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Edaphic properties override the influence of crops on the composition of the soil bacterial community in a semiarid agroecosystem☆

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ABSTRACT

Annual cropping systems are dynamic environments where soil bacterial communities are responsive to various management practices such as crop rotations, and to seasonal fluctuations of edaphic properties. However, in semiarid regions the impact of crops on the soil bacterial community appears to be modulated or affected by edaphic properties such as soil moisture availability. Therefore the objective of this study was to determine the relative influence of crops (wheat, lentil, field pea, canola, and a fallow treatment), soil chemistry, and edaphic properties on the diversity and composition of soil bacterial communities in a semiarid agroecosystem. We used a temporal sampling strategy and high throughput sequencing approach to monitor changes in the soil bacterial community in relation to crop host identity and phenology and soil properties. Structuring of the bacterial community across the 20 experimental plots was driven primarily by soil pH which varied strongly (min: 5.25, max: 6.97) across the site. Weak temporal shifts in the bacterial community were observed across the growing season and were related to seasonal variation in soil moisture (min: 8.3%, max: 20.3%), soil temperature (min. daily mean: 3.3 °C, max. daily mean: 21.1 °C), and fluctuation in available phosphate in the soil (min: 0.003 $\mu g\,cm^{-2}\,day^{-1}$, max: 0.290 $\mu g\,cm^{-2}\,day^{-1}$). These temporal and spatial shifts were not influenced by crop host identity as similar bacterial communities were observed among the crops and fallow treatment. Variance partitioning revealed that soil pH and soil moisture accounted for a high proportion of the variation of the soil bacterial community, while crops had no significant impact in the study. Edaphic factors appeared to override or level the effect of crops on the soil bacterial community. These results highlight the importance of accounting for edaphic properties for managing soil bacterial communities in agroecosystems.

1. Introduction

The soil microbiome is a highly diverse biological resource that is important in the functioning and productivity of agricultural systems. Soil bacteria account for a high proportion of this diversity and affect crop health and productivity through their functional roles in biogeochemical cycling, disease suppression, litter decomposition, and soil structure (Kennedy, 1999; Chapparo et al., 2012). However, bacterial communities are sensitive to alterations in the soil environment caused by natural and anthropogenic perturbations (Allison and Martiny, 2008). This is of critical importance in agroecosystems as these environments are constantly being modified due to intensive management practices primarily aimed at improving crop yield and production. Understanding the factors that influence the composition and function of soil bacterial communities is essential for managing this important resource.

The primary drivers of soil bacterial communities include abiotic (i.e. climate and soil physico-chemical properties) and biotic factors (i.e. plant community), both of which are constantly influenced by agricultural practices (Berg and Smalla, 2009). Extensive research has shown that many of these practices such as the application of fertilizer and pesticides, tillage, and crop rotations can alter the taxonomic and functional diversity of soil bacterial communities (Buckley and Schmidt, 2001; Allison and Martiny, 2008; Lo, 2010). Crop rotation is of particular interest because it can be easily manipulated and is a key component of enhancing the performance and sustainability of agroecosystems by maintaining soil fertility, managing disease and pests, and promoting crop yield (Karlen et al., 1994).

☆ A temporal sampling and high throughput sequencing strategy was used over a 21 week period to monitor changes in the soil bacterial community in relation to soil chemistry, edaphic factors, and crop phenology.

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Recent studies using molecular tools have provided varying evidence to support the relative importance of crop host identity or crop rotations on soil bacterial communities. These range from a strong or highly selective effect (Smalla et al., 2001; Marschner et al., 2004; Inceoglu et al., 2011; Yang et al., 2013), minimal effect (Silva et al., 2013; Zhao et al., 2014), to no effect (Li et al., 2012; Dohrmann et al., 2013; Navarro-Noya et al., 2013; Arenz et al., 2014) of the crop or crop rotation on the soil bacterial community.

Plants primarily influence the soil bacterial community through the release of an array of metabolites into the rhizosphere that can directly (e.g. carbon source for growth) or indirectly (e.g. modify soil nutrient availability) attract or inhibit the growth of specific bacteria (Bais et al., 2006). The production and composition of these rhizodeposits not only varies among plant species or genotypes, but also among growth stages which can have a selective effect on the bacterial community (Zhang et al., 2011; Baudoin et al., 2002). The influence of crop host identity is likely an important factor but it may be modulated or controlled by edaphic properties (Arenz et al., 2014; Yang et al., 2013), which are important drivers of temporal variation of bacterial communities in agricultural soils (Lauber et al., 2013). Since agricultural soils are heterogeneous and dynamic environments that are constantly changing, a temporal sampling strategy is necessary to understand the factors that influence the structure and composition of soil bacterial communities.

The objective of this study was to determine the relative influence of (i) crop host identity and phenology, (ii) edaphic properties and their seasonal variation, and (iii) soil chemical properties (site characteristics) on the spatial structuring and temporal variation of a soil bacterial community in a semiarid agroecosystem. The study was conducted in southwestern Saskatchewan, an important growing region for cereal, pulse, and oil-seed crops. We included a crop from each of these functional groups along with a fallow treatment to determine the potential influence of crop selection on soil bacterial communities. A temporal sampling and high throughput sequencing strategy was used over a 21 week period to monitor changes in the soil bacterial community in relation to soil chemistry, edaphic properties, and crop phenology. We hypothesized that (i) soil chemical properties would be important factors structuring the bacterial community, and (ii) crop host identity would modify the diversity and composition of the bacterial community, but this effect would be affected by changes in edaphic properties throughout the growing season.

2. Materials and methods

2.1. Site description and experimental design

Field plots were established in 2012 at the south farm of the Semiarid Prairie Agricultural Research Centre (50°17'N, 107 41'W). Previous crops on the site were wheat (2011), wheat (2010), fallow (2009), wheat (2008), and fallow (2007). The soil was a Swinton silt loam, an Orthic Brown Chernozem. The chemical characteristics of the field plots are summarized in Table 1.

The experiment was set up as a randomized complete block design consisting of five treatments and four blocks for a total of 20 plots. The treatments included four crop treatments (wheat, pea, lentil, and canola) and a fallow treatment. Plots were 6 m x 2 m and all blocks were separated by a 6 m border seeded to barley. Crops were seeded on May 10th in rows at 25.4 cm spacing and managed using recommended practices. A pre-seeding application of glyphosate (445 g a.i. ha^{-1}) and a post-seeding application of Solo (imazamox: 30 g a.i. ha^{-1}) were used for weed control at the sites. The fungicide Headline (pyraclostrobin: 93.22 mL a.i. ha^{-1}) was applied on June 22nd. Plots were fertilized at seeding with nitrogen only (sideband granular urea) at recommended rates for each crop (wheat: 62 kg N ha^{-1}; pea and lentil: 17 kg N ha^{-1}; canola: 67 kg N ha^{-1}). Wheat seeds were treated with the fungicide Vitaflo 280 (Chemtura) (carbathiin: 51.5 mL a.i. 100 kg^{-1}; and thiram: 43.7 mL a.i. 100 kg^{-1}). Legume seeds were treated with the fungicide Apron Maxx RTA (Syngenta) (fludioxonil: 0.61 mL a.i. 100 kg^{-1}; and mefenoxam: 0.91 mL a.i. 100 kg^{-1}) and insecticide Cruiser 4FS (Syngenta) (thiamethoxam: 39.5 mL a.i. 100 kg^{-1}) and rhizobial inoculant TagTeam C (Novozymes) (peat-based granular formulation applied at 4 kg ha^{-1} containing 1.3×10^8 *Rhizobium leguminosarum* and 1.3×10^6 *Penicillium bilaiae* propagules per gram) was added to the legume seeds prior to seeding. Canola seeds were treated with the insecticide/fungicide Helix Xtra (Syngenta) (thiamethoxam: 310.5 mL a.i. 100 kg^{-1}; difenoconazole: 18.8 mL a.i. 100 kg^{-1}; metalaxyl-M and S-isomer: 5.9 mL a.i. 100 kg^{-1}; and fludioxonil: 2.0 mL a.i. 100 kg^{-1})

2.2. Soil sampling

Sampling was conducted at 3-week intervals from April 12th (Julian day 102) to September 6th (Julian day 249). These included sampling twice prior to seeding, five times during the growing season, and once after the crops were harvested. At each sampling time, four soil cores were collected randomly on the crop row (including both bulk and rhizosphere soil) to a depth of 15 cm from each pot. The soil cores (2 cm diameter) from each plot were

Table 1
Soil chemical properties at the first sampling time (Julian day 102) in the experimental site.

	Block 1[a]	Block 2[a]	Block 3[a]	Block 4[a]	Mean[b] ± SE
pH	6.61 ± 0.16	5.78 ± 0.14	5.75 ± 0.05	5.42 ± 0.07	5.89 ± 0.11
EC (mS)	0.37 ± 0.07	0.13 ± 0.01	0.12 ± 0.01	0.14 ± 0.01	0.19 ± 0.03
Fe (mg kg^{-1})	26.65 ± 2.38	45.45 ± 6.45	46.69 ± 2.16	62.50 ± 2.59	45.32 ± 3.40
Mn (mg kg^{-1})	18.59 ± 1.59	23.93 ± 1.69	22.47 ± 1.17	28.14 ± 1.39	23.28 ± 1.03
Zn (mg kg^{-1})	1.61 ± 0.20	2.25 ± 0.76	1.25 ± 0.06	1.99 ± 0.28	1.78 ± 0.21
NH_4 (mg kg^{-1})	5.72 ± 0.26	5.67 ± 0.23	6.47 ± 0.23	5.18 ± 0.31	5.76 ± 0.16
K (mg kg^{-1})	190.98 ± 17.16	195.24 ± 19.26	215.90 ± 10.24	350.74 ± 9.70	238.22 ± 16.50
NO_3 (mg kg^{-1})	3.83 ± 0.19	3.71 ± 0.40	3.44 ± 0.43	4.43 ± 0.36	3.85 ± 0.18
PO_4 (mg kg^{-1})	22.27 ± 1.45	22.79 ± 1.39	21.20 ± 1.10	29.22 ± 1.71	23.87 ± 0.97
Ca (g kg^{-1})	2.69 ± 0.26	2.01 ± 0.14	2.00 ± 0.08	1.67 ± 0.02	2.11 ± 0.11
Mg (mg kg^{-1})	462.12 ± 16.00	408.76 ± 17.35	424.56 ± 11.50	343.66 ± 4.74	409.78 ± 11.57
Total Carbon (g kg^{-1})	16.9 ± 0.3	16.4 ± 0.6	16.5 ± 0.4	19.1 ± 0.4	17.2 ± 0.3
Organic Carbon (g kg^{-1})	16.3 ± 0.3	16.1 ± 0.6	15.7 ± 0.5	18.5 ± 0.6	16.6 ± 0.3

[a] Mean value ± standard error ($n = 5$).
[b] $n = 20$.