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Landscape level variation in soil resources and microbial properties in a no-till corn field

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Abstract

Soil microbial properties are known to exhibit high spatial and temporal variability, which can hinder our understanding of the effects of agricultural management on soil microbial activities, populations and communities. However, if this variability is explicitly considered in soil sampling schemes, experimental results can help us better understand soil microbial properties. In this initial assessment of soil resources and microbial properties in a 16-ha landscape planted to corn, we hypothesized that soil microbial properties will vary by soil type. We defined soil type based on drainage class (4 levels), series (7 levels), map unit (11 levels), and texture of the Ap horizon (3 levels). We took soil samples from 16 map units in April, June, August, and October and measured 12 physical and chemical properties, and 27 microbial properties on at least one of these dates. Soil physical and chemical properties generally varied with soil type and canonical discriminant analyses showed that soil drainage classes, series, and map units were delineated by a similar set of soil properties (total C, total N, moisture, pH, equivalent CEC (CEC_e), and available P). Ap texture classes were delineated by a different set of soil properties (available K, Mg, and Ca and CEC_e). A number of soil microbial properties varied by soil type, but, in general, a smaller proportion of measured soil microbial properties showed soil type effects compared to the proportion of soil physical and chemical properties that showed soil type effects. Method of soil classification strongly influenced which soil microbial properties varied by soil type. However, soil microbial activities, population sizes, and community structures were generally greater or most unique in mid-range soils regardless of how soils were classified, possibly because soil moisture was optimal for microbiological activity and growth in these soils. Except at the level of drainage class, there was little consistency between patterns of variation in soil physical and chemical properties and patterns of variation in soil microbial properties among soil types. Thus, different soil sampling

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strategies may be required when accounting for variation in soil physical and chemical properties than when accounting for soil microbial properties at the landscape level. While sampling soils according to soil survey-defined map units indicated that some soil microbial properties vary by soil type, a number of limitations to this approach are discussed. To improve upon results presented here, future efforts to quantify landscape level variation of soil microbial properties should probably be sampled at a finer scale that explicitly accounts for soil properties that vary at the sub-map unit level, including terrain attributes, microtopography, soil texture, soil bulk density, and other factors that impact soil temperature and moisture dynamics.

Keywords: Soil drainage class; Soil map unit; Soil microbial properties; Soil series; Spatial variability; Temporal variability

1. Introduction

Understanding soil variability at the landscape level will help refine agricultural management practices, improve our understanding of the effects of agricultural management on environmental quality, and help us understand factors controlling the distributions and activities of soil organisms (Robert et al., 1993; Cambardella et al., 1994; Pickett and Cadenasso, 1995; Ettema and Wardle, 2002). Soil variability at the landscape scale commonly is described using soil survey and classification, which are based on soil geomorphic, physical, and chemical properties. While soil biological characteristics play no direct role in soil classification and survey, edaphic factors used to classify soils are expected to influence soil biological characteristics.

It is well known that many soil physical and chemical properties, such as bulk density, water content, soil organic carbon (SOC) content, pH, and fertility vary with soil type, texture, and topographic position (Ball and Williams, 1968; Hanna et al., 1982; Kachanoski et al., 1985; Ovales and Collins, 1986; Miller et al., 1988). This variability is beginning to be incorporated into assessments of the effects of agricultural management on environmental quality. For example, recent findings show that the response of SOC to tillage management varies significantly by landscape position. There may be large differences in SOC in upslope positions but no differences in SOC in toe slope positions in no-till compared to conventional till fields (Elliott and Efetha, 1999; Bergstrom et al., 2001a,b; VandenBygaart et al., 2002). It is now recognized that models of soil dynamics must include spatial variability in order to understand the effects of agricultural management on environmental quality at the landscape level (Pennock and Frick, 2001).

While soil biologists have long recognized that soil organisms and the processes they carry out often exhibit very high spatial and temporal variability, most of the systematic study of this variability has occurred within the past decade (Ettema and Wardle, 2002). Developing a better understanding of variability among microbial processes, populations, and communities is crucial in the development of sustainable land management practices, since soil microorganisms are primary agents in soil organic matter and residue decomposition, nutrient cycling, soil structure formation and maintenance, and suppression and initiation of plant diseases (Pankhurst et al., 1997). In addition, due to their central roles in these ecosystem processes, their sensitivity to management, and because their populations, communities, and activities reflect an integration of soil physical, chemical and biological properties, soil organisms are considered central to defining soil quality, soil health, and sustainable land management (Pankhurst et al., 1997; Doran and Zeiss, 2000).

Nonetheless, we still have a limited understanding of how soil microbial activities, populations, and communities respond to agricultural management, especially at the landscape level, in large part because of high spatial and temporal variability, even in homogenously managed landscapes (Parkin, 1993; Robertson et al., 1993, 1997; Ettema and Wardle, 2002). This variability often is considered an impediment to the study of soil microorganisms, and can obscure differences among treatments. However, we can enhance our understanding of soil microorganisms if variability is considered explicitly in sampling designs (Parkin, 1993; Ettema and Wardle, 2002). A prerequisite to understanding the effect of agricultural management on soil microbial activities, populations and communities is to understand underlying spatial

variability of these parameters. Then, sampling schemes that account for variability can be devised and the effect of agricultural management on microbial activities and taxa can be better understood (Bergstrom et al., 1998).

While understanding the distributions of microorganisms at the landscape scale is complicated by interactions among soil type, topography, and water distribution (Parkin, 1993), these parameters are useful levels of demarcation for differentiating regions of soils with different microbiological properties. For example, bacterial population densities, microbial biomass, soil enzyme activities, and N cycle dynamics vary with soil type and/or drainage class (Rogers and Tate, 2001; Corre et al., 2002) although soil management also has been shown to influence soil microbial biomass more than soil type (Fromm et al., 1993). Plant-parasitic nematode population densities also vary with soil texture and drainage, with patterns varying by species (Goodell and Ferris, 1980; Noe and Barker, 1985; Ferris et al., 1990). Microbial community structure is related to soil texture (Schutter et al., 2001) and soil type is often a more important influence on soil microbial community structure than agricultural management (Bossio et al., 1998; Schutter et al., 2001; Girvan et al., 2003) and plant type (Ritchie et al., 2000; Buyer et al., 2002).

Temporal variability may be several-fold higher than spatial variability for many microbiological parameters (Parkin, 1993), which can confound comparisons among treatments. For example, soil enzyme activities, N dynamics, bacterial population sizes (plate counts), microbial community structure, and nematode population sizes vary temporally (Barker and Campbell, 1981; Barker et al., 1984; Rastin et al., 1988; Bossio et al., 1998; Bossio and Scow, 1998; Burton and McGill, 1992; Aon et al., 2001; Grayston et al., 2001; Rogers and Tate, 2001; Schutter et al., 2001; Blume et al., 2002). Microbial biomass varies temporally in some cases but not in others (Burton and McGill, 1992; Wardle, 1998; Rogers and Tate, 2001). Very few studies of spatial variability have measured soil physical, chemical, and biological properties concomitantly (Robertson et al., 1997) and we know of no studies that have included both temporal and spatial variability of a large number of soil physical, chemical, and microbiological properties.

This study was conducted as part of a detailed assessment of initial soil spatial variability at a 16-ha site in Beltsville, Maryland, USA, where a long-term cropping systems trial was later established. We tested the hypotheses that soil properties, including microbial activities, populations, and communities are distributed across the landscape in patterns that reflect soil classes as defined by soil surveying methods (drainage class, series, map unit, and texture classes). For many locations, soil maps are the finest level of description that exists. If this level of classification is useful to distinguish important soil properties, then we can use soil maps as an initial guide in sampling for soil biological properties. The site was thought to be a good location to test these hypotheses because of the diversity of soil drainage classes and soil types present. Also, the site had not been tilled for at least 10 years, thereby reducing the effect that tillage has on the distributions of soil organisms and properties (Webster and Boag, 1992; Robertson et al., 1993). To account for temporal variability, we took samples from the same locations on four different dates. One of the goals of the long-term project subsequently established at the site is to assess the effects of cropping systems on soil biotic and abiotic properties.

2. Materials and methods

2.1. Study site

The study was conducted in 1995 at the Beltsville Agricultural Research Center in Beltsville, MD, USA (39°01′N, 76°55′W). Mean annual temperature is 12.8 °C and annual precipitation is 1112 mm (30-year means). From 1993 to 1995, the entire site was cropped to corn (*Zea mays*), managed using no-till techniques, according to University of Maryland recommendations. In 1995, a hairy vetch (*Vicia villosa*) cover crop was killed with herbicide 28 March, corn (Doeblers 66XP) was planted 30 April (24,200 seed acre^{-1}) at which time 187 l ha^{-1} 12–12–4 starter fertilizer was applied. Herbicides were applied 13 May (pre-emergence) and 22 June (post-emergence), and nitrogen fertilizer was applied 22 June at a rate of 132 kg N ha^{-1}. Corn was harvested on 8 and 9 September. For the prior 8 years the field had been in alfalfa.

A soil map (1:3500) was created in 1993 using data collected from 47 soil sampling locations selected to represent geomorphic positions and landscape elements present at the site. Nineteen delineations were made using 12 map units, which were named for eight Coastal Plain Ultisol soil series (Fig. 1; Table 1). The Christiana, Keyport, Keyport variant, and Elkton soils are generally clayey (35–50% clay), dark red (2.5YR/6 being rather typical) soils that form a drainage catena from well drained to poorly drained. The Matapeake and Mattapex units, which are browner in color (10YR and 7.5YR 5/6 being typical) than the Christiana soils, have a fine-silty texture.

The 16 soil samples that were collected (see below) were classified in four different ways: according to drainage class (4 classes), soil series (7 classes), map unit (11 classes), and texture of the Ap horizon (3 classes). Drainage class, soil series, and map units are classifications determined from the soil survey and are hierarchically structured, i.e., the 11 map units are subsets of the seven soil series, which are themselves subsets of the four drainage classes. The three Ap texture classes were identified based on how the 16 soil samples mapped onto a soil textural triangle. One group had relatively high sand (0.388–0.456 g g^{-1}), and low silt

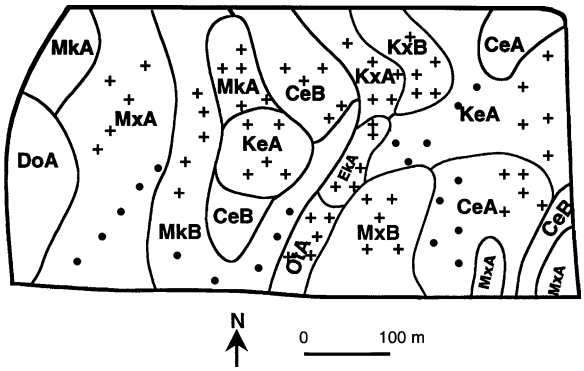

Fig. 1. Soil map of site, showing positions of individual soil sampling locations. Soil map units are as in text. Within a soil map unit, the five samples that were combined to form a composite sample have the same symbol.

Table 1
Coastal Plain Ultisols present at the study site classified by drainage class, soil series, map unit, and Ap horizon texture class

Drainage class	Soil series	Soil map unit[a]	Taxonomic class	Number of map units sampled	Ap texture class(es)[b]	Proportion of site represented by map unit
Well drained						
	Downer	DoA	Coarse-loamy, siliceous, semiactive, mesic Typic Hapludults	0	ND[c]	5
	Christiana	CeA	Fine, kaolinitic, mesic Typic Paleudults	2	2, 3	13
	Christiana	CeB	Fine, kaolinitic, mesic Typic Paleudults	1	2	9
	Matapeake	MkA	Fine-silty, mixed, semiactive, mesic Typic Hapludults	1	3	4
	Matapeake	MkB	Fine-silty, mixed, semiactive, mesic Typic Hapludults	2	2, 3	14
Moderately well drained						
	Keyport	KeA	Fine, mixed, semiactive, mesic Aquic Hapludults	3	1, 2, 2	19
	Mattapex	MxA	Fine-silty, mixed, active, mesic Aquic Hapludults	2	2, 2	19
	Mattapex	MxB	Fine-silty, mixed, active, mesic Aquic Hapludults	1	3	8
Somewhat poorly drained						
	Keyport variant	KxA	Fine, mixed, semiactive, mesic Aeric Ochraquults	1	2	3
	Keyport variant	KxB	Fine, mixed, semiactive, mesic Aeric Ochraquults	1	2	3
Poorly drained						
	Elkton	EkA	Fine-silty, mixed, active, mesic Typic Endoaquults	1	1	2
	Othello	OtA	Fine-silty, mixed, active, mesic Typic Endoaquults	1	2	2

[a] A indicates slopes of 0–3%; B indicates slopes of 3–8%.

[b] Ap textural classes are: 1: high sand (0.388–0.456 g g^{-1}), low silt (0.426–0.486 g g^{-1}); 2: medium sand (0.246–0.325 g g^{-1}), medium silt (0.506–0.621 g g^{-1}); 3: low sand (0.167–0.190 g g^{-1}), high silt (0.642–0.682 g g^{-1}).

[c] ND: not determined.

(0.426–0.486 g g^{-1}) content; another had medium sand (0.246–0.325 g g^{-1}), and medium silt (0.506–0.621 g g^{-1}) content; and a third had low sand (0.167–0.190 g g^{-1}), and high silt (0.642–0.682 g g^{-1}) content. Clay content (0.079–0.191 g g^{-1}) among all samples varied less than sand or silt content. The Ap texture classes are not hierarchically related to the drainage, series, and map unit classes. Thus, for example, the four soils that comprise the low sand, high silt Ap texture class include well drained and moderately well drained soils representing four different map units. The classification of each soil according to these four different systems is listed in Table 1. Throughout this paper we use the term soil type as a general term to refer to the four drainage classes, the seven soil series, the 11 map units, and/or the three Ap texture classes.

2.2. Soil sampling and processing

Soil samples were taken from 12 of 19 soil delineations to represent 11 soil map units (all map units except the Downer sandy loam). Samples were collected on 18 April, 19 June, 14 August, and 16 October 1995. Two samples were taken from the larger soil map units (CeA, KeA, MkB and MxA), so that 16 total samples were collected on each date. Each soil sample was comprised of five soil cores taken to a depth of 15 cm within the corn-row (except for the April sample collection date, which occurred before corn was planted). The five cores were spaced at distances of about 25–50 m to ensure that samples represented the whole of each mapped unit. Each soil core location was identified using global positioning system instrumentation to facilitate sampling nearby locations on succeeding dates.

Before the five cores for a given sample were collected, the soil probe, gloves, and ancillary equipment were rinsed with a 5% sodium hypochlorite solution. Soils were immediately placed in a cooler and brought back to the lab for immediate processing. Using sterile gloves, each soil sample was homogenized by hand. Each sample was split into six subsamples and distributed to co-investigators on the same day samples were taken. All variables except Ap depth, soil bulk density, water holding capacity, and texture were measured using these soil samples.

Depth of the Ap horizon was determined as part of the soil surveying process. Soil bulk density, water holding capacity, and texture were measured on samples collected in April from each of the 19 delineations described in the soil survey. Undisturbed soil cores, 7.6 cm in length and 7.6 cm in diameter were taken from 0- to 20-cm depth using a Uhland core sampler (Blake and Hartge, 1986). Disturbed samples were taken adjacent to cores for particle size analyses.

2.3. Soil analyses

2.3.1. Physical properties

Bulk density (Blake and Hartge, 1986) and soil water retention (at −5.0 and −1500 kPa) were determined for each undisturbed core. Matric potentials of −5.0 and −1500 kPa were achieved using a tension table and a hanging water column, and a ceramic plate apparatus, respectively (Topp and Zebchuk, 1979; Klute, 1986). Water holding capacity, on a % (v/v) basis, was determined as the difference in soil water retention at these two matric potentials. Soil texture was determined using the pipette method (Gee and Bauder, 1986). Soil moisture was determined gravimetrically (105 °C).

2.3.2. Chemical properties

Soil pH was measured in a 1:1 soil:water paste (McLean, 1982). Soil P was measured in Mehlich I extracts using the colorimetric method (Olsen and Sommers, 1982). Exchangeable soil K, Ca, and Mg were extracted using NH_4OAc and measured using atomic absorption spectrophotometry (Lanyon and Heald, 1982; Thomas, 1982). Equivalent CEC (CEC_e) is the sum of cations plus acidity. Total soil C and N were measured by dry combustion (Sollins et al., 1999). Biologically active C was extracted using $KMnO_4$ (Lefroy et al., 1993) and detected using spectrophotometry (June and August samples) or a total organic C analyzer (October samples; Tekmar-Dohrman, Mason, OH). Biologically active C is expressed per unit of total C.

2.3.3. Microbial activity

Alkaline phosphatase, acid phosphatase, β-glucosidase, and arylsulfatase activities were measured according to procedures described by Tabatabai (1994). Nitrogen mineralization potential (Nmin) was determined as the amount of NH_4^+-N produced

in a 7-day anaerobic incubation (Bundy and Meisinger, 1994). Nitrification potential was determined as described by Hart et al. (1994), using soil slurries incubated with ammonium sulfate as a substrate for 48 h. Samples were taken for NO_3^- analyses at 0, 24 and 48 h. Ammonium and NO_3^- were determined on a Lachat flow–injection analyzer (Zellweger Analytics Inc., Milwaukee, WI).

Microbial biomass C and N were determined using two separate methods, as recommended by West et al. (1986). We used chloroform fumigation–extraction (MBC_{fe} and MBN_{fe}; Horwath and Paul, 1994) and rehydration (MBC_r and MBN_r; Sikora et al., 1994). Correction factors of 0.35 and 0.54 were used for MBC_{fe} and MBN_{fe}, respectively. A correction factor of 0.23, based on ^{14}C data, was used for MBC_r. Glomalin was determined on air-dried soils (10 g) that were ground with a mortar and pestle. Glomalin was extracted and analyzed as described by Wright et al. (1996). Biologically active C, MBC_{fe}, MBN_{fe}, the four enzyme activities, and nitrification potential were not measured on samples collected in April.

All measures of soil microbial activity were standardized to reflect the fact that soil C and N fractions influence them. Since soil C and N fractions vary by soil type, standardizing soil microbial activities by these fractions provides a better basis for comparing microbial activities by soil type. Soil enzyme activities and both measures of MBC are expressed per unit of total C and active C. Glomalin is reported as a proportion of total C. Nmin, nitrification rate and both measures of MBN are expressed per unit total N.

2.3.4. Microbial populations

For all microbial population measures except for arbuscular mycorrhizal fungi (AMF), soil samples were stored at 5 °C overnight before use. Prior to subsampling, soil samples were mixed thoroughly. Ten gram of soil was added to 90 ml of sterile distilled water. During mixing on a magnetic stirrer, 1 ml subsamples were removed for 10-fold serial dilutions in sterile distilled water except as noted below. Dilutions were plated onto media semi-selective for culturable fungi, bacteria, and actinomycetes.

2.3.4.1. Fungi. Soil suspensions were plated onto Komada's medium for *Fusarium* (Komada, 1975), Trichoderma medium E for *Trichoderma* and *Gliocladium* (Papavizas and Lumsden, 1982), and Talaromyces media (Marois et al., 1984). Plates were incubated under ambient conditions and population sizes were quantified by counting colonies.

To enumerate *Pythium*, serial soil dilutions were made in 0.2% water agar plus antibiotics (Lumsden et al., 1975; Lewis and Larkin, 1998). Eight 0.12 ml drops of various dilutions were placed on glass slides and incubated for 2 days at 25 °C. The number of colony-forming units was calculated microscopically by a most probable numbers technique (Harris and Sommers, 1968).

Saprophytic ability and survival of *Rhizoctonia solani* were assessed in two separate assays with beet seed as described by Papavizas and Lewis (1986). Sterile beet seeds (*Beta vulgaris*, cultivar Detroit Red) were used to infest 100 g portions of soil adjusted to approximately 50% moisture holding capacity. After 1-week incubation under ambient conditions, beet seeds were recovered by sieving, and were plated onto water agar amended with antibiotics (Lewis and Papavizas, 1987). After 24 h, a colonization index of 0–5 based on the extent of development of hyphae from the retrieved beet seed onto a water agar surface was used as a measurement of saprophytic growth, where 0 = no observable hyphae and 5 = 100% of the agar surface covered with hyphae. For each replicate, data are reported as the sum of the colonization index times the number of seeds rated at that level.

To determine survival of *R. solani*, beet seeds were inoculated with *R. solani* Kühn isolate Rs-23 (AG-4; Lewis and Papavizas, 1987) and incubated for 3 week. Infested beet seeds were 3 weeks old when soils were collected from the field. Soils were infested with colonized beet seed and incubated as above. After 2 weeks, beet seeds were recovered and plated, and growth of *R. solani* was assessed as above.

2.3.4.2. Bacteria. Population sizes of culturable bacteria were determined by dilution plating onto nutrient agar for total bacteria (Difco), Pseudomonas Fluorescent agar for Pseudomonads (Difco), *Pseudomonas cepacia* azelic tryptamine medium for *Burkholderia cepacia* (Burbage et al., 1982), and McConkey's agar for Enterobacter (Difco).

2.3.4.3. Actinomycetes. From the original soil suspension of 10 g of soil in 90 ml sterile distilled water,

1 ml was placed in 9 ml of phenol:water (1:140, v/v) and mixed. After 2 min, 10-fold serial dilutions were made in sterile distilled water and these were plated onto actinomycete agar (Difco).

2.3.4.4. Arbuscular mycorrhizal fungi. Prior to analyses, soil samples were stored at 4 °C for up to 14 days prior to further processing. Biodiversity studies of arbuscular mycorrhizal fungi have shown that no single method of spore extraction comprehensively recovers all of the AMF species and spore morphotypes present from a soil (Bever et al., 1996, 2001; Schultz, 1996; Morton, 1985). Consequently, three complementary approaches were used to assess AMF spore morphotypes: (1) direct recovery of spores from soil (Hayman, 1984; Morton et al., 1993), (2) trap culturing in pots at a fixed dilution (Hayman, 1984; Morton et al., 1993), and (3) culturing in a pasteurized soil:sand mix using a series of soil dilutions (Porter, 1979; Morton, 1985). Spore counting and trap culturing were conducted only on samples collected in April; dilution culturing was conducted only on samples collected in August. The total numbers of different spores and fungal types by soil type are reported here. More detailed accounts of the AMF counting methods and data are presented in Millner et al. (submitted for publication).

2.3.4.5. Nematodes. Soil samples were stored and processed in the laboratory within a week after collection. Nematodes from each composite sample were extracted from a representative 250 ml subsample using Cobb's sieving and decanting technique (Cobb, 1918), followed by a modified Baermann funnel method (Hooper, 1986). U.S. Standard Sieves 100, 200, and 325 mesh (openings of 150, 75 and 45 μm, respectively) were used. Nematodes were fixed in 3% formaldehyde solution, identified to genus level, and counted using a stereoscope. Some fixed specimens were processed with anhydrous glycerin (Seinhorst, 1959) and examined under a compound microscope for species identification. Nematode identifications were based on the morphology of adult and larval forms and their identities were confirmed with recent taxonomic keys (Handoo and Golden, 1992; Mai et al., 1996; Sher, 1966; Handoo, 2000).

All measures of soil microbial population size were standardized by MBC_{fe} and MBC_r to eliminate possible effects of soil type or date on microbial biomass that might influence population sizes of individual components of the biomass. Measures of AMF population size were not standardized since they were only measured on one date (date had the greatest influence on soil microbial population sizes).

2.3.5. Microbial community structure

Fatty acid analysis, based on the MIDI procedure for bacterial isolates (Microbial ID Inc., Newark, Delaware, USA), was performed according to the procedure described by Cavigelli et al. (1995) except that two final washings were conducted. The MIDI eukaryotic standard and peak library were used. Fatty acid methyl esters (FAMEs) were grouped into saturated, branched, monounsaturated, polyunsaturated, 2-hydroxy, 3-hydroxy, unsaturated, and cyclo groups to reduce the number of dependent variables in multivariate analyses.

2.4. Statistical analyses

All statistical analyses were conducted using SAS v. 8.2 (SAS Institute Inc., 1999). Since many variables exhibited heterogeneous residual variance among class variable levels and we wished to compare means of non-transformed values, the distinct sizes of residual variance were modeled by partitioning (i.e., grouping) the total residual variance in two-way univariate ANOVAs, with date and one measure of soil classification as the two class variables. Variance grouping assigns levels of class variables with similar variances into groups and adds a class variable to the analysis to reflect this grouping. Henceforth, appropriate residual variability is associated with all ANOVA effect tests and means comparisons. We used the PDMIX800 SAS macro to assign letter groupings to the Proc MIXED LSMeans output (Saxton, 1998). To analyze count data (AMF, nematodes) we used Proc GENMOD to fit Poisson regressions with a log link function. We used increasingly conservative means separation methods as the number of soil types per class increased. Thus, we used LSD to compare means among drainage and Ap texture classes, Tukey's to compare means among soil series, and Sidak's to compare means among soil map units.

We also conducted canonical discriminant analysis (CDA) on subsets of the data. We ran four separate sets of analyses: (1) on soil physical and chemical

properties (9 variables), (2) on measures of soil microbial activity (11 variables expressed per unit total C or total N), (3) on microbial populations (plate counts; 10 variables expressed per unit MBC_{fe}), and (4) on FAMEs (8 variables). When correlation coefficients were statistically significant, we ran two-way ANOVAs (date plus the relevant soil class) on the first two or three canonical variates to determine if there were differences among soil classes.

3. Results

Mean soil properties for the site, averaged across all dates, are shown in Table 2. In general, soil physical and chemical properties showed the least amount of variation and microbial populations showed the most variability across all dates and sampling locations. There were not sufficient replicates to allow for statistical analyses of soil nematode data by species so statistical analyses were conducted on total number of species only. In total, 37 species of nematodes were identified among all 16 sampling locations on four dates (Table 3). Two important plant parasitic nematodes, *Pratylenchus thornei*, a root lesion nematode, and *Xiphinema rivesi*, a virus-transmitting nematode, were found in almost all samples on all dates. Other common species included *Aphelenchus avenae* and *Pratylenchus neglectus*. *Pratylenchus pinguicaudatus*, which was found in two samples in October, represents the first record of this species in the United States.

3.1. Soil drainage class effects

According to univariate analyses of soil physical and chemical properties, well drained soils had greater bulk density and less available K than did less well drained soils (Table 4). Poorly drained soils had higher total C and N than did better drained soils, and poorly and somewhat poorly drained soils had higher CEC_e than did the better drained soils. Active C/total C was greater in moderately well drained soils than in somewhat poorly drained and poorly drained soils. The other six measured soil physical and chemical properties were not significantly different among drainage classes when analyzed using univariate methods. CDA conducted on the nine soil physical and chemical properties that were measured on more than one date showed that there was a significant drainage class effect (Wilks' Lambda, $P < 0.0001$; Fig. 2a). ANOVA of the first canonical variate shows that the poorly drained soil is distinct from the other three drainage classes (Table 4), due largely to differences in total C, total N, pH, moisture and CEC_e, and secondarily to differences in available P and Ca (Table 5). ANOVA of the second canonical variate shows that the three drainage classes that clustered together along the first axis are distinct along the second axis (Table 4). These differences are due primarily to differences in soil available K among drainage classes (Table 5).

Univariate analyses showed that four measures of soil microbial activity and three measures of microbial population size varied by soil drainage class (Table 4). Acid phosphatase activity/active C was greater in somewhat poorly drained soils than in moderately well drained soils, and β-glucosidase activity/total C was greater in well drained and somewhat poorly drained soils than in poorly drained soils. Nmin/total N was greater in somewhat poorly drained soils than in poorly drained soils, and MBC_r/active C was greater in poorly drained soils than in moderately well drained soils. There were more total bacteria/MBC_r, and more actinomycetes, whether reported per unit of MBC_{fe} or MBC_r, in the somewhat poorly drained soils than in the other three drainage classes (Table 4). There were also fewer actinomycetes/MBC_r in the well drained soil than in the moderately well drained soils. CDAs were not able to distinguish among soil drainage classes based on soil microbial activities, populations, or community structure (data not shown).

3.2. Soil series effects

Soil pH and CEC_e were the only soil physical and chemical properties that varied with soil series according to univariate analyses (Table 6). The two poorly drained Ot and Ek soils had lower pH than all but the somewhat poorly drained Mx soil. The well drained Mk soil had higher pH than the well drained Ce soil. The two poorly drained soils had higher CEC_e than all but the somewhat poorly drained Kx soil. Although only two soil physical and chemical properties varied with soil series according to univariate analyses, CDA showed that there were differences among soil series (Wilks' Lambda,

Table 2
Descriptive statistics for soil physical, chemical, and microbiological properties, averaged across all dates collected

Soil property	Mean	Median	Minimum	Maximum	C.V.[a] (%)
Physical properties					
Ap depth (cm)	24	23	19	32	14.3
Sand	31.0	30.1	16.7	45.6	25.2
Clay	13.1	13.0	7.9	19.1	22.4
Silt	55.9	57.6	42.6	68.2	13.2
Bulk density (Mg m^{-3})	1.32	1.31	1.21	1.48	7.0
Water holding capacity (%, v/v)	0.32	0.33	0.26	0.40	14.8
Moisture (g g^{-1})	20.6	21.2	13.1	27.4	19.9
Chemical properties					
pH	6.71	6.70	6.2	7.1	3.2
Available P (kg ha^{-1})	201	202	109	330	23.3
Available K (cmol kg^{-1})	0.30	0.30	0.16	0.55	27.6
Available Mg (cmol kg^{-1})	1.2	1.2	0.9	1.6	15.2
Available Ca (cmol kg^{-1})	6.8	7.0	5.3	7.8	9.4
CEC_e (cmol kg^{-1})	9.3	9.1	6.6	11.6	10.7
Total C (g kg^{-1})	15.8	15.5	12	22.6	14.4
Total N (g kg^{-1})	1.38	1.35	1.00	1.95	14.5
Active C (μg g^{-1})	89	87	34	175	35.1
Microbial activities					
Acid phosphatase (μg PNP[b] g^{-1} h^{-1})	387	378	231	754	24.8
Alkaline phosphatase (μg PNP g^{-1} h^{-1})	213	209	98	385	28.2
β-Glucosidase (μg PNP g^{-1} h^{-1})	108	107	41	184	26.4
Arylsulfatase (μg PNP g^{-1} h^{-1})	93	97	33	135	23.1
Nmin (μg g^{-1})	72	73	46	103	15.9
Nitrification rate (μg ml^{-1} h^{-1} g^{-1})	0.43	0.41	0.21	0.75	30.3
MBC_{fe} (μg g^{-1})	335	326	10	692	40.7
MBC_r (μg g^{-1})	421	400	184	717	29.0
MBN_{fe} (μg g^{-1})	49	49	18	104	33.4
MBN_r (μg g^{-1})	61	62	23	101	30.9
Glomalin (μg g^{-1})	1.43	1.41	0.86	1.86	16.3
Microbial populations					
Fusaria (CFU g $soil^{-1}$)	886	229	0	1.47×10^4	281
Gliocladium + *Trichoderma* (CFU g $soil^{-1}$)	3.43×10^5	3.78×10^4	7.41×10^3	2.31×10^6	171
Talaromyces (CFU g $soil^{-1}$)	923	236	0	5.24×10^4	162
Pythium (CFU g $soil^{-1}$)	6.83×10^3	1.85×10^3	115	1.27×10^5	255
Rhizoctonia survival	14.4	6.1	2.8	55.4	112
Rhizoctonia saprophytic ability (1–5)	1.2	0.3	0.0	5.0	144
Total bacteria (CFU g $soil^{-1}$)	3.76×10^5	3.51×10^5	1.70×10^4	3.36×10^6	119
Pseudomonads (CFU g $soil^{-1}$)	199	0	0	1.16×10^4	728
Burkholderia cepacia (CFU g $soil^{-1}$)	2.07×10^3	0	0	5.12×10^4	374
Enterobacter (CFU g $soil^{-1}$)	9.42×10^4	2.33×10^5	3.02×10^4	3.71×10^7	489
Actinomycetes (CFU g $soil^{-1}$)	7.16×10^4	1.47×10^4	0	7.30×10^5	196
AMF[c] spore incidence	4.1	4.5	0	7	56.5
AMF incidence by trap culturing	2.9	2.0	1	8	72.8
AMF incidence by MPN	7.3	7.0	4	14	30.4
Total nematode sp.	4.6	4.5	1	9	38.4

All data are for soil samples collected to a depth of 15 cm except for texture, bulk density, and water holding capacity, which were collected to a depth of 20 cm. Ap depth was determined in 1993 during soil surveying.

[a] C.V.: coefficient of variation.

[b] PNP: *p*-nitrophenol.

[c] AMF: arbuscular mycorrhizal fungi.

Table 3
Number of nematode species detected in 16 sampling locations in a no-till corn field on four dates

Species	April	June	August	October	Total
Aphelenchoides sp.	1	2	0	0	3
Aphelenchus avenae	13	6	6	4	29
Aphelenchus sp.	0	0	1	0	1
Axonchium sp.	1	1	0	0	2
Coslenchus costatus	1	0	1	0	2
Coslenchus sp.	0	5	2	0	7
Ditylenchus myceliophagus	1	0	0	0	1
Dorylaimellus sp.	0	0	1	0	1
Dorylaimida group	0	0	1	0	1
Dorylaimus sp.	0	2	9	0	11
Eudorylaimus sp.	3	0	3	0	6
Helicotylenchus digonicus	1	2	1	0	4
Helicotylenchus pseudorobustus	2	1	1	5	9
Helicotylenchus sp.	0	1	0	0	1
Hoplolaimus galeatus	1	1	0	0	2
Merlinius brevidens	1	0	1	1	3
Mesodorylaimus sp.	1	1	1	0	3
Mononchus sp.	0	0	3	0	3
Plectus sp.	0	1	5	0	6
Pratylenchus neglectus	6	5	7	2	20
Pratylenchus penetrans	4	2	1	3	10
Pratylenchus pinguicaudatus	0	0	0	2	2
Pratylenchus projectus	1	0	0	0	1
Pratylenchus thornei	16	12	15	15	58
Pratylenchus zeae	0	0	0	2	2
Pratylenchus sp.	0	0	3	0	3
Psilenchus hilarulus	3	0	0	0	3
Psilenchus sp.	0	3	3	0	6
Pungentus sp.	0	1	0	0	1
Rhabditid group	0	4	0	0	4
Thonus sp.	1	2	0	0	3
Tylenchorhynchus sp.	1	2	1	2	6
Tylenchus davini	0	1	0	0	1
Tylenchus exiguus	2	0	0	0	2
Tylenchus hamatus	2	0	0	0	2
Tylenchus sp.	1	5	10	1	17
Xiphinema rivesi	16	15	13	15	59

$P < 0.0001$; Fig. 2b) and that these differences were due to differences in multiple soil physical and chemical variables. ANOVA of the first canonical variate showed that the poorly drained Ek and Ot soils are each different from all other soils, and that the well drained Ce and Mk soils and the moderately well drained Ke soil are different than the moderately well drained Mx soil (Table 6). Differences among soils along the first axis are due primarily to differences in total soil C and N, pH, and moisture; secondly, to available P and CEC_e; and thirdly, to available K and Mg (Table 5). ANOVA of the second canonical variates indicates that the Ce and Ke soils are distinct from each other and from the Mk soil (Table 6). These differences are due primarily to differences in available K and secondly to differences in available Mg and P, and total N (Table 5). In two dimensions, the seven soil series could be divided into six distinct groups, with only the moderately well drained Ke and the somewhat poorly drained Kx soil not distinguishable from each other.

Univariate analyses showed that three measures of soil microbial activity and no measures of microbial population varied with soil series. Arylsulfatase activity/total C and nitrification rate/total N were

Table 4
Means of soil properties, including canonical variates, that were significantly different among soil drainage classes according to two-way analyses of variance

Soil property	Drainage class				Significance level		
	Well drained	Moderately well drained	Somewhat poorly drained	Poorly drained	Drainage class	Date	Drainage class × date
Physical and chemical properties							
Bulk density (Mg m^{-3})	1.40 a	1.31 b	1.22 b	1.21 b	<0.01	ns[a]	ns
Available K (cmol kg^{-1})	0.25 b	0.33 a	0.39 a	0.33 a	<0.05	<0.0001	ns
CEC_e (cmol kg^{-1})	9.05 b	9.01 b	9.90 a	10.51 a	<0.0001	ns	ns
Total C (g kg^{-1})	15.2 b	14.9 b	15.8 b	20.1 a	<0.01	ns	ns
Total N (g kg^{-1})	1.34 b	1.33 b	1.36 b	1.68 a	<0.05	ns	ns
Active C/total C (mg g^{-1})	5.79 ab	6.32 a	4.44 b	4.89 b	<0.05	ns	ns
Canonical variate 1	−1.87 b	−1.80 b	−1.04 b	2.42 a	<0.0001	ns	ns
Canonical variate 2	−34.9 c	−33.0 b	−32.1 a	−34.1 c	<0.0001	ns	ns
Microbial activities							
Acid phosphatase/active C (g PNP g^{-1} h^{-1})	4.90 ab	4.06 b	5.51 a	5.94 ab	<0.05	ns	ns
β-Glucosidase/total C (mg PNP g^{-1} h^{-1})	7.61 a	6.76 ab	7.98 a	5.36 b	<0.05	<0.001	ns
Nmin/total N (mg g^{-1} 7 d^{-1})	52.5 ab	53.6 ab	60.3 a	46.0 b	<0.05	<0.0001	ns
MBC_r/active C (g g^{-1})	4.56 ab	4.02 b	5.39 ab	5.63 a	<0.05	ns	ns
Microbial populations							
Total bacteria (CFU μg MBC_r^{-1})	7.77 ab	3.41 ab	5.68 a	1.83 b	<0.05	<0.05	ns
Actinomycetes (CFU μg MBC_{fe}^{-1})	36.1 b	58.8 b	141.5 a	62.2 b	<0.01	ns	ns
Actinomycetes (CFU μg MBC_r^{-1})	0.10 c	0.18 b	0.34 a	0.14 bc	<0.01	ns	ns

Means within a row followed by a different letter are significantly different according to $LSD_{0.05}$.
[a] ns: not significant.

greater in the moderately well drained Ke soil than in the poorly drained Ek and Ot soils, respectively. Arylsulfatase activity/active C was greater in the Ot soil than in the Mx soil. CDAs were not able to distinguish soil series based on soil microbial activities, populations, or community structure (data not shown).

3.3. Soil map unit effects

According to univariate analyses of soil physical and chemical properties, soil map units differed only in pH (Table 7). pH was greater in the well drained MkA and MkB soils and the moderately well drained KeA soil than in the poorly drained EkA and OtA soils

Table 5
Canonical structures for linear canonical discriminant analyses of soil physical and chemical properties analyzed by soil drainage class, series, map unit, and Ap texture class

Soil property	Class factor used to conduct analysis								
	Drainage class		Soil series		Soil map unit			Ap texture class	
	Can[a] 1	Can 2	Can 1	Can 2	Can 1	Can 2	Can 3	Can 1	Can 2
Moisture	0.97	0.21	0.80	−0.08	0.69	0.15	0.07	0.98	0.20
pH	−0.97	−0.01	−0.80	0.09	−0.53	−0.03	0.35	0.49	0.87
Available P	0.79	0.02	0.67	0.40	0.65	0.14	−0.57	−0.39	−0.92
Available K	0.34	0.93	0.34	0.77	0.07	0.73	0.37	0.93	−0.36
Available Mg	0.06	−0.16	−0.34	−0.47	−0.06	−0.46	0.84	0.90	0.44
Available Ca	0.58	0.30	0.08	−0.12	0.26	−0.01	0.79	0.99	0.16
CEC_e	0.93	0.17	0.70	−0.12	0.57	0.10	0.46	0.89	−0.45
Total C	0.99	−0.10	0.92	−0.25	0.93	−0.02	0.27	0.58	−0.82
Total N	0.99	−0.15	0.87	−0.36	0.89	−0.17	0.26	0.78	−0.63

[a] Can: canonical variate.

and the somewhat poorly drained MxB soil. CDA of soil physical and chemical properties showed a soil map unit effect (Wilks' Lambda, $P < 0.0001$; Fig. 2c). ANOVA of canonical variate 1 identified four separate groups of distinct soil: (1) the poorly drained OtA soil, (2) the poorly drained EkA soil, (3) the well drained CeA and MkB soils and the moderately well drained MxA soil, and (4) the well drained CeB and MkA soils, the moderately well drained MxB and KeA soils and the somewhat poorly drained KxB soil (Table 7). These differences were due to differences in total C, total N, moisture, available P, CEC_e, and pH (Table 5). Further distinctions among soils along axis 2 (Table 7) were mostly due to differences in available K (Table 5), and distinctions among soils along axis 3 (Table 7), which explains 18% of variability, were primarily due to differences in available Mg and Ca and secondarily to differences in P and CEC_e (Table 5). In three dimensions, nine separate groups can be distinguished, with only two pairs of soils not

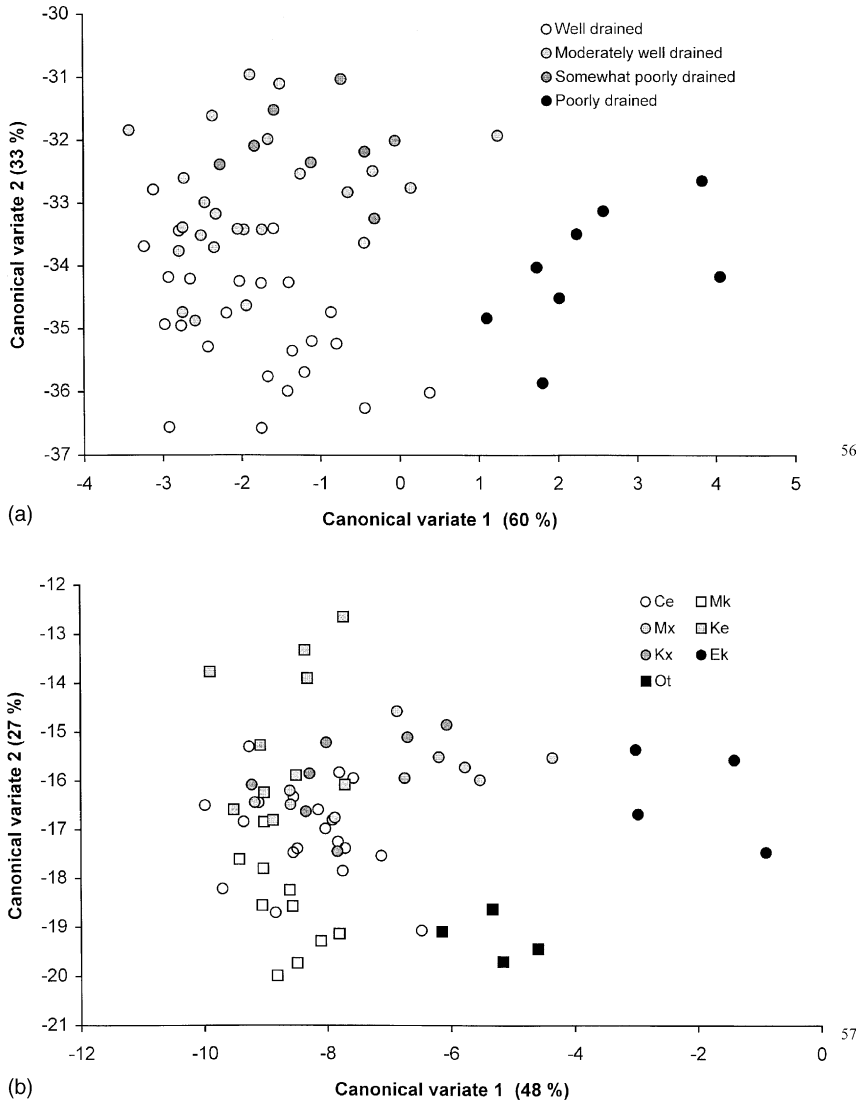

Fig. 2. Canonical linear discriminant analysis of soil physical + chemical properties by (a) drainage class, (b) series, (c) map unit, and (d) Ap texture class.

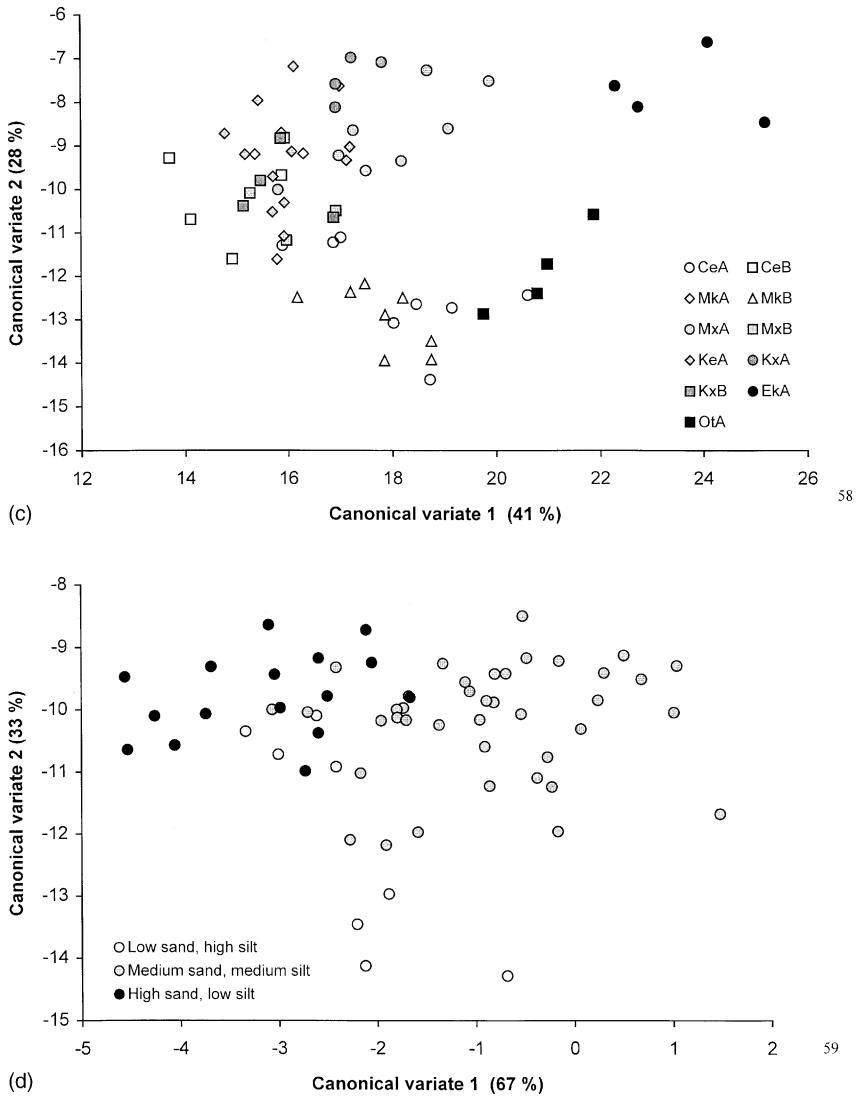

Fig. 2. (*Continued*).

being distinguishable from each other: the well drained CeB and MkA soils, and the moderately well drained MxB and KeA soils.

Univariate analyses of measures of microbial activity showed that MBC_r/total C was greater in the moderately well drained MxB soil than in all but the well drained CeB and MkA soils and the somewhat poorly drained KxB soil (Table 7). MBC_r/total C was also less in the moderately well drained KxA soil than in the well drained CeB, the moderately well drained MxB and the somewhat poorly drained KxB soils. MBC_r/active C was greater in the somewhat poorly drained KxB soil than in the moderately well drained KeA soil. These two soils did not have different active C/total C. CDA conducted on measures of soil microbial activity showed that there was a map unit effect (Wilks' Lambda, $P < 0.05$). The first canonical variate, which was the only significant one, explained 35% of variability. ANOVA showed that the moderately well drained MxB soil was unique and that the well drained CeA soil was similar to the moderately well drained KeA soil, the somewhat poorly drained

Table 6
Means of soil properties, including canonical variates, that were significantly different among soil series according to two-way grouped variance analysis of variance

Soil property	Soil series (and drainage class)							Significance level		
	Ce (well)[a]	Mk (well)	Mx (modw)[a]	Ke (modw)	Kx (swpo)[a]	Ek (poor)[a]	Ot (poor)	Soil series	Date	Soil series × date
Physical and chemical properties										
pH	6.67 bc	6.87 a	6.62 abc	6.83 ab	6.75 ab	6.45 c	6.45 c	<0.0001	ns	ns
CEC_e (cmol kg^{-1})	9.2 bc	8.9 c	8.9 bc	9.1 bc	9.9 abc	10.3 ab	10.7 a	<0.001	ns	ns
Canonical variate 1	−8.48 d	−8.70 d	−7.21 c	−8.54 d	−7.65 cd	−2.07 a	−5.31 b	<0.0001	ns	ns
Canonical variate 2	−17.2 b	−18.5 c	−16.2 ab	−15.2 a	−15.9 a	−16.3 ab	−19.2 c	<0.0001	ns	ns
Microbial activities										
Arylsulfatase/total C (mg PNP g^{-1} h^{-1})	5.69 ab	5.85 ab	5.93 ab	6.76 a	6.05 ab	5.55 b	5.83 ab	<0.05	<0.01	ns
Arylsulfatase/active C (g PNP g^{-1} h^{-1})	1.14 ab	1.20 ab	1.02 b	1.13 ab	1.45 ab	1.16 ab	1.70 a	<0.05	<0.01	ns
Nitrification rate/total N (mg ml^{-1} h^{-1} g^{-1})	0.31 ab	0.35 ab	0.28 ab	0.38 a	0.34 ab	0.24 ab	0.22 b	<0.05	<0.0001	ns

Means followed by a different letter are significantly different within a row according to Tukey's $LSD_{0.05}$ for univariate analyses and $LSD_{0.05}$ for multivariate analyses.
[a] well: well drained; modw: moderately well drained; swpo: somewhat poorly drained; poor: poorly drained.

KxA and KxB soils and the poorly drained EkA soil. The well drained MkB soil was similar to the well drained CeB and MkA soils and the moderately well drained MxA soil. The canonical structure showed that these differences were determined primarily by differences among soil map units in acid phosphatase/total C, and glomalin/total C, and secondly by differences in alkaline phosphatase/total C, arylsulfatase/total C, MBC_{fe}/total C, MBC_r/total C, MBN_{fe}/total N, MBN_r/total N, and Nmin/total N (Table 8).

Univariate analyses showed that actinomycete populations, expressed per unit MBC_{fe} or MBC_r, were the only microbial populations that differed by soil map unit independent of date (Table 7). In both cases, actinomycete populations were greater in the somewhat poorly drained KxB soil than in the well drained CeB, MkA, and MkB soils (data for actinomycetes/MBC_r not shown). When expressed per unit MBC_{fe}, actinomycete populations were also greater in the KxB soil than in the moderately well drained MxA and KeA soils.

Six microbial populations differed by soil map unit on only one date. In August, Pseudomonads/MBC_{fe} varied by soil map unit, being greater in the somewhat poorly drained KxA soil than in all other soils (Table 7). *Fusarium* population size in October was greater in the KxA soil than in all other soils. In October, *Gliocladium* + *Trichoderma*, the saprophytic ability of *R. solani*, survival of *R. solani*, and total bacteria, expressed per unit of MBC_{fe}, all varied by soil map unit, being greater in the CeB soil than in all other soils. Results were almost identical when microbial population sizes were expressed per unit MBC_r (data not shown). CDAs were not able to distinguish soil map units based on either soil microbial populations, or community structure (data not shown).

In this landscape, soil map units differ from soil series only in that those series with a wide range of slopes are divided into regions of 0–3% slope and regions of 3–8% slope. Each soil series for which there were two soil map units (Ce, Mk, Mx, and Kx) showed differences in soil physical and chemical and/or soil microbial properties between map units (Table 7). Thus, soil slope influenced soil physical, chemical, and microbial properties.

3.4. Ap texture class effects

Univariate analyses of soil physical and chemical properties showed that bulk density was greater in the high sand, low silt soils than in the other two groups (Table 9). Available K was higher in medium sand, medium silt soils than in high sand, low silt soils, and available Mg was higher in medium sand, medium silt

Table 7
Means of soil properties that were significantly different among soil map units according to two-way grouped variance analysis of variance

Soil property	Soil map unit (and drainage class)											Significance level		
	CeA (well)[a]	CeB (well)	MkA (well)	MkB (well)	MxA (modw)[a]	MxB (modw)	KeA (modw)	KxA (swpo)[a]	KxB (swpo)	EkA (poor)[a]	OtA (poor)	Soil map unit	Date	Soil map unit × date or date (soil map unit)
Physical and chemical properties														
pH	6.89 ab	6.63 ab	6.93 a	6.84 a	6.71 ab	6.43 b	6.83 a	6.78 ab	6.73 ab	6.45 b	6.45 b	<0.0001	ns	ns
Canonical variate 1	18.1 c	14.7 e	15.8 de	17.8 c	17.9 c	16.0 de	16.0 de	17.2 cd	15.8 de	23.6 a	20.9 b	<0.0001	ns	ns
Canonical variate 2	−12.4 d	−10.3 c	−9.7 c	−13.0 d	−8.8 abc	−10.1 c	−9.2 bc	−7.4 a	−9.9 c	−7.7 ab	−11.9 d	<0.0001	ns	ns
Canonical variate 3	5.9 d	7.7 bc	8.4 bc	9.3 ab	7.9 bc	5.2 d	7.7 bcd	9.1 abc	10.5 a	7.3 cd	9.5 ab	<0.001	ns	ns
Microbial activities														
MBC_r/total C (mg g^{-1})	26.7 bcd	31.7 ab	27.2 abcd	24.6 cd	26.6 bcd	32.4 a	25.4 cd	23.6 d	29.7 abc	26.3 bcd	25.2 cd	<0.001	<0.0001	<0.01
MBC_r/active C (g g^{-1})	4.68 ab	5.20 ab	3.57 ab	4.35 ab	4.42 ab	3.90 ab	3.79 b	3.57 ab	6.48 a	5.46 ab	5.81 ab	<0.05	<0.05	ns
Canonical variate 1	17.5 b	15.0 de	15.3 cde	14.6 e	15.3 cde	19.6 a	16.6 bcd	16.5 bcd	16.8 bc	16.4 bcd	14.7 c	<0.001	ns	ns
Microbial populations														
August Pseudomonads (CFU μg MBC_{fe}^{-1})	0 b	0 b	0 b	0 b	0.5 b	0 b	0 b	19.8 a	0 b	0 b	0 b	<0.0001	<0.0001	<0.001
Actinomycetes (CFU μg MBC_{fe}^{-1})	72.1 ab	18.5 b	22.7 b	24.9 b	53.5 b	69.9 ab	58.7 b	12.3 ab	186 a	71.6 ab	52.8 ab	<0.05	ns	ns
October *Fusaria* (CFU μg MBC_{fe}^{-1})	9.39 b	0 b	0 b	1.61 b	0 b	0.47 b	0 b	94.6 a	0 b	0 b	0 b	<0.001	<0.05	<0.001
October *Gliocladium* + *Trichoderma* (CFU × 10^3 μg MBC_{fe}^{-1})	2.96 b	77.4 a	4.42 b	16.0 b	3.63 b	2.43 b	2.08 b	5.18 b	11.8 ab	3.15 b	3.37 b	<0.001	<0.0001	<0.001
October *Rhizoctonia* survival (μg MBC_{fe}^{-1})	0.01 b	0.59 a	0.02 b	0.05 b	0.01 b	0.02 b	0.01 b	0.04 b	0.08 b	0.02 b	0.01 b	<0.001	<0.0001	<0.001
October *Rhizoctonia* saprophytic ability (μg MBC_{fe}^{-1})	0.008 b	0.313 a	0.012 b	0.030 b	0.011 b	0.007 b	0.011 b	0.017 b	0.045 b	0.010 b	0.008 b	<0.001	<0.0001	<0.01
October total bacteria (CFU × 10^3 μg MBC_{fe}^{-1})	1.24 b	32.4 a	1.53 b	2.96 b	1.03 b	1.00 b	2.79 b	1.89 b	5.35 ab	1.00 b	0.79 b	<0.01	<0.001	<0.05

Means followed by a different letter are significantly different within a row according to Sidak's $LSD_{0.05}$ for univariate analyses and $LSD_{0.05}$ for multivariate analyses.
[a] well: well drained; modw: moderately well drained; swpo: somewhat poorly drained; poor: poorly drained.

Table 8
Canonical structure of the first canonical variate for soil microbial activities analyzed by soil map unit

Soil microbial activities	Canonical variate 1
Acid phosphatase/total C (mg PNP[a] g^{-1} h^{-1})	0.85
Alkaline phosphatase/total C (mg PNP g^{-1} h^{-1})	−0.34
β-Glucosidase/total C (mg PNP g^{-1} h^{-1})	0.27
Arylsulfatase/total C (mg PNP g^{-1} h^{-1})	0.49
Nmin/total N (mg g^{-1} 7 d^{-1})	0.43
Nitrification rate/total N (mg ml^{-1} h^{-1} g^{-1})	−0.15
MBC_{fe}/total C (mg g^{-1})	0.40
MBC_r/total C (mg g^{-1})	0.46
MBN_{fe}/total N (mg g^{-1})	−0.33
MBN_r/total N (mg g^{-1})	0.39
Glomalin/total C (mg g^{-1})	0.88

[a] PNP: *p*-nitrophenol.

soils than in the other two texture groups. CDA distinguished among the three textural classes (Wilks' Lambda, $P < 0.0001$; Fig. 2d). ANOVA showed that the three soil classes were distinguished along canonical axis 1 (Table 9) primarily by moisture, available K, Mg, and Ca, and CEC_e (Table 5). The low sand, high silt soils were different from the other two groups along axis 2 (Table 9) based largely on total C, pH, and available P (Table 5).

Univariate analyses showed that three measures of microbial activity and one measure of microbial population size varied by Ap texture class. Alkaline phosphatase and β-glucosidase activities, and MBC_{fe}, each expressed per unit of active C, and the incidence of AMF spores, were higher in the medium sand, medium silt soils than in the low sand and high silt soils (Table 9). CDAs were not able to distinguish soil Ap texture classes based on soil microbial activities or on soil microbial populations (data not shown), but CDA was able to detect differences among texture classes based on FAME profiles (Wilks' Lambda, $P < 0.05$; Fig. 3). ANOVAs of canonical variates 1 and 2 showed that the three texture groups were different in two dimensions (Table 9).

3.5. Date effects

Among soil physical and chemical properties, only soil moisture, and available K and Ca showed significant date effects in the two-way univariate

Table 9
Means of soil properties that were significantly different among Ap textural classes according to one-way (bulk density and canonical variates) or two-way analyses of variance

Soil properties	Ap texture class			Significance level		
	Low sand, high silt	Medium sand, medium silt	High sand, low silt	Ap texture class	Date	Ap texture class × date
Physical and chemical properties						
Bulk density (Mg m^{-3})	1.21 b	1.30 b	1.44 a	<0.001	NA[a]	NA
Available K (cmol kg^{-1})	0.32 ab	0.33 a	0.22 b	<0.05	<0.0001	ns[b]
Available Mg (cmol kg^{-1})	1.01 b	1.28 a	1.09 b	<0.05	ns	ns
Active C/total C (mg g^{-1})	6.05 ab	5.23 b	6.95 a	<0.01	ns	ns
Canonical variate 1	−2.28 b	−0.88 a	−3.13 c	<0.0001	ns	ns
Canonical variate 2	−12.1 b	−10.2 a	−9.8 a	<0.0001	ns	ns
Microbial activities						
Alkaline phosphatase/active C (g PNP g^{-1} h^{-1})	1.78 b	2.90 a	2.45 ab	<0.001	ns	ns
β-Glucosidase/active C (g PNP g^{-1} h^{-1})	0.99 b	1.48 a	1.36 ab	<0.01	<0.001	ns
MBC_{fe}/active C (g g^{-1})	3.07 b	4.49 a	4.20 ab	<0.05	ns	ns
Microbial populations						
AMF spore incidence	0.6 b	5.2 a	3.0 ab	<0.05	NA	NA
Microbial communities						
FAME canonical variate 1	3.10 a	2.04 b	3.67 a	<0.001	NA	NA
FAME canonical variate 2	−0.55 a	−1.46 b	−2.38 c	<0.01	NA	NA

Means within a row followed by a different letter are significantly different row according to $LSD_{0.05}$.
[a] NA: not applicable.
[b] ns: not significant at $P < 0.05$.

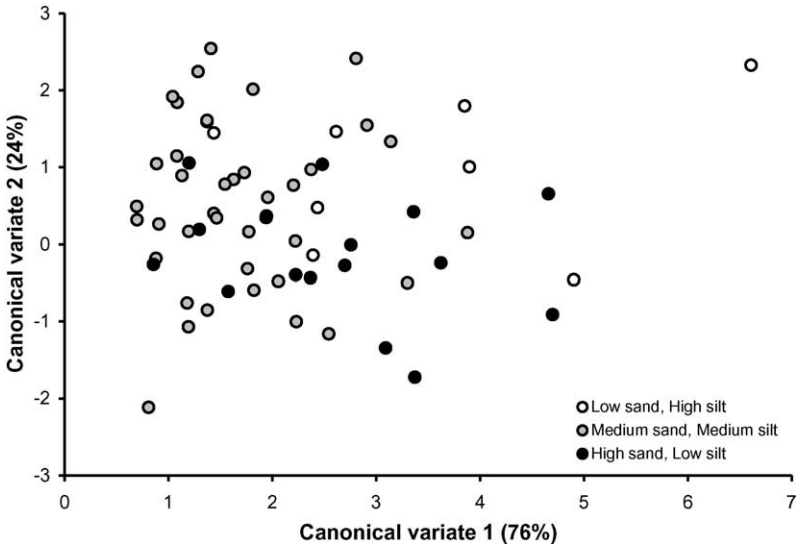

Fig. 3. Canonical linear discriminant analysis of FAME profiles by Ap texture class.

analyses. For example, soil moisture in October (25%) was higher than in April (22%), June (20%), and August (15%) ($P < 0.05$; K and Ca data not shown). These effects were evident regardless of how soils were classified. Two-way ANOVAs of canonical variates from CDAs of soil physical and chemical properties showed no significant date effects (Tables 4, 6, 7, and 9). Most measures of microbial activity and microbial population sizes were influenced by date of sampling (Table 10). The method of classifying soils had little effect on the influence of date on microbial activity parameters but method of classifying soils had an effect on the influence of date on microbial population sizes (Table 10).

4. Discussion

4.1. Soil type effects

4.1.1. Soil physical and chemical properties

All four methods of classifying soils—soil drainage class, soil series, soil map unit, and Ap texture class—showed that soil physical and chemical properties varied with soil type. While the individual soil physical and chemical properties that differed by soil type, based on univariate analyses, varied based on the method of classifying the soils (Tables 4, 6, 7, and 9), multivariate analyses showed a more consistent picture of differences among soils. CDAs of soil physical and chemical properties and subsequent ANOVAs of canonical variate 1 showed that poorly drained soils were always clearly distinct from other soils, and that the two poorly drained soils were distinct from each other (Fig. 2a–c; Tables 4, 6, and 7). Well, moderately well, and somewhat poorly drained soils were distinct when classified by drainage class (canonical variate 2, Table 4). Although soil type effects were evident at finer hierarchical scales (series and map unit), these three drainage classes were not always distinct at these scales. Since there were fewer samples in each class level at finer hierarchical levels, and since differences among soil types at finer hierarchical levels, by definition, ought to be less distinct than at coarser hierarchical levels, this result is not surprising.

Soil type groupings by means separations, whether determined by univariate or multivariate methods, however, were not always intuitive. While it might be expected that soil series and map units within the same soil drainage class should be more similar to each other than to soils in different drainage classes, this was not always the case. And, while it might be expected that differences among soil types should increase with increasing differences in soil drainage, this was also not always the case. For example, for

Table 10
Soil microbial activities and populations that showed date effects when analyzed by two-way ANOVA using grouped variance

	First class variable in two-way ANOVAs			
	Drainage class	Soil series	Soil map unit	Ap texture class
Acid phosphatase/total C (mg PNP[a] g^{-1} h^{-1})	x	x	x	x
Acid phosphatase/active C (g PNP[a] g^{-1} h^{-1})				
Alkaline phosphatase/total C (mg PNP g^{-1} h^{-1})	x	x	x	x
Alkaline phosphatase/active (g PNP g^{-1} h^{-1})				
β-Glucosidase/total C (mg PNP g^{-1} h^{-1})	x	x	x	x
β-Glucosidase/active (g PNP g^{-1} h^{-1})	x	x	x	x
Arylsulfatase/total C (mg PNP g^{-1} h^{-1})	x	x	x	
Arylsulfatase/active (g PNP g^{-1} h^{-1})	x	x	x	x
N min/total N (mg g^{-1} 7 day^{-1})	x	x	x	x
Nitrification rate/total N (mg ml^{-1} h^{-1} g^{-1})	x	x	x	x
MBC_{fe}/total C (mg g^{-1})				
MBC_{fe}/active C (g g^{-1})				
MBC_r/total C (mg g^{-1})	x	x	x	x
MBC_r/active C (g g^{-1})				
MBN_{fe}/total N (mg g^{-1})	x	x	x	
MBN_r/total N (g g^{-1})			x	x
Glomalin/total C (mg g^{-1})	x	x	x	x
Fusaria (CFU μg MBC_{fe}^{-1})			x	
Fusaria (CFU μg MBC_r^{-1})			x	
Gliocladium + *Trichoderma* (CFU μg MBC_{fe}^{-1})	x	x	x	x
Gliocladium + *Trichoderma* (CFU μg MBC_r^{-1})		x	x	x
Talaromyces (CFU μg MBC_{fe}^{-1})				
Talaromyces (CFU μg MBC_r^{-1})				
Pythium (CFU μg MBC_{fe}^{-1})	x		x	x
Pythium (CFU μg MBC_r^{-1})	x			
Rhizoctonia survival (number μg MBC_{fe}^{-1})	x	x	x	x
Rhizoctonia survival (number μg MBC_r^{-1})	x	x	x	x
Rhizoctonia saprophytic ability (number μg MBC_{fe}^{-1})			x	
Rhizoctonia saprophytic ability (number μg MBC_r^{-1})			x	
Total bacteria (CFU μg MBC_{fe}^{-1})	x	x	x	x
Total bacteria (CFU μg MBC_r^{-1})	x		x	x
Pseudomonads (CFU μg MBC_{fe}^{-1})			x	
Pseudomonads (CFU μg MBC_r^{-1})	x		x	
Burkholderia cepacia (CFU μg MBC_{fe}^{-1})			x	x
Burkholderia cepacia (CFU μg MBC_r^{-1})	x	x	x	
Enterobacter (CFU μg MBC_{fe}^{-1})	x			x
Enterobacter (CFU μg MBC_r^{-1})				
Actinomycetes (CFU μg MBC_{fe}^{-1})				
Actinomycetes (CFU μg MBC_r^{-1})				x
Total nematode sp.		x	x	

An x denotes that the soil type in a two-way ANOVA showed a date effect at $P < 0.05$.
[a] PNP: *p*-nitrophenol.

soils classified by soil map unit, canonical variate 1 shows that well drained CeA and MkB soils were clearly distinct from the three moderately well drained and the two somewhat poorly drained soils, but the well drained CeB and MkA soils were not different than the three moderately well drained and one of the somewhat poorly drained soils (Table 7). This example highlights the effect that slope had on soil properties. It also indicates that the complex patterns of soil physical and chemical properties among soil types makes interpretation of differences among soil types challenging.

Despite these complex patterns, differences among soil types at each hierarchical level of classification

(drainage, series, and map unit) were driven by a similar set of soil properties (Table 5). Total soil C and N were dominant influences on canonical variate 1 for each hierarchical level of soil classification. Soil moisture, pH, CEC_e, and available P were also important determinants of differences among soil types, but with varying degrees of importance among the different hierarchical levels of classification. Available K was always the dominant soil property influencing canonical variate 2 (Table 5).

Since the activity and growth of soil microorganisms are influenced by multiple environmental factors, we suggest that the multivariate descriptions of soil types based on soil physical and chemical properties are better descriptions of microbial environments than are the univariate analyses. One line of evidence supporting this position is that the same soil properties defined canonical variates 1 and 2 regardless of the hierarchical level of soil classification, while different soil properties varied by soil type at the three hierarchical levels of soil classification when univariate analyses were used.

When soils were classified according to Ap texture class, the three soil types were distinguished by a different set of factors than those responsible for distinguishing among drainage classes, series, and map units. Soil moisture, available K, Mg and Ca, and CEC_e distinguished the three soil texture classes along canonical axis 1 (Table 5). Thus, classifying soils by Ap texture would be expected to provide qualitatively different results for soil microbial parameters compared to the classification schemes based on the hierarchical soil survey categories.

4.1.2. Soil microbial properties

Soil microbial properties showed fewer soil type effects than did soil physical and chemical properties. Based on results of univariate analyses, 8 of 12 measured soil physical and chemical properties showed a soil type effect, while 11 of 17 measured soil microbial activities (includes activities expressed per unit active C and per unit total C), and 13 of 26 measured soil microbial population sizes (includes populations expressed per unit MBC_{fe} and per unit MBC_r) varied by soil type according to at least one of four methods of classifying soils. In addition, while all four classification schemes showed soil type effects based on CDAs of soil physical and chemical properties, among the 12 CDAs conducted on soil microbial properties (microbial activities, microbial populations, and FAMEs by four methods of soil classification), only CDA conducted on microbial activities by soil map unit and CDA conducted on FAMEs by soil texture class showed a significant soil type effect. Also, the specific soil microbial properties that distinguished soil types were different when soil types were defined by drainage class, series, map unit, and Ap texture class (Tables 4, 6, 7, and 9). Based on the CDA results for soil physical and chemical properties, we expected that unique soil microbial properties would show soil type effects when soil type was defined by Ap texture class rather than by the other three methods of classifying soils. However, based on CDA results for soil physical and chemical properties, we also expected that the same or similar soil microbial properties would show soil type effects when soil type was defined according to the three hierarchical soil classification methods. Thus, in contrast to CDA results for soil physical and chemical properties, the effect of soil type on soil microbial properties was highly dependent on how soil type is defined.

One slight exception to this conclusion is that MBC_r/active C and actinomycetes/MBC_{fe} both varied by soil drainage class and by soil map unit (but not by soil series). There was also some consistency in means separations for these two variables when the two soil classification methods were used. MBC_r/active C was lowest in moderately well drained soils (Table 4) and in the moderately well drained KeA soil (Table 7). Actinomycetes/MBC_{fe} were greatest in somewhat poorly drained soils and in the somewhat poorly drained KxB soil. Perhaps MBC_r and actinomycete population sizes are more strongly influenced by soil type than the other soil microbial properties we measured; further investigations into the spatial and temporal variability of soil microbial properties at the landscape level may benefit by studying these two variables.

The degree of similarity between means separations for soil physical and chemical properties versus that for soil microbial properties were different for each method of soil classification. When classified by drainage class, means separations of canonical variates from a CDA conducted on soil physical and chemical properties and means separations of seven

soil microbial properties showed clear and consistent differences between the poorly drained soils and the better drained soils (Table 4). Thus, there seems to be some relationship between soil physical and chemical properties and soil microbial properties when soils are classified by drainage class. Among soil series, while significant differences in soil microbial properties were evident between poorly drained soils and better drained soils, as was the case for soil physical and chemical properties, the more subtle differences in soil physical and chemical properties evident among soil series were not evident for soil microbial properties (Table 6). Among soil map units, means separations for the first canonical variate of CDAs conducted using soil physical and chemical properties are very different than the means separations for the first canonical variate of CDAs conducted using soil microbial activities (Table 7). And, while univariate analyses showed that four different measures of microbial population size were greater in the CeB soil than in any other soil, the CeB soil was not identified as unique using any measure of soil physical and/or chemical properties. There also did not seem to be any relationship between means separations for other soil microbial properties that showed significant soil map unit effects and soil physical and chemical properties that showed soil map unit effects (Table 7). Thus, it seems that at finer hierarchical delineations of soil types, there are fewer relationships between soil physical and chemical properties and soil microbial properties than there are at coarser hierarchical levels.

Among Ap texture classes, there was much more consistency between soil type delineations elucidated by soil physical and chemical properties and those elucidated by soil microbial properties (Table 9). The medium sand and medium silt soils were distinct from at least one of the other Ap texture classes in available K, available Mg, active C/total C, alkaline phosphatase/active C, β-glucosidase/active C, MBC_{fe}/active C, number of microbial spores, and the first two canonical variates for CDAs of soil physical and chemical properties and for CDAs of FAMEs.

The complex patterns of soil physical, chemical, and microbial properties among soil types, especially at finer hierarchical levels, could be due to a number of factors. As already noted, with increasing sampling resolution, fewer soil samples were collected per soil type. Having fewer samples per soil type reduces the ability of the statistical analyses to identify differences among soil types. Many soil properties varied with soil type at $0.05 < \alpha < 0.10$ (data not shown), which is an indication that greater replication may have revealed a larger number of soil properties that vary by soil type and may have revealed more differences among soil types. Also, our soil sampling protocol, which was designed to capture the spatial breadth of each soil map unit (Fig. 1), may have contributed to variability by integrating large spatial areas into each soil sample. While this method captured the full spatial breadth of each soil map unit, the number of soil cores (five) comprising each sample may have been inadequate to capture the breadth of the spatial variability of soil properties, especially the soil microbiological properties, within each soil map unit (Speir et al., 1984). In addition, we based our sampling design on the soil map shown in Fig. 1. The lines demarcating individual soil map units are the result of a semi-quantitative process of soil surveying and mapping. It is possible that individual soil cores taken at the edge of a given map unit may have less distinct soil properties than samples taken further from map boundaries, and these cores may have reduced the distinctiveness of individual samples. Also, observations made during subsequent wet years at this site have identified the region from which most of the cores comprising one of the moderately well drained MxA samples were taken seems to be more poorly drained than a moderately well drained soil would be. This potential mapping discrepancy might explain why the MxA samples often grouped more closely with the poorly and somewhat poorly drained soils than with the moderately well drained soils. Finally, we suspect that although the entire field was managed as one field for at least 10 years prior to the year of this study, unequal manure applications even before this time may have impacted soil properties independent of soil type. Our site is just to the west of a dairy that has historically applied manure preferentially to the east end of the site. This practice may have contributed to the complex patterns of soil physical and chemical properties among soil series and map units. Dairy manure applications would impact all the factors that influenced means separations of soil types along canonical variate 1: total soil C and N, moisture, pH, CEC_e, and available P. Since these variables are also likely to influence soil microbial properties, it is

possible that historical differences in management might also have reduced our ability to detect differences in soil microbial properties among soil types and contributed to complex patterns of soil microbial properties among soil types.

Given the limitations of this study, our results should be interpreted as conservative estimates of landscape level variation among soil physical, chemical, and microbiological properties. We suggest that future efforts at characterizing soil variation by soil type consider within soil map unit variability carefully and that a relatively large number of cores be taken per map unit. And, in light of the limitations described above, describing landscape level variability of soil microbial properties based on sampling by soil map unit might best serve only as a starting point for future investigations. Just as soil curvature and other terrain attributes that vary within soil map units are proving to be useful explanatory variables in efforts to predict crop yields (Timlin et al., 1998; Nielsen and Wendroth, 2003), it is likely that predicting soil microbial properties across landscapes will benefit by considering these additional descriptors of landscape level variability. Since soil microbial properties are likely to vary at a scale smaller than that at which crop yields vary, it is also likely that soil sampling within a map unit may need to be further stratified by microtopography, soil texture, soil bulk density, and other factors that influence the variability of soil temperature and moisture dynamics within a soil map unit.

4.2. Date effects

Among soil physical and chemical properties only moisture, and available K and Ca varied by date. We found that almost all soil microbial properties exhibited higher temporal variability (Table 10) than did soil chemical properties, which is consistent with many literature reports (Barker and Campbell, 1981; Barker et al., 1984; Speir et al., 1984; Rastin et al., 1988; Bossio et al., 1998; Bossio and Scow, 1998; Burton and McGill, 1992; Aon et al., 2001; Grayston et al., 2001; Rogers and Tate, 2001; Schutter et al., 2001; Blume et al., 2002). Seasonal fluctuations among soil biological properties were likely related to fluctuations in soil temperature, soil moisture, substrate availability, and root growth (Kirchner et al., 1993). The lack of temporal variability exhibited by acid and alkaline phosphatases when expressed per unit active C compared to significant date effects, when expressed per unit total C, suggests that active C and the activity of these two enzymes varied temporally in unison. We also found high temporal variability among soil populations, as have others (e.g., Aon et al., 2001). Among microbial populations, the only taxa that did not vary by date were Talaromyces, Enterobacter/MBC_r, and actinomycetes/MBC_{fe}. Lack of temporal variability in population size of actinomycetes/MBC_{fe} suggests an additional benefit to using actinomycetes/MBC_{fe} in studies of landscape level variability of soil microbial properties.

4.3. Soil physical and chemical properties

Among soil drainage classes, soil physical and chemical properties generally followed predictable patterns: poorly drained soils had greater total C and N, CEC_e, and moisture, and lesser pH than did better drained soils. At finer hierarchical levels, however, patterns of soil physical and chemical properties were sometimes complex, which may have been due to limitations in our sampling scheme, as discussed above.

4.4. Soil microbial activities

Most measures of soil microbial activity were greatest in mid-range soil types (somewhat poorly drained; moderately well drained; and medium silt, medium sand soils; Tables 4, 6, 7, and 9). These patterns suggest that soil moisture in these mid-range soil types may have been more optimal for soil microbial activity than in other soil types in 1995. Although no significant differences were found in soil moisture among soil types according to univariate analyses, soil moisture was an important factor in the first canonical variate of soil physical and chemical properties for all four soil classification methods (Table 5).

Date, drainage class, and soil map unit affected MBC_r but not MBC_{fe}, MBN_r or MBN_{fe}. These discrepancies support the concept of measuring soil microbial biomass using more than one method (West et al., 1986). The reason that MBC_r but not MBN_r was affected by date, drainage class, and soil map unit might be related to the sensitivity of the analyses. Soil MBC is seven to almost 10 times greater than soil MBN.

4.5. Soil microbial populations and community structure

As with soil microbial activity, those microbial populations that varied with soil type were greatest in mid-range soil types: total bacteria, actinomycete, and August Pseudomonad population sizes were greatest in somewhat poorly drained soils (Tables 4 and 7); and AMF spore incidence was highest in the medium sand, medium silt Ap texture class (Table 9). Greater microbial population sizes in these mid-range soils may have been due to these soils having more favorable water contents for microbial growth than the better or more poorly drained soils in 1995.

In October, population sizes of total bacteria and *Gliocladium* + *Trichoderma*, and *Rhizoctonia* survival and saprophytic ability were greater in the well drained CeB soil than in all other soils. Soil moisture in October was higher than at previous sampling dates, which should have made the better drained soils a better environment for microbial growth in October than during the year as a whole or during drier periods, such as August. *Fusaria* were the only microbial populations that showed a soil type effect that did not fit this pattern.

Patterns of soil microbial populations, including total bacteria, among soil types were very different than those found for FAMEs, a result which supports the contention that FAMEs identify different portions of the soil microbial community than those that can be readily cultured in the lab (Cavigelli et al., 1995). Although others (Bossio et al., 1998; Ritchie et al., 2000; Schutter et al., 2001; Buyer et al., 2002; Girvan et al., 2003) have shown that FAME profiles vary with soil type, we did not find any differences in FAME profiles among soil drainage classes, series or map units. We did, however, find differences among FAMEs based on soil texture, as did Schutter et al. (2001). As with microbial activities and populations, FAME profiles in the mid-range soil types proved to be different from both the more extreme soil types.

5. Conclusions

We found support for our hypothesis that soil microbial properties vary by soil type. Eleven measures of microbial activity, 13 measures of microbial population size, and 1 measure of microbial community structure varied by soil type using at least one of four methods of classifying soils in a 16-ha no-till corn field. However, while CDAs showed that the majority of soil physical and chemical properties varied by soil type, regardless of soil classification method used, only a relatively small subset of soil microbial properties varied by soil type for any individual soil classification method. In addition, while a similar set of soil physical and chemical properties varied by soil type regardless of soil classification method used, soil classification method influenced which soil microbial properties varied by soil type. These inconsistencies in the effect of soil type on soil microbial properties suggest that patterns of soil microbial properties across a landscape are complex. They also suggest that soil delineations derived from soil surveying and mapping may not contain sufficient information or may not be at an adequate resolution to allow for more powerful predictions of variation in soil microbial properties across landscapes. Further increasing our level of understanding of variation in soil microbial properties across landscapes will likely require that sub-soil map unit variation be explicitly sampled. For example, sampling within a soil map unit may need to be stratified by landscape elements, soil microtopography, soil texture, soil bulk density, and/or other factors that influence soil temperature and moisture dynamics.

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References

Aon, M.A., Cabello, M.N., Sarena, D.E., Colaneri, A.C., Franco, M.G., Burgos, J.L., Cortassa, S., 2001. I. Spatio-temporal patterns of soil microbial and enzymatic activities in an agricultural soil. Appl. Soil Ecol. 18, 239–254.

Ball, D.F., Williams, W.M., 1968. Variabilitiy of soil chemical properties in two uncultivated brown earths. J. Soil Sci. 19, 379–391.

Barker, K.R., Campbell, C.L., 1981. Sampling nematode populations. In: Zuckerman, B.M., Rohde, R.A. (Eds.), Plant Parasitic

Nematodes, vol. III. Academic Press, New York, NY, pp. 451–474.

Barker, K.R., Schmitt, D.P., Noe, J.P., 1984. Role of sampling for crop-loss assessment and nematode management. Agric. Ecosyst. Environ. 12, 355–369.

Bergstrom, D.W., Monreal, C.M., Millete, J.A., King, D.J., 1998. Spatial dependence of soil enzyme activities along a slope. Soil Sci. Soc. Am. J. 62, 1302–1308.

Bergstrom, D.W., Monreal, C.M., St. Jacques, E., 2001a. Spatial dependence of soil organic carbon mass and its relationship to soil series and topography. Can. J. Soil Sci. 81, 53–62.

Bergstrom, D.W., Monreal, C.M., St. Jacques, E., 2001b. Influence of tillage practice on carbon sequestration is scale-dependent. Can. J. Soil Sci. 81, 63–70.

Bever, J.D., Morton, J., Antonovics, J., Schultz, P.A., 1996. Host-dependent sporulation and species diversity of mycorrhizal fungi in a mown grassland. J. Ecol. 75, 1965–1977.

Bever, J.D., Schultz, P.A., Pringle, A., Morton, J.B., 2001. Arbuscular mycorrhizal fungi: more diverse than meets the eye, and the ecological tale of why. BioScience 51, 923–931.

Blake, G.R., Hartge, K.H., 1986. Bulk density. In: Klute, A. (Ed.), Methods of Soil Analysis: Physical and Mineralogical Methods. second ed. American Society of Agronomy, Madison, WI, pp. 363–376.

Blume, E., Bischoff, M., Reichert, J.M., Morrman, T., Konopka, A., Turco, R.F., 2002. Surface and subsurface microbial biomass, community structure and metabolic activity as a function of soil depth and season. Appl. Soil Ecol. 20, 171–181.

Bossio, D.A., Scow, K.M., 1998. Impacts of carbon and flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. Microb. Ecol. 35, 265–278.

Bossio, D.A., Scow, K.M., Gunapala, N., Graham, K.J., 1998. Determinants of soil microbial communities: effects of agricultural management, season, and soil type on phospholipid fatty acid profiles. Microb. Ecol. 36, 1–12.

Bundy, L.G., Meisinger, J.J., 1994. Nitrogen availability indices. In: Weaver, R.W., Angle, S., Bottomley, P., Bezdicek, D., Smith, S., Tabatabai, A., Wollum, A. (Eds.), Methods of Soil Analysis: Microbiological and Biochemical Properties. American Society of Agronomy, Madison, WI, pp. 951–984.

Burbage, D.A., Sasser, M., Lumsden, R.D., 1982. A medium selective for *Pseudomonas cepacia*. Phytopathology 72, 706.

Burton, D.L., McGill, W.B., 1992. Spatial and temporal fluctuation in biomass, nitrogen mineralizing reaction and mineral nitrogen in a soil cropped to barley. Can. J. Soil Sci. 72, 31–42.

Buyer, J.S., Roberts, D.P., Russek-Cohen, E., 2002. Soil and plant effects on microbial community structure. Can. J. Microbiol. 48, 955–964.

Cambardella, C.A., Moorman, T.B., Novak, J.M., Parkin, T.B., Karlen, D.L., Turco, R.F., Konopka, A.E., 1994. Field-scale variability of soil properties in central Iowa soils. Soil Sci. Soc. Am. J. 58, 1501–1511.

Cavigelli, M.A., Robertson, G.P., Klug, M.J., 1995. Fatty acid methyl ester (FAME) profiles as measures of soil microbial community structure. Plant Soil 170, 99–113.

Cobb, N.A., 1918. Estimating the nema population of the soil. Agric. Tech. Circ. Bur. Pl. Ind. U.S. Dept. Agric. 1, 48.

Corre, M.D., Schnabel, R.R., Stout, W.L., 2002. Spatial and seasonal variation of gross nitrogen transformations and microbial biomass in a Northeastern US grassland. Soil Biol. Biochem. 34, 445–457.

Doran, J.W., Zeiss, M.R., 2000. Soil health and sustainability: managing the biotic component of soil quality. Appl. Soil Ecol. 15, 3–11.

Elliott, J.A., Efetha, A.A., 1999. Influence of tillage and cropping system on soil organic matter, structure and infiltration in a rolling landscape. Can. J. Soil Sci. 79, 457–463.

Ettema, C.H., Wardle, D.A., 2002. Spatial soil ecology. TREE 17, 177–183.

Ferris, H., Mullens, T.A., Foord, K.E., 1990. Stability and characteristics of spatial description parameters for nematode populations. J. Nematol. 22, 427–439.

Fromm, H., Winter, K., Filser, J., Hantschel, R., Beese, F., 1993. The influence of soil type and cultivation system on the spatial distributions of the soil fauna and microorganisms and their interactions. Geoderma 60, 109–118.

Gee, G.W., Bauder, J.W., 1986. Particle-size analysis. In: Klute, A. (Ed.), Methods of Soil Analysis: Physical and Mineralogical Methods. second ed. American Society of Agronomy, Madison, WI, pp. 377–382.

Girvan, M.S., Bullimor, J., Pretty, J.N., Osborn, A.M., Ball, A.S., 2003. Soil type is the primary determinant of the composition of the total and active bacterial communities in arable soils. Appl. Environ. Microbiol. 69, 1800–1809.

Goodell, P., Ferris, H., 1980. Plant-parasitic nematode distributions in an alfalfa field. J. Nematol. 12, 136–141.

Grayston, S.J., Griffith, G.S., Mawdsley, J.L., Campbell, C.D., Bardgett, R.D., 2001. Accounting for variability in soil microbial communities of temperate upland grassland ecosystems. Soil Biol. Biochem. 33, 533–551.

Handoo, Z.A., 2000. A key and diagnostic compendium to the species of the genus *Tylenchorhynchus* Cobb (Nematoda: Belonolaimidae). J. Nematol. 32, 20–34.

Handoo, Z.A., Golden, A.M., 1992. A key and diagnostic compendium to the species of genus *Pratylenchus* Filipjev (Lesion nematodes). J. Nematol. 21, 202–218.

Hanna, A.Y., Harlan, P.W., Lewis, D.T., 1982. Soil available water as influenced by landscape position and aspect. Agron. J. 74, 999–1004.

Harris, R.F., Sommers, L.E., 1968. Plate-dilution frequency technique for assay of microbial ecology. Appl. Microbiol. 16, 330–334.

Hart, S.C., Stark, J.M., Davidson, E.A., Firestone, M.K., 1994. Nitrogen mineralization, immobilization, and nitrification. In: Weaver, R.W., Ange, S., Bottomley, P., Bezdicek, D., Smith, S., Tabatabai, A., Wollum, A. (Eds.), Methods of Soil Analysis: Microbiological and Biochemical Properties. American Society of Agronomy, Madison, WI, pp. 985–1018.

Hayman, D.S., 1984. Methods for evaluating and manipulating vesicular–arbuscular mycorrhiza. In: Grainger, J.M., Lynch, J.M. (Eds.), Microbiological Methods for Environmental Biotechnology. Academic Press Inc., London, UK, pp. 95–117.

Hooper, D.J., 1986. Structure and classification of nematodes. In: Southey, J.F. (Ed.), Laboratory Methods for Work with Plant and

Soil Nematodes. sixth ed. Her Majesty's Stationary office, London, p. 202.

Horwath, W.R., Paul, E.A., 1994. Microbial biomass. In: Weaver, R.W., Ange, S., Bottomley, P., Bezdicek, D., Smith, S., Tabatabai, A., Wollum, A. (Eds.), Methods of Soil Analysis: Microbiological and Biochemical Properties. American Society of Agronomy, Madison, WI, pp. 753–774.

Kachanoski, R.G., Rolston, D.E., de Jong, E., 1985. Spatial and spectral relationships of soil properties and microtopography. I. Density and thickness of A horizon. Soil Sci. Soc. Am. J. 49, 804–812.

Kirchner, M.J., Wollum II, A.G., King, L.D., 1993. Soil microbial populations and activities in reduced chemical input agroecosystems. Soil Sci. Soc. Am. J. 57, 1289–1295.

Klute, A., 1986. Water retention: laboratory methods. In: Klute, A., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis: Physical and Mineralogical Methods. second ed. American Society of Agronomy, Madison, WI, pp. 635–662.

Komada, H., 1975. Development of a selective medium for quantitative isolation of *Fusarium oxysporum* from natural soil. Rev. Plant Prot. Res. 8, 115–125.

Lanyon, L.E., Heald, W.R., 1982. Magnesium, calcium, strontium, and barium. In: Page, A.L., Klute, A., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis: Chemical and Microbiological Properties. second ed. ASA, Madison, WI, pp. 247–262.

Lefroy, R.D.B., Blair, G.J., Strog, W.M., 1993. Changes in soil organic matter with cropping as measured by organic carbon fractions and ^{13}C natural isotope abundance. Plant Soil 155–156, 399–402.

Lewis, J.A., Larkin, R.P., 1998. Formulation of the biocontrol fungus *Cladorrhinum foecundissimum* to reduce damping-off diseases caused by *Rhizoctonia solani* and *Pythium ultimum*. Biological Contr. 12, 182–190.

Lewis, J.A., Papavizas, G.C., 1987. Reduction of inoculum of *Rhizoctonia solani* in soil by germlings of *Trichoderma hamatum*. Soil Biol. Biochem. 19, 195–201.

Lumsden, R.D., Ayers, W.A., Dow, R.L., 1975. Differential isolation of Pythium species from soil by means of selective media, temperature, and pH. Can. J. Microbiol. 21, 606–612.

Mai, W.F., Mullin, P.G., Lyon, H.H., Loeffler, K., 1996. Plant-parasitic nematodes. In: A Pictorial Key to Genera, fifth ed. Comstock Publishing Associates, Cornell University Press, Ithaca, NY, 276 pp..

Marois, J.J., Fravel, D.R., Papavizas, G.C., 1984. Ability of *Talaromyces flavus* to occupy the rhizosphere and its interactions with *Verticillium dahliae*. Soil Biol. Biochem. 16, 387–390.

McLean, E.O., 1982. Soil pH and lime requirement. In: Page, A.L., Klute, A., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis: Chemical and Microbiological Properties. second ed. ASA, Madison, WI, pp. 199–224.

Miller, M.P., Singer, M.J., Nielsen, D.R., 1988. Spatial variability of wheat yield and soil properties on complex hills. Soil Sci. Soc. Am. J. 52, 1133–1141.

Millner, P.D., Watson, D., Cavigelli, M., Lengnick, L., submitted for publication. Diversity of arbuscular mycorrhizal fungi in an agricultural field. Appl. Soil Ecol.

Morton, J.B., 1985. Underestimation of most probable numbers of vesicular–arbuscular endophytes because of non-staining mycorrhizae. Soil Biol. Biochem. 17, 383–384.

Morton, J.B., Bentivenga, S.P., Wheeler, W.W., 1993. Germplasm in the International Collection of Arbuscular Mycorrhizal Fungi (INVAM) and procedures for culture development, documentation and storage. Mycotaxon 48, 491–528.

Nielsen, D.R., Wendroth, O., 2003. Spatial and Temporal Statistics: Sampling Field Soils and their Vegetation. Catena Verlag GmbH, Reiskirchen, Germany, 350 pp.

Noe, J.P., Barker, K.R., 1985. Relation of within-field spatial variation of plant-parasitic nematode population densities and edaphic factors. Phytopathology 75, 247–252.

Olsen, S.R., Sommers, L.E., 1982. Soil pH and lime requirement. In: Page, A.L., Klute, A., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis: Chemical and Microbiological Properties. second ed. ASA, Madison, WI, pp. 403–422.

Ovales, F.A., Collins, M.E., 1986. Soil–landscape relationships and soil variability in North Central Florida. Soil Sci. Soc. Am. J. 50, 401–408.

Pankhurst, C., Doube, B.M., Gupta, V.V.S.R. (Eds.), 1997. Biological Indicators of Soil Health. CAB International, Wallingford, 451 pp..

Papavizas, G.C., Lewis, J.A., 1986. Isolating, identifying, and producing inoculum of *Rhizoctonia solani*. In: Dickey, K.D. (Ed.), Methods for Evaluating Pesticides for Control of Plant Pathogens. APS Press, St. Paul, MN, pp. 50–53.

Papavizas, G.C., Lumsden, R.D., 1982. Improved medium for isolation of *Trichoderma* spp. from soil. Plant Dis. 66, 1019–1020.

Parkin, T.B., 1993. Spatial variability of microbial processes in soil—a review. J. Environ. Qual. 22, 409–417.

Pennock, D.J., Frick, A.H., 2001. The role of field studies in landscape-scale applications of process models: an example of soil redistribution and soil organic carbon modeling using CENTURY. Soil Tillage Res. 58, 183–191.

Pickett, S.T.A., Cadenasso, M.L., 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science 269, 331–334.

Porter, W.M., 1979. The 'most probable number' method for enumerating infective propagules of vesicular-arbuscular mycorrhizal fungi in soil. Aust. J. Soil Res. 17, 515–519.

Rastin, N., Rosenplanter, K., Huttermann, A., 1988. Seasonal variation of enzyme activity and their dependence on certain soil factors in a beech forest soil. Soil Biol. Biochem. 20, 637–642.

Ritchie, N.J., Schutter, M.E., Dick, R.P., Myrold, D.D., 2000. Use of length heterogeneity PCR and fatty acid methyl ester profiles to characterize microbial communities in soil. Appl. Environ. Microbiol. 66, 1668–1675.

Robert, P.C., Rust, R.H., Larson, W.E. (Eds.), 1993. Soil Specific Crop Management. American Society of Agronomy, Madison, WI, p. 395.

Robertson, G.P., Crum, J.R., Ellis, B.G., 1993. The spatial variability of soil resources following long-term disturbance. Oecologia 96, 451–456.

Robertson, G.P., Klingensmith, K.M., Klug, M.J., Paul, E.A., Crum, J.R., Ellis, B.G., 1997. Soil resources, microbial activity, and primary production across an agricultural ecosystem. Ecol. Appl. 7, 158–170.

Rogers, B.F., Tate III, R.L., 2001. Temporal analysis of the soil microbial community along a toposequence in Pineland soils. Soil Biol. Biochem. 33, 1389–1401.

SAS Institute Inc., 1999. SAS/STAT User's Guide, version 8.2. SAS Institute Inc., Cary, NC, 3884 pp.

Saxton, A.M., 1998. A macro for converting mean separation output to letter groupings in Proc Mixed. In: Proceedings of 23rd SAS Users Group International, SAS Institute, Cary, NC, pp. 1243–1246.

Schultz, P.A., 1996. Arbuscular mycorrhizal species diversity and distribution in an old-field community. Ph.D. Dissertation, Duke University, Durham, NC, 126 pp.

Schutter, M.E., Sandeno, J.M., Dick, R.P., 2001. Seasonal, soil type, and alternative management influences on microbial communities of vegetable cropping systems. Biol. Fertil. Soils 34, 397–410.

Seinhorst, J.W., 1959. A rapid method for the transfer of nematodes from fixative to anhydrous glycerine. Nematologica 4, 67–69.

Sher, S.A., 1966. Revision of the Hoplolaimidae (Nematoda) VI. *Helicotylenchus* Steiner, 1945. Nematologica 12, 1–56.

Sikora, L.J., Yakovchenko, V., Kaufman, D.D., 1994. Comparison of the rehydration method for biomass determination to fumigation–incubation and substrate-induced respiration method. Soil Biol. Biochem. 26, 1443–1445.

Sollins, P., Glassman, C., Paul, E.A., Swanston, C., Lajtha, K., Heil, J.W., Elliott, E.T., 1999. In: Robertson, G.P., Bledsoe, C.S., Coleman, D.C., Sollins, P. (Eds.), Standard Soil Methods for Long-Term Ecological Research. Oxford University Press, New York, NY, pp. 89–105.

Speir, T.W., Ross, D.J., Orchard, V.A., 1984. Spatial variability of biochemical properties in a taxonomically uniform soil under grazed pasture. Soil Biol. Biochem. 16, 153–160.

Tabatabai, M.A., 1994. Soil enzymes. In: Weaver, R.W., Angle, S., Bottomley, P., Bezdicek, D., Smith, S., Tabatabai, A., Wollum, A. (Eds.), Methods of Soil Analysis: Microbiological and Biochemical Properties. American Society of Agronomy, Madison, WI, pp. 775–826.

Thomas, G.W., 1982. Exchangeable cations. In: Page, A.L., Klute, A., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis: Chemical and Microbiological Properties. second ed. ASA, Madison, WI, pp. 159–165.

Timlin, D.J., Pachepsky, Y., Snyder, V.A., Bryant, R.B., 1998. Spatial and temporal variability of corn grain yield on a hillslope. Soil Sci. Soc. Am. J. 62, 764–773.

Topp, G.C., Zebchuk, W., 1979. The determination of soil–water desorption curves for soil cores. Can. J. Soil Sci. 59, 19–26.

VandenBygaart, A.J., Yang, X.M., Kay, B.D., Aspinall, J.D., 2002. Variability in carbon sequestration potential in no-till soil landscapes of southern Ontario. Soil Tillage Res. 65, 231–241.

Wardle, D.A., 1998. Controls of temporal variability of the soil microbial biomass: a global-scale synthesis. Soil Biol. Biochem. 30, 1627–1637.

Webster, R., Boag, B., 1992. Geostatistical analysis of cyst nematodes in soil. J. Soil Sci. 43, 583–595.

West, A.W., Sparling, G.P., Grant, W.D., 1986. Correlation between four methods to estimate total microbial biomass in stored, air-dried and glucose-amended soils. Soil Biol. Biochem. 18, 569–576.

Wright, S.F., Franke-Snyder, M., Morton, J.B., Upadhyaya, A., 1996. Time-course study and partial characterization of a protein on hyphae of arbuscular mycorrhizal fungi during active colonization of roots. Plant Soil 181, 193–203.