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Spatial patterns of soil microbial communities and implications for precision soil management at the field scale

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Abstract

Understanding the spatial patterns of soil microbial communities and influencing factors is a prerequisite for soil health assessments and site-specific management to improve crop production. However, soil microbial community structure at the field scale is complicated by the interactions among topography and soil properties. The objectives of this study were to (1) characterize the spatial variability patterns of soil microbial communities at the field scale; (2) assess the influence of soil physico-chemical properties, topography and management on soil microbial biomass spatial variability. This study was conducted in a 194-ha commercially-managed field in Hale County, Texas, in 2017. A total of 212 composite soil samples were collected at 0–0.15 m depth and analyzed via the ester-linked fatty acid methyl ester (EL-FAME) method to characterize the microbial community structure and biomass. Soil electrical conductivity (EC), pH, soil texture, soil water content (SWC), soil organic carbon (SOC) and total nitrogen (TN) were determined for each soil sample. Topographic attributes, including elevation and slope, were derived from real-time kinematic (RTK) point elevation data. Interpolated microbial community maps at this scale revealed a spatially structured distribution of microbial biomass and diversity with patches of several hundred meters in different directions corresponding to the distribution of soil types and topography. Most of the microbial communities were autocorrelated at greater ranges within the same soil types than across different soils. The distribution of total soil microbial biomass was mainly affected by SOC and SWC. Soil pH and C:N ratio had a negative impact on the biomass of bacterial communities. Biomass of fungal communities was negatively influenced by slope and elevation. The results of this study have the potential to provide a basis for designing soil sampling plans in characterizing microbial community distribution and site-specific soil health management.

Keywords Site-specific management · Soil biology · Soil physico-chemical properties · Ester-linked fatty acid methyl ester (EL-FAME) · Topography

Extended author information available on the last page of the article

Introduction

Soil micro-organisms are an essential component of soil ecosystems that perform functions related to soil health and plant growth (Cano et al., 2018; Le Guillou et al., 2019). Although soil biota typically represents less than 0.05% of dry soil weight, they have the greatest diversity among all ecosystems. They are responsible for organic matter decomposition, carbon sequestration, nutrient cycling, water availability and other ecosystem services in soils (Lehman et al., 2015). These micro-organisms, in interaction with other environmental variables, can influence crop growth and production (Lehman et al., 2015). They contribute to healthy crop production by enhancing water acquisition by plants, suppressing diseases and weeds, increasing aeration, reducing soil compaction for proper root growth and exuding enzymes that recycle plant nutrients (Brussaard, 1997; Parkin, 1993; Wall et al., 2004).

An in-depth understanding of the effects of management practices, soil physico-chemical properties and topography on soil microbial community size, composition and activity can help the precision management of soil micro-organisms in the field (Bhandari et al., 2018; Le Guillou et al., 2019). Various management practices can influence soil biological components that affect the efficiency of other agricultural inputs (Ryan & Peigné, 2017). For example, tillage affects soil physico-chemical properties such as soil moisture and nutrient distribution, which influences the size and distribution of soil micro-organisms (Le Guillou et al., 2019). The spatial and temporal distribution of micro-organisms at the landscape scale is also complicated by the interactions among topography, soil type and SWC (Cavigelli et al., 2005; Constancias et al., 2015). The soil properties, such as texture, organic matter and management-derived compaction, influences soil pore characteristics that, in turn, affect the spatio-temporal distribution of soil microbial biomass (Rasiah & Kay, 1999).

Recent studies have shown that the spatial distribution of soil organisms influences plant growth and possibly yield (Liu et al., 2020; Tautges et al., 2016). Geostatistical analysis of soil microbial community composition can reveal the underlying soil processes that fully or partially contribute to crop growth and yield variability. This is especially important in field-scale studies where intensive soil sampling is challenging and various factors such as soil properties and topography complicate the analysis (Piotrowska-Długosz et al., 2012, 2019; Robertson, 1987). As a result, few field studies have evaluated the spatial variability patterns of soil microbial groups (Piotrowska-Długosz et al., 2019; Powell et al., 2015; Shi et al., 2018). A study conducted in France showed that microbial indicators exhibited a high spatial heterogeneity at a field level that masked the effect of soil and crop management treatments (Peigné et al., 2009). This study also showed that the biological variables exhibited spatial variability of the same order of magnitude as physico-chemical parameters. Several studies indicated the presence of autocorrelation among selected microbial variables at different spatial scales (Constancias et al., 2015; Franklin & Mills, 2003; Naveed et al., 2016; Piotrowska & Długosz, 2012; Serna-Chavez et al., 2013). The variations in microbial community and its turnover could be due to environmental factors (Karimi et al., 2018; Le Guillou et al., 2019; Powell et al., 2015; Ranjard et al., 2013). Such information can facilitate site-specific management of crop inputs based on the spatial variability of organisms, such as earthworms, nematodes, protozoa, fungi, bacteria and arthropods (Osman, 2013). However, most of the studies on spatial variability of soil microbes are conducted either at a small or global scale that might not represent the field-scale soil microbiological processes.

Despite their critical roles in soil productivity and plant growth, the spatial variability of soil organisms is not considered in most site-specific studies because the measurements of soil microbial communities are complex, time-consuming, labor-intensive and cost-prohibitive. However, it is imperative to evaluate the spatial patterns of soil microbes and associated influencing factors for assessing soil health and site-specific management. The hypotheses were (a) soil microbial communities have significant spatial variability and (b) the variability structures are affected by soil properties, such as SWC, soil texture, organic matter pH and topography at the field scale. Hence, the objectives of this study were to (1) characterize the spatial variability patterns of soil microbial communities at the field scale; (2) assess the effects of soil physico-chemical properties and topography on soil microbial spatial variability.

Materials and methods

Study field and management

The study was conducted in a 194-ha field (33°57'26.31" N, 101°47'20.31" W) in the Southern High Plains of Texas in 2017 (Fig. 1). This semi-arid area has an annual rainfall ranging from 260 mm to 600 mm, with a median summer rainfall of 292 mm, about one-third of the potential crop evapotranspiration of 846 mm (Mauget et al., 2017). Continuous cotton cropping was practiced for more than five years before the study. The soils in this area are characterized by well-developed deep soils with increasing clay and accumulations of calcium carbonate in subsoil horizons (NRCS, 2008; Steiner et al., 2018). The surface soil texture of the field varies from sand to sandy loam, which is representative of the soils in this region (USDA-NRCS, 2018). The soil types are mainly Pullman clay loam (Fine, mixed, superactive, thermic Torrertic Paleustolls) and Olton loam (Fine, mixed, superactive, thermic Aridic Paleustolls), as indicated by the soil map units from the NRCS Soil Survey Geographic Database (SSURGO) (Fig. 1). The Pullman soils occur on nearly level to very gently sloping plains or playa slopes, consisting of very deep, well-drained, slowly permeable soils formed in clayey eolian deposits from the Blackwater Draw Formation. It typically contains a profile of Ap and several Bt and Btk horizons that extends up to 2 m depth. The Olton loam occurs on plains with low slopes and upper side slopes of playas and draws. This soil consists of very deep, well-drained, moderately slowly permeable soils formed in clayey, calcareous eolian sediments in the Blackwater Draw Formation. An Olton loam typically contains a profile of A and several Bt and Btk horizons that extends up to 2.5 m depth (Soil Survey Staff, 1974). The playa lake area with Randall clay (Fine, smectitic, thermic Ustic Epiaquerts) on the southeast side of the field was not cultivated.

Soil sampling

A total of 212 core soil samples were collected in April 2017 from eight circular transects spaced 100 m apart (Fig. 1). The sample spacing was 100 ± 30 m along each transect, depending on its distance from the field center. The sampling locations were determined using a real-time kinematic (RTK) GNSS receiver (AgGPS 214, Trimble, Sunnyvale, CA, USA). Composite soil samples, each with three cores within 2 m from the target location,

were collected at 0–0.15 m depth. The south half of the field was tilled two months before soil sampling. No samples were collected in or around the playa lake.

Soil physical and chemical analyses

Soil particle size analysis was performed using the hydrometer method (Gee & Bauder, 1986) with an ASTM 152-H hydrometer (Thermo Fisher Scientific, Waltham, WA, USA). Soil pH was measured using a pH meter (Model 89231-582, VWR, Radnor, PA, USA) at a soil to water ratio of 1:1 (w/v) and electrical conductivity (EC) was measured using an EC meter (Model 89231-614, VWR, Radnor, PA, USA) at a soil to water ratio of 1:5 (w/v). The SWC was determined using the gravimetric method. Each soil sample of approximately 50 g was oven-dried at 105 °C for 24 h for computing gravimetric water content. The total

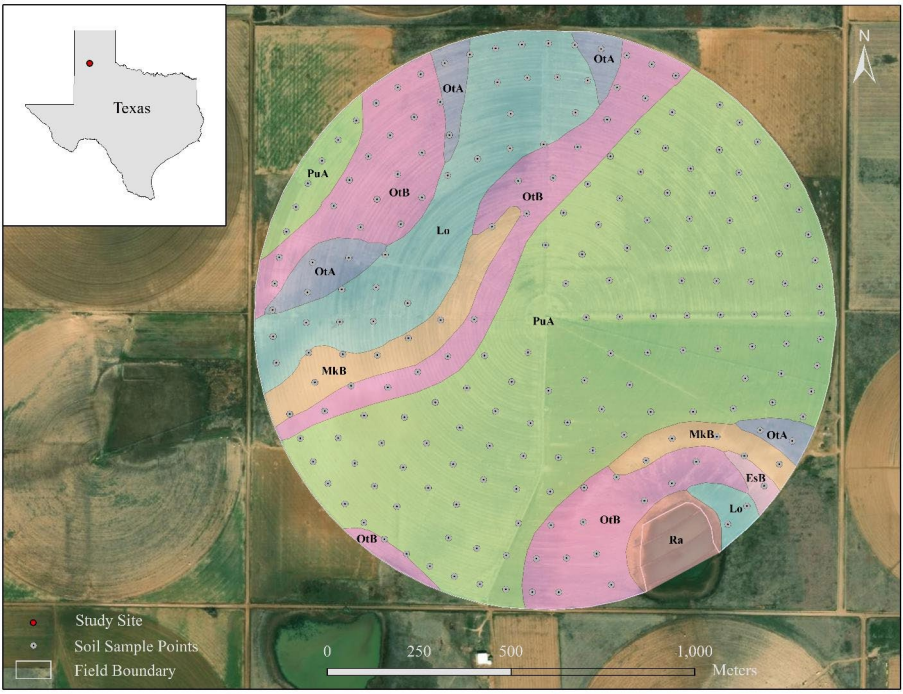

Fig. 1 Study site with soil sample locations and soil map units for a 194-ha field in Hale County, Texas in 2017 [1]

[1] (Basemap source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopoand the GIS User Community) [EsB: Estacado loam, 1–3% slopes (Fine-loamy, mixed, superactive, thermic Aridic Paleustolls); MkB: Mansker loam, 0–3% slopes (Coarse-loamy, carbonatic, thermic Calcidic Paleustolls); Lo: Lofton clay loam: 0.5% slopes (Fine, mixed, superactive, thermic Vertic Argiustolls); OtA: Olton loam, 0–1% slopes (Fine, mixed, superactive, thermic Aridic Paleustolls); OtB: Olton loam, 1–2% slopes (Fine, mixed, superactive, thermic Aridic Paleustolls); PuA: Pullman clay loam, 0–1% slopes (Fine, mixed, superactive, thermic Torrertic Paleustolls); Ra: Randall clay (Fine, smectitic, thermic Ustic Epiaquerts) (Soil Survey Staff, 1974)]

nitrogen (TN) and total SOC were measured via dry combustion using a TruSpec CN analyzer (LECO Corporation, St. Joseph, MI, USA).

Soil microbial analyses

Soil microbial community size and biomass were characterized using the ester-linked fatty acid methyl ester (EL-FAME) method (Schutter & Dick, 2000). This analysis provides information on microbial community size and composition (Cano et al., 2018). In the EL-FAME method, each soil sample of 3 g was analyzed in four steps. First, the release and methylation of ester-linked fatty acids were conducted at 37 °C by adding 15 ml of 0.2 KOH in methanol for 60 min. Second, the neutralization was performed with 3 ml of 1.0 M acetic acid. Third, hexane layer evaporation under N_2 was carried out. Finally, 100 µL of hexane containing the 19:0 internal standard (150 nmol g^{-1} soil) was used to redissolve the FAMEs, which was transferred to 250 µL glass inserts in 2 mL GC vials. The FAMEs were analyzed using an Agilent 6890 N gas chromatograph equipped with a 25 mm × 0.20 mm (5% phenyl)—methylpolysiloxane Agilent HP-5 fused silica capillary column (Agilent, Santa Clara, CA, USA) and flame ionization detector (Hewlett Packard, Palo Alto, CA, USA) with ultra-high-purity nitrogen as the carrier gas. Peak identification and area calculation were performed using the Phospholipid Fatty Acid calibration method from MIDI (Microbial ID, Inc., Newark, DE, USA). Selected FAMEs were used as microbial markers according to previous research (Zelles, 1999). Bacterial markers included gram-positive bacteria (i15:0, a15:0, i17:0, a17:0), gram-negative bacteria (cy17:0, cy19:0)and actinobacteria (10Me16:0, 10Me17:0, 10Me18:0); fungal markers included saprophytic fungi (18:1ω9c, 18:2ω6c) and arbuscular mycorrhizal fungi (AMF) (16:1ω5c); one marker was used for protozoa (20:4ω6c) (Li et al., 2020). The bacterial sum was calculated using the gram-positive (G+) bacteria, gram-negative (G−) bacteria and actinobacteria markers. The fungal sum was calculated using saprophytic and AMF fungal markers listed above. The fungal to bacterial ratio was calculated by dividing total fungi by total bacteria. Soil microbial community size was estimated as a sum of all the biomarker fatty acids associated with bacteria, fungi andand protozoa.

Topographic data collection and analysis

Point elevation data were collected using a real-time kinematic (RTK) GNSS receiver with an accuracy of 10 mm (Gan-Mor et al., 2007). The elevation data were collected during planting on transects spaced ~15 m, resulting in one data point every 15 m. The elevation point data were converted to a digital elevation model (DEM) using the Spatial Analyst tool of ArcGIS (Version 10.5.1, ESRI, Redlands, CA, USA) by interpolating the point datasets to 4 m raster grids. The slope was then derived from this DEM using the Slope routine of the Spatial Analyst tool of ArcGIS.

Data Aggregation

The soil sample locations were used to spatially coincide all the data layers for sand content, clay content, silt content, SOC, TN, C:N ratio, elevation, slope, pH, EC, G+ bacteria, G− bacteria, actinobacteria, AMF, saprophytic fungi, total bacteria, total fungi, protozoa

and total biomass. Except for elevation and slope, all the aforementioned variables were measured on the collected soil samples. The means of elevation and slope were calculated for each sampling location using the Zonal Statistics as a Table routine in the Spatial Analyst extension of ArcGIS. The variability map for each layer was created using ordinary kriging of ArcGIS.

Statistical and geostatistical analyses

Summary statistics, including minimum, maximum, mean, median, range, standard deviation and coefficient of variation (CV), were determined for the response and explanatory variables using the R software (R Core Team, 2017). Pearson correlation between soil microbes and other variables was performed using the *cor* function. Data normality for each microbial type was evaluated using the Shapiro Wilk test and heteroskedasticity was assessed using the Breusch Pagan test (Breusch & Pagan, 1979; Shapiro & Wilk, 1965). Biomass of soil microbial communities showed the presence of non-normality and global trends. Hence, a log-transformation was performed for each microbial community and a first-order trend was removed before the analysis for spatial autocorrelation of each microbial community.

A multiple regression model was used to explore the relationship between the biomass of soil microbial communities as a function of soil physico-chemical properties and topography. The explanatory variables for this model were selected by performing the backward stepwise regression at $\alpha = 0.05$ significance level for each microbial community resulting in multiple models. The spatial ecological data typically contain spatially autocorrelated model residuals that violate the assumption of independence and hence need to be addressed (Davis, 2002; Webster & Oliver, 2007). The residual of the model for each microbial community was tested for spatial autocorrelation using Moran's I test (Cliff & Ord, 1981). The model was adjusted for spatial autocorrelation using the SAR models based on the Lagrange multiplier test (Anselin, 1988).

Results

Variability in elevation and slope

The field exhibited large variability in topography, with elevation ranging from 1005.51 to 1014.02 m, the lowest around the playa lake in the southeast part (Fig. 2). Two depres-

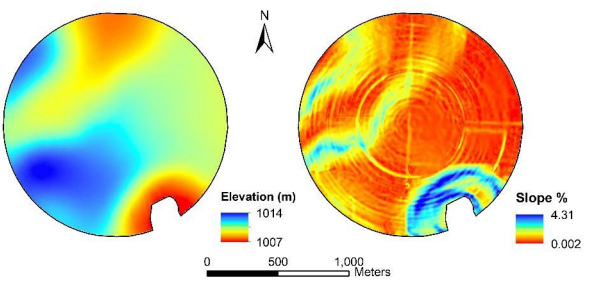

Fig. 2 Variation of elevation and slope in a 194-ha field in Hale County, Texas

sions were evident in the northwest part of the field. The slope varied from 0 to 4.31%, with higher slopes in the areas leading to the playa lake and depressions with rapid elevation changes. The slope appeared to be associated with soil types. For instance, the slope was low in Pullman clay loam but high in Mansker loam and Estacado loam close to the playa lake or depression areas. In general, there was higher variability in elevation and slope in the southern part of the field.

Variability in soil physical properties

The clay content of the 0–0.15 m depth was generally higher in the northern part with a maximum of 38.7%, especially in depression areas with Lofton clay soils (Figs. 1 and 3; Table 1). Sand content was higher in areas with low clay and silt contents both in the north and south. However, the CV was higher for silt (23.59%) as compared to sand (17.36%) and clay (12.78%), indicating higher variability in silt content across the field.

Variability in soil chemical properties

Higher soil pH values were observed in the south part of the field (Fig. 4). These areas also corresponded to lower EC. This was especially evident in the areas leading to the playa lake where the slope was higher. Field observations indicated these areas had experienced some

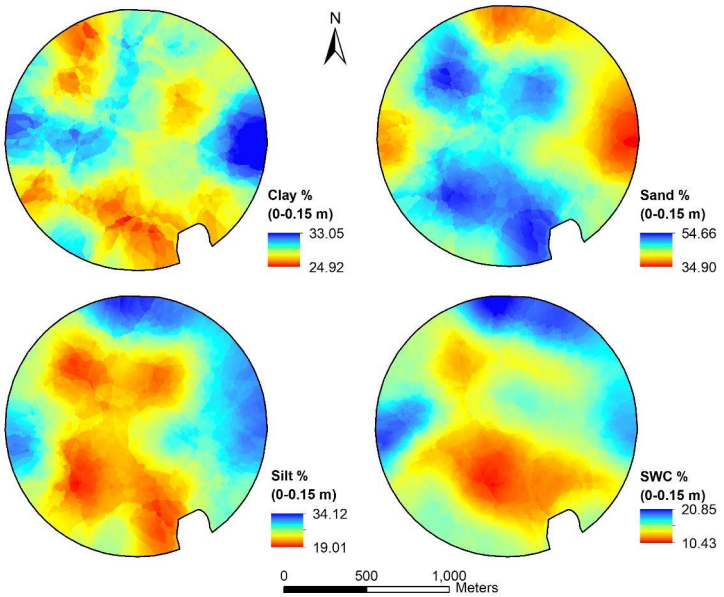

Fig. 3 Soil particle size and soil water content (SWC) at a depth of 0–0.15 m for a 194-ha field in Hale County, Texas, in 2017

Table 1 Summary statistics of soil microbial biomass (0–0.15 m depth), soil physico-chemical properties and topography for a 194-ha field in Hale County, Texas, in 2017

Variable	Min	Max	Range	Median	Mean	Stdev	CV %
G+ bacteria	6.29	40.07	33.78	13.75	15.02	5.63	37.47
G−bacteria	0.77	12.65	11.88	3.53	3.66	2.01	55.02
Actinobacteria	5.04	28.94	23.90	9.41	10.38	3.93	37.88
AMF	0.74	13.43	12.69	3.66	4.08	1.73	42.41
SF	10.90	89.07	78.18	26.88	30.35	14.10	46.44
Protozoa	0.00	2.92	2.92	0.88	0.97	0.55	57.29
Bacteria	13.55	80.35	66.79	26.50	29.05	11.01	37.91
Fungi	13.22	94.58	81.35	30.79	34.43	14.54	42.21
Total microbes	28.87	165.57	136.70	58.38	64.51	24.84	38.51
Clay	13.20	38.70	25.50	28.05	28.37	3.63	12.78
Silt	10.50	51.50	41.00	25.90	26.12	6.16	23.59
Sand	23.80	65.90	42.10	45.05	45.51	7.90	17.36
SWC	7.00	27.00	20.00	15.00	15.20	3.29	21.63
SOC	0.41	3.20	2.79	0.87	0.97	0.38	39.65
TN	0.03	0.14	0.11	0.07	0.07	0.02	25.36
EC	18.8	65.5	46.7	27.4	30.0	8.46	28.21
pH	7.45	9.04	1.59	8.32	8.27	0.32	3.82
Elevation	1006.8	1014.0	7.2	1010.5	1010.7	1.43	1.14
Slope	0.04	3.41	3.37	0.58	0.81	0.70	85.63

Bacteria is the sum of FAME markers for G+ (gram-positive bacteria), G−(gram-negative bacteria) and ACT (Actinobacteria) in nmol g^{-1}; Fungi is the sum of FAME markers for SF (Saprophytic fungi) and AMF (arbuscular mycorrhizal fungi) nmol g^{-1}; Elevation (m); EC = Electrical conductivity (µS mm^{-1}); Clay, silt, sand, slope, SWC (soil water content), TN (Total Nitrogen), and SOC (soil organic carbon) are in %

water and wind erosion, which exposed some calcareous layers with carbonates, leading to higher pH values. In addition, soils in these areas were low in water content and organic matter. Soils with high organic matter are associated with lower soil pH due to the release of hydrogen ions from organic matter or by nitrification in an open system (Ritchie & Dolling, 1985). Soil organic carbon was lower in the south part of the field in areas leading to the playa lake, which might be the cause for the lower C:N ratio in these areas. However, TN ranged from 0.056 to 0.098%, with a mean of 0.067% and was higher in the north part of the field. This might explain the overall lower C:N ratios in most of the north part.

Variability in biomass of soil microbial communities

Total microbial biomass (estimated by FAME) ranged from 40 nmol g^{-1} to 93.57 nmol g^{-1} with a mean of 64.51 nmol g^{-1} (Table 1). The soil microbial biomass was greater in the north part of the field compared to the south (Fig. 5). Most of the microbial communities showed similar spatial distribution patterns for biomass except for protozoa, which had lower biomass towards the center and higher concentrations towards the edge of the field. Fungal communities contributed the greatest to the total FAME biomass with a mean of 34.43 nmol g^{-1} and median of 30.79 nmol g^{-1}. Among fungal communities, saprophytic fungi were most abundant, with a mean biomass of 30.35 nmol g^{-1}. AMF biomass ranged

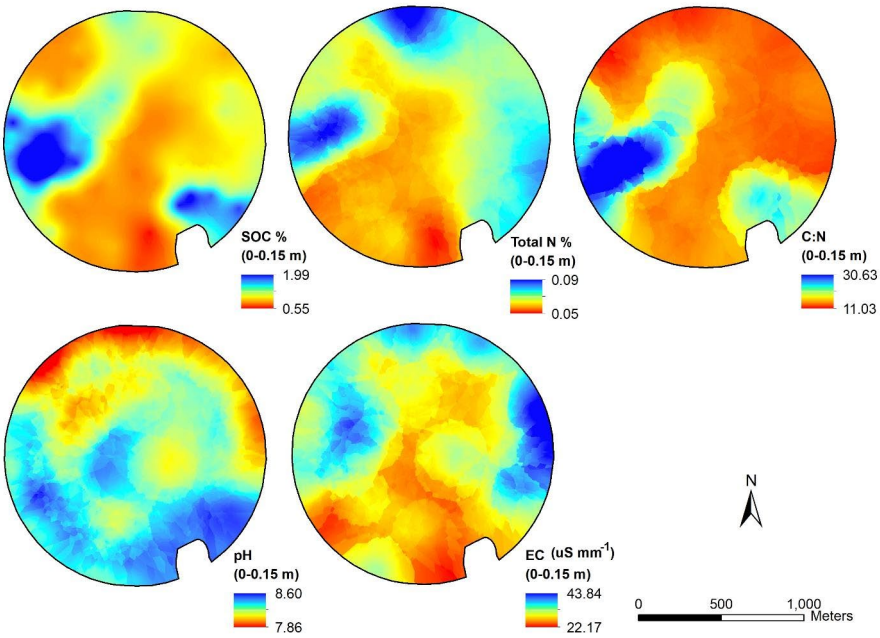

Fig. 4 Soil chemical properties at 0–0.15 m depth for a 194-ha field in Hale County, Texas, in 2017

from 2.57 to 6.62 nmol g^{-1} with a mean of 4.08 nmol g^{-1}. Among bacterial groups, G+ bacteria contributed the highest to the total microbial biomass with a mean of 15.02 nmol g^{-1}. The actinobacteria had a mean biomass of 10.38 nmol g^{-1}. The biomass of total bacterial (G+ > actinobacteria > G−) ranged from 13.55 to 80.35 nmol g^{-1} with a mean of 29.05 nmol g^{-1}. Overall, the fungal biomass was greater than that of bacteria, as reflected in the fungi:bacteria ratio ranging from 0.98 to 1.37. Protozoa exhibited the highest variation (CV = 57.29%) and G+ bacteria had the lowest variation (CV = 37.47%) in biomass. Both AMF and Saprophytic fungi had relatively high variations in biomass, with CV values of 42.41% and 46.44%, respectively.

Relationship between soil microbial properties, soil physico-chemical properties and topography

Total microbial biomass had a significant positive correlation ($p < 0.001$) with silt content, EC, SWC and TN and a significant negative correlation with elevation (Table 2). Total bacteria were positively correlated with silt content, EC, SWC and TN of soil, but negatively correlated to sand content, elevation and pH. The biomass of G+ and G − bacteria was negatively correlated with sand content, elevation and pH but positively correlated with silt content, EC, SWC and TN. The biomass of actinobacteria was negatively correlated with sand content and elevation and positively correlated with silt content, EC, SWC and TN.

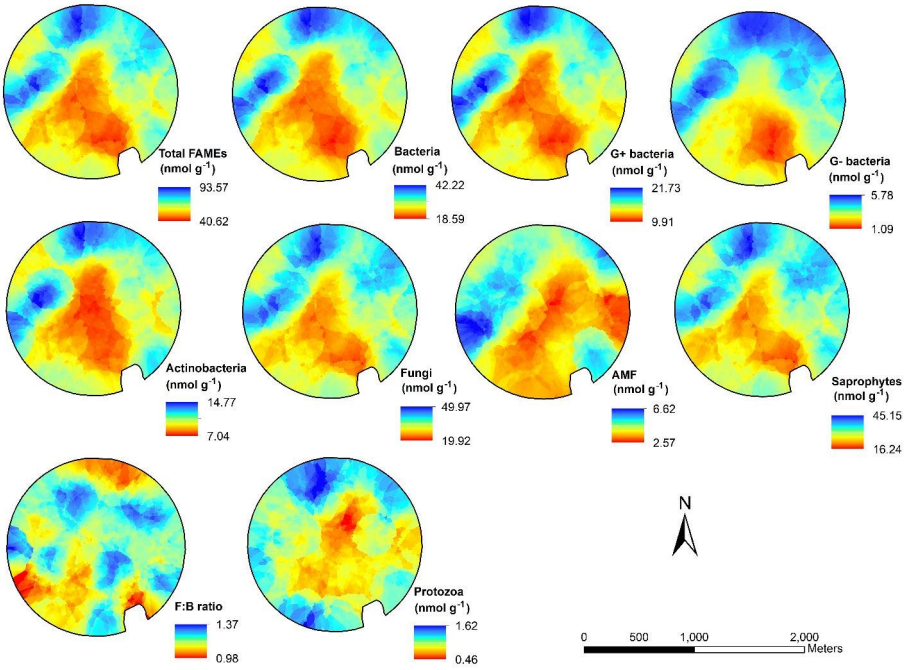

Fig. 5 Variability of soil microbial biomass at 0–0.15 m depth for a 194-ha field in Hale County, Texas, in 2017

The fungal biomass was significantly positively correlated with SWC and TN, but negatively correlated with elevation. AMF biomass was positively correlated with slope, SOC and C:N ratio. Biomass of saprophytic fungi was positively correlated to SWC and TN but negatively correlated to elevation. Protozoa biomass was not significantly correlated with any variables under study.

Table 2 Correlation between soil microbial biomass, soil physico-chemical properties (0–0.15 m depth) and topography for a 194-ha field in Hale County, Texas, in 2017

Variable	G+	G−	ACT	AMF	SF	Bacteria	Fungi	Total FAMEs
Silt	0.23	0.25	0.25			0.25		0.23
Sand	−0.21	−0.21	−0.22			−0.22		
EC	0.22	0.34	0.22			0.25		0.21
Elevation	−0.27	−0.32	−0.25		−0.25	−0.29	−0.26	−0.28
Slope				0.33				
SWC	0.38	0.38	0.35		0.24	0.39	0.24	0.31
pH	−0.24	−0.27				−0.23		
TN	0.37	0.36	0.32		0.28	0.37	0.28	0.33
SOC				0.42				
C:N				0.37				

Correlation coefficients are significant at $p<0.001$; C:N = Ratio of SOC and TN; F:B = ratio of fungi and bacteria; Bacteria is the sum of FAME markers for G+ (gram-positive bacteria), G− (gram-negative bacteria) and ACT (Actinobacteria); Fungi is the sum of FAME markers for SF (Saprophytic fungi) and AMF (arbuscular mycorrhizal fungi); Elevation (m), EC = Electrical conductivity (μS mm^{-1})

Spatial variability of soil microbial groups

All of the soil microbial communities except protozoa exhibited spatially autocorrelated variation in their biomass. A spherical semivariogram model was fit for the rest of the microbial communities (Table 3). The nugget:sill ratio for most of the microbial communities was greater than 0.55, indicating moderate spatial dependency (Cambardella et al., 1994). Except for G−bacteria, all of the microbial communities showed an anisotropic variation in their biomass with the major range along the northeast-southwest direction (around 50 degrees). The orientation of the minor range was approximately perpendicular to this direction. This anisotropic pattern was consistent with the distribution of soil types, i.e., greater variability in soil type and properties in the northwest-southeast direction. The anisotropic ratio, the ratio of the major range to the minor range, was highest for gram-positive bacteria, followed by saprophytic fungi. The total microbial biomass was distributed spatially with an anisotropic ratio of 2.66. The range of semivariogram represents the distance of spatial influence or the maximum distance up to which the property of the variable is spatially autocorrelated (Gooaverts, 1997). The major range was 743 mand the minor range was 279 m for total microbes. This result is consistent with the results from a study conducted across an agricultural landscape in France (Constancias et al., 2015), which showed that the spatial variation of soil microbes ranged up to hundreds of meters at the landscape scale.

Soil microbial community as affected by topography and soil properties

Topography and soil physico-chemical properties influenced the distribution of soil microbial communities and their biomass (Table 4). The results from multiple regression analysis for each microbial community indicate that SWC, clay content and SOC were the most important factors influencing the variability of total microbial biomass (Table 4). Besides these factors, the distribution of total bacterial biomass was also influenced by soil pH. The negative coefficients for soil pH indicate that areas with high pH had a lower distribution of bacterial communities. The C:N ratio also had a significant negative influence on the biomass

Table 3 Semivariogram models for soil microbial biomass at a depth of 0–0.15 m for a 194-ha field in Hale County, Texas, in 2017 (Lag size = 70 m, number of lags = 12)

Variable	Model	Nugget	Sill	Nugget :Sill	Major range (m)	Minor range (m)	Anisotropy direction (°)	Anisotropy ratio
Total FAMEs	Spherical	0.08	0.12	0.67	743	279	51	2.66
G+	Spherical	0.07	0.11	0.64	748	250	48	2.99
G−	Spherical	0.21	0.29	0.72	840	510	144	1.65
Act	Spherical	0.07	0.11	0.63	601	383	58	1.56
Bacteria	Spherical	0.07	0.11	0.63	694	269	50	2.57
AMF	Spherical	0.10	0.14	0.71	840	430	50	1.95
SF	Spherical	0.12	0.17	0.70	689	231	57	2.98
Fungi	Spherical	0.11	0.15	0.73	840	305	49	2.75

Bacteria is the sum of FAME markers for G+ (gram-positive bacteria), G−(gram-negative bacteria) and Act (Actinobacteria); Fungi is the sum of FAME markers for SF (Saprophytic fungi) and AMF (arbuscular mycorrhizal fungi); Anisotropy ratio is the ratio of major range to minor range at the direction of anisotropy

Table 4 Summary of multiple regression analysis for soil properties and topography predicting soil microbial biomass for a 194-ha field in Hale County, Texas, in 2017

Variable	Coefficient	p-value	Variable	Coefficient	p-value
Total FAMEs			*Actinobacteria*		
Clay	−1.11	0.03	Clay	−0.18	0.02
SOC	18.21	0.03	SOC	3.58	<0.01
SWC	1.88	<0.01	SWC	0.40	<0.01
Total bacteria			C:N ratio	−0.15	0.02
Clay	−0.58	<0.01	*Total fungi*		
SOC	10.59	<0.01	SWC	0.78	0.03
pH	−4.88	0.03	Elevation	−2.18	<0.01
SWC	1.16	<0.01	Slope	−3.18	0.05
C:N ratio	−0.47	<0.01	*AMF*		
G+ bacteria			Clay	−0.01	0.05
Clay	−0.27	0.01	SOC	0.30	<0.01
SOC	5.28	<0.01	Slope	−0.11	<0.01
pH	−2.66	0.02	*Saprophytic fungi*		
SWC	0.55	<0.01	Elevation	−2.31	<0.01
C:N ratio	−0.26	<0.01	Slope	−3.19	0.02
G − bacteria			*Protozoa*		
Clay	−0.11	<0.01	SWC	0.03	0.02
SOC	0.85	0.01			
pH	−1.08	0.01			
SWC	0.19	<0.01			
Elevation	−0.26	<0.01			

Bacteria is the sum of FAME markers for G+ (gram-positive bacteria), G−(gram-negative bacteria) and Act (Actinobacteria); Fungi is the sum of FAME markers for SF (Saprophytic fungi) and AMF (arbuscular mycorrhizal fungi); C:N=Ratio of SOC and TN, F:B=ratio of fungi and bacteria, EC=Electrical conductivity

distribution of G+ and Actinobacteria. Soil EC had no significant effect on soil microbial biomass distribution. Specifically, clay content, SWC, pH, C:N ratio and SOC influenced the distribution of biomass of G+ bacteria. However, elevation had a significant effect only on the distribution of biomass of G−bacteria among bacterial communities. For fungal communities, SWC, elevation and slope were important factors influencing the total fungal biomass distribution. The variation in AMF biomass was mainly influenced by SOC and slope. The biomass of saprophytic fungi was primarily influenced by topographic attributes, including elevation and slope. The protozoa biomass was mainly affected by the distribution of SWC across the field. Overall, SOC and SWC had a significant positive effect on the biomass of most of the microbial communities. Contrarily, pH, elevation, slope and clay content had a significant negative effect on the biomass of most of the microbial communities.

The regression model for biomass of each soil microbial community as a function of soil and topographical properties showed no presence of spatial autocorrelation except for the AMF case. A Gaussian model was found as the best fitting model for AMF. The nugget:sill ratio for this model was greater than 0.55, indicating moderate spatial dependency. The range of autocorrelation was 662 m. The LM test indicated that the spatial lag model fitted the data better for AMF.

Discussion

Soil microbial distribution and influencing factors

The effects of environmental factors on soil microbes varied with the microbial type. While all the microbial variables were related to soil properties and topography, protozoa were only significantly correlated to SWC content. Tajik et al. (2020) also found that protozoa behaved differently than other microbial groups, possibly due to the grazing behavior and unicellular nature of protozoa. Soil particle size had a significant effect on the distribution of bacterial groups. Clay content had a significant negative effect on the biomass of G+ bacteria, G−bacteria, Actinobacteria and total bacteria. Contrarily, most studies have shown that clay particles have a beneficial impact on the soil microbial community. Soil micro-organisms are primarily attached to soil particles with small pore sizes and more water holding capacity could protect from predators and suitable growth environment (Bach et al., 2010; Tajik et al., 2020). The association of a low microbial community with high clay content in this study might be due to some management-induced environments in some areas of the field.

Although topography was correlated to all microbes, elevation and slope had no significant influence on total FAME distribution. Specific microbial groups such as G−bacteria, total fungi, AMF and saprophytic fungi were negatively influenced by elevation and/or slope. This could be due to erosion and deposition of finer particles from higher areas to the low-lying areas that could foster favorable conditions for microbial growth (Constancias et al., 2015; Naveed et al., 2016). The effect of topography, including slope and elevation, on soil microbial distribution might be through its impact on the distribution of soil properties, especially SWC and SOC, which influence total FAMEs.

The SWC and SOC are sources of nutrition and cell structure maintenance for microbes and control their activity and growth (Sorensen et al., 2013; Yan et al., 2015). Interestingly, SWC had no significant effect on the distribution of saprophytic fungi and AMF, possibly due to their high tolerance to matric potential because of the stronger cell walls as compared to other microbial groups (Schimel et al., 2007). Higher C:N ratios tend to indicate low organic matter decomposability (Dequiedt et al., 2011) and hence had a negative relationship with the microbial variables, especially bacteria. TN, which is essential for microbial survival, was significantly and positively correlated with most of the microbial variables. However, TN was not included in the regression model during stepwise selection, probably because SOC is a keystone driver of micro-organisms compared to TN (Table 5, Appendix).

Generally, pH is regarded as one of the main predictors of variation in soil microbial communities and biomass (Cao et al., 2016; Constancias et al., 2015). In this study, however, only soil bacterial communities were significantly and negatively correlated to soil pH. This is consistent with previous studies that suggested that soil pH could either impose a physiological constraint on bacteria or influence microbial growth conditions, such as salinity and nutrient availability, which affect bacterial distribution (Cao et al., 2016; Lauber et al., 2009; Rousk et al., 2010). Contrarily, fungal communities were found to survive in a wide range of soil pH, which might be due to the multicellular nature of most of the fungal communities as compared to unicellular bacterial communities (Lauber et al., 2009; Tajik et al., 2020).

Implications for site-specific management and research

Knowledge about the spatial variability of soil microbes and influencing factors can help researchers to design strategies for site-specific soil management. The results in the spatial variability of soil microbes, including the magnitude and potential causes, have implications for relevant research and site-specific soil management at the field scale. While SWC and SOC were two important factors influencing soil microbial biomass distribution, in general, areas with high slope, high pH, low SOC, low TN, low EC and low SWC showed a lower abundance of soil microbes. This implies that management activities, such as irrigation, fertilization and manure application, could be managed site-specifically to improve the microbial communities, especially in sloped areas. Studies showed that adding organic amendments such as manure resulted in increased microbial biomass (soil bacteria and fungi) and higher microbial activity (Graham et al., 2012; Watts et al., 2010). This can ultimately contribute to promoting agricultural practices to maximize the benefits from soil microbes and at the same time preserve financial and environmental resources (Cano et al., 2018; Le Guillou et al., 2019; Lehman et al., 2015). Further, saprophytic fungi and AMF have been found to improve soil aggregate formation to protect against erosion, increase water and nutrient uptake by plant roots attributed to hyphal extension, especially in this semi-arid region (Davinic et al., 2013). Therefore, field management practices, such as cover cropping and mulching, could be implemented to improve fungal biomass where needed in the field. The F:B ratio is a good indicator of shifts in the microbial community in extreme weather conditions such as drought (Wardle & Parkinson, 1990) and tillage (Frey et al., 1999). This information can be used in implementing several soil and crop management strategies, such as crop selection, fertilizer application and irrigation (Acosta-Martínez et al., 2014).

This study showed an anisotropic spatial variation of microbes across the field and the spatial patterns were mainly corresponding to the distribution of soil types. Most of the microbial communities showed less spatial variability of biomass within the soil type, but exhibited greater spatial variability across different soil types. Studies have shown that spatial descriptors vary with ecological context and spatial extent (Constancias et al., 2015; Dequiedt et al., 2011; Naveed et al., 2016). Therefore, the spatial variability of microbial communities and biomass provides valuable information for designing soil sampling plans in fields with diverse soil types and topographic properties. For example, in areas with similar soil types and topographic properties, fewer samples at greater distances could be collected to understand the spatial variability of certain micro-organisms. However, in areas with varying soil types, sampling should be performed at shorter distances since the range of spatial autocorrelation is lower. Further, the information of spatial variability of soil microbes can help create management zones or experimental plots across the field and evaluate the effects of various treatments (Cassel et al., 2000; Peigné et al., 2009). This ability to differentiate the effects due to the initial spatial variability of the field from those related to soil management techniques can ultimately provide a base for long-term site-specific management of crop inputs.

Limitations and future research

The study unveils several important factors related to soil microbiology and underlying soil properties. A grid-based sampling scheme, commonly used in precision agriculture, was

adopted to investigate the spatial patterns of soil properties (Van Groenigen et al., 1999; Yfantis et al., 1987; Zimmerman, 2006). However, the sampling distance and sampling depth are limited due to the cost and time constraints of soil sampling and microbial analyses. Sampling distance and depth could influence the output of the spatial analysis of soil microbial properties (Bhattarai et al., 2015; Cavigelli et al., 2005; McBratney & Webster, 1983; Turner et al., 2017; Warrick & Myers, 1987). Studies have also shown that about 65% of soil microbial density is present at the top 0.25 m layer of soil and has high spatial variability (Fierer et al., 2003; Nunan et al., 2002). Although most soil microbial studies use 0–0.20 m depth as representative for soil microbial activities (Constancias et al., 2015; Piotrowska-Długosz et al., 2019), sampling depth at 0–0.15 m was used to create uniformity among other soil properties analyzed in this study.

The main focus of this study lies in the understanding of various factors influencing soil microbes and how this information can be applied in precision soil management. Hence, given the scenario where there is limited prior information about soil microbial characteristics in this 194-ha field and limited studies conducted to understand the spatial variability of soil microbes at this scale, sampling at a distance of 70–100 m and depth 0–0.15 m depth is appropriate for these two purposes. However, additional sampling schemes at shorter distances (e.g., nested with the current regular grids) and varied sampling depths would provide information on the spatial structure at finer scales, which may be warranted in the future. Temporal analyses of soil microbial distribution could also help in implementing site-specific as well as time-specific management decisions since seasonal variation has a huge influence on soil microbes (Cavigelli et al., 2005; Piotrowska & Długosz, 2012). Future research in multiple years is necessary to provide a more comprehensive characterization of the spatial and temporal variability of soil microbial properties for site-specific management of soil health.

Conclusions

In this study, the effects of soil physico-chemical properties and topography on the spatial variability of soil microbial communities were evaluated at the field scale. Given the scale of soil sampling distance and depth, soil texture, SOC and SWC were the main factors influencing the spatial variability of total soil microbial biomass. The effect of topography on soil microbial biomass is likely through its impact on the distribution of soil properties, especially SWC and SOC. The fungal communities were significantly influenced by topographical properties such as elevation and slope and soil texture had a significant influence on bacterial communities. The information on soil microbes as affected by soil physico-chemical properties and topography could be used to develop strategies for site-specific management to enhance soil health. For example, microbial communities in areas with high slopes and high sand content could be enhanced by applying more crop residue as organic material for SOC development. The spatial analysis of soil microbial properties could be utilized to assist in designing soil sampling strategies for microbial analysis. Overall, the results of spatial patterns of soil microbes and associated influencing soil properties from this study extend understanding of site-specific soil health management research and application, especially in semi-arid crop production systems. Further studies are required to evaluate the sampling scales in multiple years and multiple fields for site-specific soil microbial management.

Appendix

Table 5 Correlation between soil physico-chemical properties (0–0.15 m depth) and topography for a 194-ha field in Hale County, Texas, in 2017

	Clay	Silt	Sand	EC	Ele	Slope	SWC	pH	TN	SOC
Silt (%)	0.25									
Sand (%)	−0.66	−0.90								
EC (µS mm−1)		0.28	−0.30							
Elevation (m)		−0.24	0.22							
Slope (%)		−0.30	0.32	−0.21						
SWC (%)	0.46	0.52	−0.62	0.28	−0.33	−0.31				
pH		−0.21	0.23	−0.51		0.33	−0.24			
TN (%)	0.39	0.56	−0.62	0.38	−0.45	−0.32	0.59	−0.29		
SOC (%)		0.23	−0.24			0.34			0.29	
C:N						0.50	−0.29	0.29	−0.30	0.79

Correlation coefficients significant at $p < 0.001$; C:N = Ratio of SOC to TN, EC = Electrical conductivity

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Declarations

Conflict of interest The authors declare no conflict of interest.

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