



Soil texture affects soil microbial and structural recovery during grassland restoration

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ABSTRACT

Many biotic and abiotic factors influence recovery of soil communities following prolonged disturbance. We investigated the role of soil texture in the recovery of soil microbial community structure and changes in microbial stress, as indexed by phospholipid fatty acid (PLFA) profiles, using two chronosequences of grasslands restored from 0 to 19 years on silty clay loam and loamy fine sand soils in Nebraska, USA. All restorations were formerly cultivated fields seeded to native warm-season grasses through the USDA's Conservation Reserve Program. Increases in many PLFA concentrations occurred across the silty clay loam chronosequence including total PLFA biomass, richness, fungi, arbuscular mycorrhizal fungi, Gram-positive bacteria, Gram-negative bacteria, and actinomycetes. Ratios of saturated:monounsaturated and iso:anteiso PLFAs decreased across the silty clay loam chronosequence indicating reduction in nutrient stress of the microbial community as grassland established. Multivariate analysis of entire PLFA profiles across the silty clay loam chronosequence showed recovery of microbial community structure on the trajectory toward native prairie. Conversely, no microbial groups exhibited a directional change across the loamy fine sand chronosequence. Changes in soil structure were also only observed across the silty clay loam chronosequence. Aggregate mean weighted diameter (MWD) exhibited an exponential rise to maximum resulting from an exponential rise to maximum in the proportion of large macroaggregates (>2000 μm) and exponential decay in microaggregates (<250 μm and >53 μm) and the silt and clay fraction (<53 μm). Across both chronosequences, MWD was highly correlated with total PLFA biomass and the biomass of many microbial groups. Strong correlations between many PLFA groups and the MWD of aggregates underscore the interdependence between the recovery of soil microbial communities and soil structure that may explain more variation than time for some soils (i.e., loamy fine sand). This study demonstrates that soil microbial responses to grassland restoration are modulated by soil texture with implications for estimating the true capacity of restoration efforts to rehabilitate ecosystem functions.

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1. Introduction

More than 86% of the historical 162 million hectares of tallgrass prairie has been altered for agricultural purposes (Samson et al., 2004). Conventional tillage disrupts soil structure, reduces organic matter storage, alters nutrient supply rates, increases soil temperature fluctuations, and causes more extreme wet/dry cycles in soils (Tisdall and Oades, 1982; Mann, 1986; Tisdall, 1994). The

USDA's Conservation Reserve Program (CRP) was introduced within the Food and Security Act of 1985 with the goal of reducing erosion by converting highly erodible croplands to perennial vegetation. During fiscal year 2007, the CRP reduced soil erosion by 426 million metric tons, soil runoff by 188 million metric tons, nitrogen runoff by 218,000 metric tons, phosphorous runoff by 49,000 metric tons, and was estimated to sequester 50 million metric tons of atmospheric carbon (CO_2) (USDA FSA, 2008). Planting perennial grasses on formerly cultivated soil can increase C and nitrogen (N) storage (Parton et al., 1988; Baer et al., 2002; McLaughlan, 2006a; Matamala et al., 2008; Baer et al., 2010), but accrual rates likely depend in part upon recovery of the soil microbial community and soil aggregate structure (Six et al., 2006).

Soil microorganisms play a critical role in providing ecosystem services through their effects on the development and maintenance

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of soil structure by binding soil particles and organic matter to create aggregates (Jastrow et al., 1998; Six et al., 2000a). During grassland restoration, soil microbial biomass increases over time in response to the development of perennial root systems and concomitant increases in labile C pools (Baer et al., 2002, 2010). Phospholipid fatty acid (PLFA) profiles have been used to examine microbial community change in response to agricultural management (Petersen et al., 1997), disturbance (DeGroot et al., 2005) and during recovery from disturbance through restoration (Allison et al., 2005; McKinley et al., 2005). Additionally, PLFA markers have been used to document changes in biomass of different functional groups and to elucidate changes in nutrient stress associated with C limitations following the cessation of tillage and reestablishment of perennial grasses (Allison et al., 2005; McKinley et al., 2005).

The generality of microbial response to restoration, however, likely varies with soil texture. Silt and clay particles generally support larger and more diverse microbial communities than sand particles, which are dominated by fungi (Sessitsch et al., 2001). Soils with high clay content better protect the microbial biomass (Six et al., 2006), form more and larger aggregates (Angers and Caron, 1998; Kristiansen et al., 2006; McLauchlan, 2006b; Wick et al., 2009), and have inherently greater water holding capacity (Voroney, 2007). Soil moisture has been correlated with increases in microbial biomass, particularly fungal biomass and hyphal length (Frey et al., 1999). Furthermore, clay content has been positively related to nutrient retention in soils (Knops and Tilman, 2000). Thus, texture may modulate nutrient and environmental stress experienced by soil microbial communities and thereby influence restoration of the microbial community and belowground recovery in general.

The intimate connection between soil microbes and aggregate formation, C sequestration, as well as soil pore space and hydrology (Tisdall, 1994; Edgerton et al., 1995; Jastrow, 1996; DeGroot et al., 2005) emphasizes the importance of considering the role of microbial communities during soil restoration. Therefore, the objectives of this study were to compare microbial community and soil structural recovery between two contrasting soil textures during the transition from long-term conventional tillage to perennial native grass systems by (1) quantifying rates of soil microbial community recovery as indexed by PLFA profiles during grassland reestablishment on former cropland, (2) determining whether physiological stress of the soil microbial community changes during restoration, and (3) relating changes in soil microbial community structure to recovery of soil C and N, and soil structure. Specifically, we hypothesized that total PLFA biomass and richness would increase and PLFA indicators of microbial stress would decrease with time since cessation of tillage and years of grassland establishment, but to a greater extent in soil with higher clay content. We also hypothesized that fungi would be most highly correlated with soil structural recovery. Lastly, we predicted that microbial community structure and stress would vary between the soil textures, with a relatively larger proportion of fungal biomass and higher levels of PLFA stress indicator ratios in the loamy fine sand soil.

2. Methods

2.1. Study area

A chronosequence of independently restored grasslands ($n = 22$), cultivated fields ($n = 3$), and native prairies ($n = 3$) on silty clay loam soil with 0–6% slope (Fine smectitic, mesic Aquertic Argiudolls) was located across Gage (40.26508 N, 96.69347 W) and Saline (40.53134 N, 97.14231 W) counties, Nebraska, USA (USDA,

1990, 2003). Soils from these sites contained 71–90% silt and clay (Baer et al., 2010). During the years encompassing the restoration chronosequence (1988–2008; complete dataset acquired from weather station Beatrice 1n, 40.2994 N, 96.75 W), total precipitation ranged from 1022 to 376 mm, with an average of 757 ± 198 (± 1 standard deviation, SD) mm of total precipitation, of which an average of 616 ± 181 mm was received during the growing season (April–September). Average annual temperature from 1988 to 2008 was 10.9 ± 0.8 °C with an average minimum temperature of 4.2 ± 0.9 °C and maximum of 17.6 ± 0.9 °C.

A second chronosequence of independently restored grasslands ($n = 19$), cultivated fields ($n = 3$), and native prairies ($n = 3$) was located on well-drained loamy fine sand soil (mixed, mesic, Udorthentic Haplustolls) (USDA, 1984) across Stanton (41.92203 N, 97.19040 W), Madison (41.92186 N, 97.59950 W), and Pierce (42.27134 N, 97.61061 W) counties, Nebraska, USA. Sand content in these sites ranged from 80 to 93% and clay content was <10% (USDA, 1984; Baer et al., 2010). During the years encompassing the restoration chronosequence (1988–2008; complete dataset acquired from the Norfolk Karl Stefan Memorial Airport, 41.9806 N, 97.436 W), total precipitation ranged from 960 to 420 mm, with an average of 685 ± 134 mm of total precipitation, of which an average of 550 ± 107 mm was received April–September. Average annual temperature from 1988 to 2008 was 9.8 ± 0.86 °C with an average minimum temperature of 3.5 ± 0.8 °C and maximum of 16.2 ± 1.0 °C.

All restored grasslands were formerly cropped with corn (*Zea mays* L.), wheat (*Triticum aestivum* L.), oat (*Avena sativa* L.), sorghum (*Sorghum bicolor* L.), and/or soybean (*Glycine max* (L.) Merr). Upon enrollment in CRP, most sites were seeded with the same 6 perennial grasses (*Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., *Pascopyrum smithii* (Rybd.) A. Löve, *Bouteloua curtipendula* (Michx.) Torr., and *Sorghastrum nutans* (L.) Nash) sown at similar rates (Table 1). Sites planted after 1997 were seeded with two additional legumes (*Medicago sativa* L. and *Trifolium pratense* L.) and *P. smithii* was frequently substituted for *P. virgatum* (Table 1). The loamy fine sand sites often included *Eragrostis trichodes* (Nut.) Alph. Wood, substituted *Andropogon hallii* Hack. for *A. gerardii*, and used *Melilotus officinalis* (L.) Lam. for one of the legumes. Two older restorations on loamy fine sand were planted exclusively with *P. virgatum* and one younger restoration included five native forbs in addition to the grasses (Table 1). Nomenclature follows the USDA PLANTS Database (USDA, 2009).

2.2. Soil PLFA profiles

Soil for phospholipid fatty acid (PLFA) analyses was collected from each field using 2 cm diameter cores to a depth of 10 cm in May 2007 (all loamy fine sand sites and silty clay loam sites >8 y) and May 2008 (4 y, 10 y, and cultivated silty clay loam sites). Approximately 20 cores were removed from random locations in each field and composited. Composited soil samples were kept cold (~ 4 °C) and transported to the laboratory where the soil was passed through a 4 mm diameter sieve within 1 week of collection. A subsample (30 g) was frozen immediately after sieving and shipped on dry ice to the Soil Microbial Ecology Laboratory at the University of California Davis (Dr. K.M. Scow).

PLFAs were extracted from soil using the chloroform extraction method developed by Bligh and Dyer (1959) and modified by Bossio et al. (1998) and DeGroot et al. (2005). Briefly, fatty acids were extracted from soil into a 1:2:0.8 chloroform (CHCl₃):methanol(MeOH):phosphate buffer through centrifugation (2500 rpm 10 min, 30 min). Additional CHCl₃ and phosphate buffer (12 mL each) were added and phases were allowed to separate. The CHCl₃ phase was removed, evaporated under nitrogen (N₂), and

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