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A chronosequence of soil health under tallgrass prairie reconstruction

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ABSTRACT

Soil health changes induced by prairie reconstruction (cultivated fields to tallgrass prairie) were assessed in Central Missouri within sites representing a chronosequence of 0, 2, 3, 4, 6, 9, 10, 11, 12, and 13-yr post-reconstruction. In addition, a nearby remnant native prairie, two long-term reconstructed prairies (~25 and ~57-yr post-reconstruction), and a biofuel prairie 9-yr post-reconstruction were evaluated for comparative purposes. From 0 to 8-yr, prairie reconstruction increased soil aggregation, total soil organic carbon (SOC), total nitrogen (TN), active C and N (permanganate oxidizable C and total protein), and mineralizable C and N (soil respiration and potentially mineralizable nitrogen), becoming more similar to levels in the remnant prairie. Further, four enzymes involved in the cycling of C (β-glucosidase), N (β-glucosaminidase), P (acid phosphatase), and S (arylsulfatase) demonstrated amplified activities within samples collected to a depth of 15-cm. Over time, the ratios of active C to SOC and active N to TN declined, reflecting the conversion of active C/N pools into more stable C/N pools due to continued organic inputs and increased microbial activity. In contrast, from 8- to 13-yr post-reconstruction, the number of these same soil health indicators declined, which may be attributed to historical land use, the improvement of prairie reconstruction and management strategies, and ecological processes related to succession. Overall, prairie reconstruction holds great potential for soil health restoration in degraded agricultural landscapes, and further study is needed to understand how historical land use and prairie reconstruction practices affect soil health and ecological resilience.

1. Introduction

Historically, much of the tallgrass prairie in the central United States (U.S.) was converted to cultivated agriculture (Samson and Knopf, 1994; Kirt, 1995) and less than 1% of the original tallgrass prairie in this region exists today (Samson and Knopf, 1994). Conversion of native systems (*i.e.*, tallgrass prairie) to agricultural fields has led to soil degradation including nutrient depletion and soil compaction. Specifically, it has led to loss of soil organic matter and, in turn, decreased soil aggregate stability, weakened soil structure, reduced soil water holding capacity, and increased potential wind- and water-induced soil erosion (Karlen and Rice, 2015). These changes result in deteriorated soil conditions that decrease the ability of soil to perform crucial functions, such as nutrient cycling and productivity (Karlen et al., 2019).

Evidence suggests that reverting croplands back to native prairie systems (*i.e.*, prairie reconstruction) can have many potential benefits for the ecosystem, including soil erosion control and increased wildlife habitat (Jiang et al., 2007). Prairie reconstruction is expected to improve hydraulic conductivity, organic matter content, soil bulk density (Udawatta et al., 2008), microbial community activity, and nutrient cycling (Upton et al., 2018). Previous research has studied the effects of grassland restoration (or reconstruction) on soil physical (Jastrow et al., 1998; Camill et al., 2004; Chandrasoma et al., 2016), chemical (Sherman et al., 2005; Kucharik et al., 2006), and biological (Jastrow et al., 1998; McKinley et al., 2005; Kucharik et al., 2006; Li et al., 2018) properties. However, few studies have investigated changes in soil

Abbreviations: PFCA, Prairie Fork Conservation Area; SOC, soil organic carbon; TN, total nitrogen; WAS, wet aggregate stability; C, carbon; N, nitrogen; AC, active C; AN, active N; MC, mineralized C; MN, mineralized N.

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health indicators across a chronosequence of reconstruction to determine how rapidly soil health and function may recover.

Soil organic matter is quantified through measurements of soil organic carbon (SOC) and total nitrogen (TN) to provide insight into the decomposition and stabilization of plant and animal residues, root exudates, living and dead microorganisms, and soil biota (Nieder and Benbi, 2008). However, SOC and TN changes induced by soil management may be difficult to detect in short-term studies. Smith (2004) reported that a minimum of 6- to 10-yr is required to detect an increase in SOC when annual C inputs increase by 20–25% and result in a 3% change in background SOC levels. Thus, active C (AC), active N (AN), mineralizable C (MC), and mineralizable N (MN) measurements can serve as early indicators of soil degradation or improvement (Drinkwater et al., 1996; Weil et al., 2003; Li et al., 2017; Hurisso et al., 2018). Active C (permanganate oxidizable C) and AN (autoclaved citrate extractable protein) are pools of soil organic C and N, respectively, that provide readily available carbon and nutrient sources for soil microbial metabolism. Active C is closely correlated with other labile C pools such as microbial biomass C (Weil et al., 2003) and particulate organic C (Mirksy et al., 2008). A meta-analysis by Hurisso et al. (2016) showed that AC is more related to soil organic matter stabilization, whereas MC is heterotrophically respired C measured from rewetted soils during a short-term aerobic incubation and is more related to soil organic matter mineralization and nutrient release. The labile AN pool reflects the capacity of soils to supply N (Ros et al., 2011; Hurisso et al., 2018), and the incubation-based MN pool represents the fraction of organic N easily decomposed by soil microorganisms and potentially supplied to plants over the growing season (Drinkwater et al., 1996; Keeney and Bremner, 1966). Along with quantification of various C and N pools, the ratios of AC:SOC, MC:SOC, AC:MC, AN:TN, MN:TN, and AN:MN indicate C and N flow among different pools, which are associated with ecosystem processes such as decomposition and nutrient cycling. Together, these pools provide information on ecosystem processes and insight into soil health restoration status.

The soil microbial community is vital to soil health, as microorganisms play a key role in maintaining a healthy ecosystem functionality and sustainability by regulating processes such as C sequestration, N fixation and transformation, and P transformation and absorption in soil (Kandeler et al., 1996). Microbes utilize resources and acclimate to stress by altering their allocation of resources to maintenance, resource acquisition, and growth (Schimel et al., 2007). Soil enzymes are primarily produced by microbes when the substrate concentrations are sufficient for a positive return on resource investment (Allison et al., 2010). Enzyme activity is controlled by enzyme production and turnover (Steinweg et al., 2013), which reflect changes in microbial biogeochemical cycling and soil organic matter dynamics induced by management practices (Dick and Tabatabai, 1993; Lehman et al., 2015). Soil enzymes commonly assessed include hydrolases such as β-glucosidase, β-glucosaminidase, phosphatases, and sulfatases as indices of C, N, P, and S cycling, respectively (Acosta-Martinez et al., 2018). β-glucosidase activity is the only enzyme currently included as an indicator of C cycling in the Soil Management Assessment Framework (Stott et al., 2010). It provides information on cellulose degradation, which is the most common polysaccharide in nature. β-glucosaminidase plays a significant role in C and N cycling by hydrolyzing chitooligosaccharides (the degraded product of chitin) and releasing simple amino-sugars, which are major sources of mineralized N in soils (Ekenler and Tabatabai, 2004). Phosphomonoesterases are responsible for removing phosphate groups from many types of molecules, including nucleotides, proteins, and alkaloids. Phosphorus is needed for energy transfer and as a back-bone for DNA but is another limiting nutrient after N in agricultural production worldwide (Acosta-Martinez et al., 2018). Arylsulfatase catalyzes the hydrolysis of ester sulfates, which is considered the most labile form of organic S in soil (Scherer, 2001).

Soil physical properties, such as wet aggregate stability (WAS), influence important soil functions such as resistance to soil erosion and water partitioning (Amézketa, 1999). Compared to other physical properties, changes in aggregate stability can serve as early indicators of recovery or degradation of soils. Aggregate stability is a physical property but strongly influenced by soil biological properties such as organic matter content, biological activity, and nutrient cycling in soil (Amezketa, 1999). Soil texture (particle size distribution) is typically considered an inherent soil property stable during a short period. However, soil texture strongly influences other soil properties such as structure, carbon sequestration rate, and water holding capacity (Hassink, 1994.) and can be modified by erosion. Soil pH is the foundation of all soil chemical and biological reactions. The deficiencies of many nutrients, declines of microbial activity and crop yield, and deterioration of environmental conditions are often associated with changes in pH levels (Thomas,1996).

The tallgrass prairie reconstruction chronosequence is located in the unique topographic and climatic setting of Missouri's dissected till plains. This region includes the Central Claypan Region of Major Land Resource Area 113 in the central U.S (USDA-NRCS, 2006). Claypan soils cover approximately 10 million acres in the Midwestern U.S. and pose many unique management challenges for agricultural production including poor drainage, a shallow restrictive layer, high erosion, and high N loss (Jamison, Smith, & Thornton, 1968). Producers have historically resorted to intensive tillage to manage crop residues and dry soils, leading to the loss of nearly half of the original topsoil since European settlement in the 1800s (Bird and Miller, 1960). Improving soil health and sustainability have become key goals of soil restoration in this region in response to the erosion and degradation from intensive agricultural practices (Kremer and Anderson, 2005).

Revitalizing soil health requires a comprehensive approach including multiple soil health indicators that can provide insight into changes in the soil ecosystem and reveal the benefits of prairie reconstruction. The primary goal of reconstructing ecosystems on degraded sites is to promote re-establishment of functional equivalency to native ecosystems (Zedler and Lindig-Cisneros, 2001), meaning that the structure and function found in undisturbed ecosystems are regained during the reconstruction process. Thus, the main objective of this study was to evaluate physical, chemical, and biological soil health indicators across a chronosequence of reconstructed prairies in central Missouri that ranged from 0 to 13 yr and in comparison with a nearby remnant native prairie, two long-term reconstructed prairies (~25 and ~ 57-yr post-reconstruction), and a 9-yr post-reconstruction biofuel prairie. We hypothesized that: 1) pools of SOC and TN, AC and AN, MC and MN, soil enzyme activities, and soil aggregation would increase with time after reconstruction but not necessarily reach levels observed in the nearby native prairie; and 2) soil health improvement would result from interactions among soil physical, chemical, and biological indicators. Our study will provide a better understanding of the belowground prairie reconstruction process and inform management decisions.

2. Materials and methods

2.1. Sites description and soil sampling

Sites selected for this study are located in the Central Claypan Region (MLRA 113) of the Dissected Till Plains, including one row-cropped field planted to soybean [*Glycine* max (L.) Merr.] representing 0 yr of prairie reconstruction (R0), and reconstructed tallgrass prairie fields of varying ages (2- to 13-yr; R2–13) located at the Prairie Fork Conservation Area (PFCA) on Callaway County, MO (38.8923, −91.7350). Ages of the reconstructed prairie studied were 0, 2, 3, 4, 6, 9, 10, 11, 12, and 13 yr. Four reference sites outside PFCA were selected for comparative purposes: 1) a 9-yr post-reconstruction biofuel prairie at the Bradford Research and Extension Center (BF9) located 18 km east of the University of Missouri campus (38.8989, −92.2070); 2) a ~25-yr post-reconstruction prairie (LT25) located in the F.O. and Leda J. Sears Memorial Wildlife Area in Audrain County, MO (39.2622, −91.7198); 3) a

~57-yr post-reconstruction prairie (LT57) located in the Redman Conservation Area in Macon County, MO (39.8578, −92.3376); and 4) a remnant prairie, never cultivated (RP) located in the Tucker Prairie Natural Area in Callaway County, MO (38.9499, −91.9918) and approximately 22 km from PFCA.

Sites selected for this study do not differ in climate conditions and experience a mean annual temperature of 12 to 14 °C and mean annual precipitation of 960 to 1220 mm (USDA-NRCS, 2006). The sites also have comparable soil series that are poorly drained with little topographic relief. Soils at the sites are mainly silt loams with an argillic subsoil horizon that has an aquic condition and vertic properties such as shrink-swell and cracking behavior (*i.e.*, claypan horizon) (Baer and Anderson, 1997; Soil Survey Staff, 2019). The soil series include Calwoods (Fine, smectitic, mesic Aeric Epiaqualfs), Mexico (Fine, smectitic, mesic Vertic Epiaqualfs), Keswick and Gorin (Fine, smectitic, mesic Aquertic Chromic Hapludalfs), and Armster (Fine, smectitic, mesic Mollic Hapludalfs). Epiaqualfs are generally present on less sloping portions of the landscape (less than 5%) and Hapludalfs are generally found on steeper slopes up to 20% (Soil Survey Staff, 2019).

The younger PFCA sites (2 to 6-yr) were managed as fescue pasture or native warm-season grass from the 1980s onward and prior to prairie reconstruction. In contrast, the older PFCA sites (9 to 13-yr) were previously under long-term cultivation for more than 20 yr (personal communication with Jeff Demand, site historical manager). The prairie reconstruction at PFCA employs a variety of management strategies and techniques, including: (1) site preparation; (2) seeding native plants collected from nearby native prairies (<75 km) including Tucker Prairie; and (3) mowing, prescribed fire, and exotic species control for establishment and maintenance of the natural plant communities (Newbold et al., 2019). Site preparation included two treatments to remove undesirable species: (1) 3-, 4-, 6-, 9-, 13-yr PFCA were prepared using no-till cropping of glyphosate-resistant crops (*e.g.*, soybeans or corn) for ≥3 yr prior to seeding prairie species; and (2) 2-, 10-, 11-, 12-yr sites were prepared using nonnative and native grass planting followed by 1–2 yr of herbicide applications. Both treatments removed residual vegetation, prepared the seedbed for good soil-seed contact, and employed the same seeding methods for native species, although the composition of the native seed mix differed slightly each year (>75% overlap of seed rates/species composition each year).

The reconstructed biofuel prairie (BF9) was previously row-cropped with soybean then managed for biofuel production with annual mowing at the end of each growing season during the prairie reconstruction (Udawatta et al., 2020). A mix of native grasses and forbs were planted in the early 2000s at Sears Prairie, and the site is managed with periodic prescribed burns (MDC, 2017). Redman Prairie, a 48-ha area, was converted from cultivation to prairie in *ca.* 1960 and has been managed by alternating prescribed burns in two blocks (24 ha) on a 3-yr rotation to limit woody plant invasion and increase grassland plant species diversity (MDC, 2015). Tucker Prairie is the largest tallgrass prairie remnant in central Missouri (59 ha). It was managed by winter or early spring burns from 1958 through 2002. Since 2002, it was divided into five units with a burn rotation where each unit is burned twice within a 5-yr period. Detailed descriptions of the Tucker Prairie plant community and soil characteristics can be found in Kucera (1956, 1958).

Soil samples were collected in July of 2017 from the 14 sites at from 0 to 5-cm and 5- to 15-cm depths at each site from three transects crossing summit, backslope, and toeslope landscape positions. The only exception was BF9 where four transects were sampled. Each transect represented an average of 3 ha. The specific soil series for each sampling transect is provided in Table S1. Five soil cores (31.75-mm diameter) were collected from each transect using a soil sampling auger and composited. A total of 15 soil cores (5 cores × 3 transects) were taken per site and separated into 0–5 cm and 5–15 cm depth segments. The 5 cores from each transect were then mixed (composited) in the field (one composite sample for each depth). The composited soil samples were immediately transferred to the laboratory under refrigeration and processed within 48-h after sample collection. Bulk soil samples were sieved (< 2-mm) and homogenized before being air-dried.

2.2. Soil biological measurements

Ground air-dried soil was analyzed on a Leco TruMac CN combustion analyzer (Leco Corp., St. Joseph MI) for SOC and TN content. Active C (AC) was measured by the weak potassium permanganate (0.02 M $KMnO_4$) solution method (Weil et al., 2003). Active N (AN) was determined following the autoclaved citrate extractable protein method using the Thermo Pierce BCA protein assay kit (Thermo Scientific, IL, USA) according to Moebius-Clune et al. (2016). This method was modified from the "easily extractable glomalin" analysis of Wright and Upadhyaya (1996) and has been shown to consist of a broad pool of proteins (Rosier et al., 2006; Gillespie et al., 2011) that reflect organically bound, labile N (Hurisso et al., 2018). Potentially mineralizable N (MN) was evaluated based on a 7-day anaerobic incubation at 40 °C (Drinkwater 1996) and was calculated as the difference between the initial and post-incubation ammonium content as quantified by the colorimetric reaction of Rhine et al. (1998). Mineralizable C (MC) was measured *via* heterotrophic respiration on 20-g air-dried soil through a 4-day incubation at 20 °C where released CO_2 was trapped by KOH and quantified by the change in electrical conductivity of the KOH solution (Moebius-Clune et al., 2016).

The activities of four enzymes were quantified: the C-cycling enzyme β-glucosidase (EC 3.2.1.21; C-EA); N-cycling enzyme β-glucosaminidase (EC 3.2.1.52; N-EA); P-cycling enzyme acid phosphatase (EC 3.1.3.2; P-EA); and S-cycling enzyme arylsulfatase (EC 3.1.6.1; S-EA). Acid phosphatase was selected over alkaline phosphatase because the soil pH of sampling sites was acidic to neutral where acid phosphatase is more dominant. For all assays, 0.5-g air-dried soil was incubated for 1 h at 37 °C with the appropriate *p*-nitrophenyl derivative substrate and buffer following the methodology described by Tabatabai (1994) and Parham and Deng (2000). The amount of *p*-nitrophenyl released was measured using a spectrophotometer at 405 nm.

2.3. Soil physicochemical measurements

Gravimetric water content was determined by drying in the oven at 105 °C. Soil pH was measured on air-dried soils in a 1:2 mixture of soil: water (Thomas, 1996) using a Fisher Scientific Accumet® XL600 Dual pH/ISE meter with a Fisherbrand accuTupH® rugged bulb pH combination electrode (Hampton, NH). Soil particle size was analyzed following a rapid soil texture assessment method developed by Kettler et al. (2001) and adapted by Moebius-Clune et al. (2016) where 7-g air-dried soil was wet sieved through a 0.053-mm sieve to collect sand-sized particles, silt particles were settled out from suspension after 2-h, and the clay fraction was calculated by difference. Wet aggregate stability (WAS) was determined on the 1–2 mm aggregate size fraction of undisturbed air-dried soil following an adapted method of Kemper and Rosenau (1986) as described in Burt (2011) by submerging 3 g of 2-to-1 mm particle size on a 0.5 mm sieve underwater overnight followed by wet sieving (raising and lowering the sieve 20 times in 40 s). Aggregate stability was reported as a percent of aggregates (2 to 0.5 mm) retained after wet sieving.

2.4. Statistical analysis

2.4.1. Linear regression analysis for soil health indicators

Statistical analyses were conducted using R statistical software (R Core Team, 2019). To evaluate the impacts of reconstructed prairie age on soil health indicators, descriptive analyses of soil properties with prairie reconstruction age were conducted first on the chronosequence analysis, including 10 PFCA sites (0, 2, 3, 4, 6, 9, 10, 11, 12, and 13 yr post-reconstruction). Data from BF9, LT25, and LT57 were not included in the prairie reconstruction chronosequence analysis due to different

post-reconstruction management practices. The remnant prairie (RP) was excluded because "reconstruction age" does not apply.

Multiple linear regression and multiple quadratic regression were explored to describe the change in soil properties across the chronosequence. Akaike Information Criterion (AIC) was used for model selection, where lower AIC scores indicate a better model fit (Sakamoto et al., 1986). When AIC scores of two models between the linear and multiple quadratic regressions were similar, the model with a greater R^2 was selected. Multiple regression analysis with two predictors (prairie reconstruction age and soil depth) was conducted for all soil properties. Where soil depth was significant, a separate regression was conducted with prairie reconstruction age for each soil depth. If soil properties did not differ due to years post-reconstruction, analysis of variance (ANOVA) was conducted for comparisons among the post-reconstruction age groups [0-yr (R0), 2–6 yr (R2–6), 9–13 yr (R9–13), BF9, LT25, LT57, and RP]. Type III sums of squares was used to test the null hypotheses in the ANOVA to account for unbalanced data (four sites for R2–6, five sites for R9–13, and one site each for R0, BF9, LT25, LT57, and RP) with two soil depths and three or four replicates (transects).

2.4.2. Multivariate ordination analysis

Constrained ordination Distance-based redundancy analysis (dbRDA) (*capscale* function in *vegan* package) was conducted for 20 soil health indicators (water content, WAS, pH, SOC, TN, AC, AN, MC, MN, C-EA, N-EA, S-EA, P-EA, C:N, AC:SOC, MC:SOC, AC:MC, AN:TN, MN:TN, and AN:MN) at 0–5 and 5–15 cm. Soil particle size distribution (sand, silt, and clay content) were not included in the ordination since they are quite stable during this timeframe. To illustrate the soil health changes in the dbRDA ordination biplot, sampling sites were divided into seven reconstruction groups: R0, R2-6, R9-13, BF9, LT25, LT57, and RP. The R2-13 sites were divided into two groups due to land-use history (long-term cropping *versus* grass), which is expected to have long-term impacts on SOC and overall soil health condition. Each group was presented with confidence ellipses using the *ordiellipse* function in the *vegan* package. Differences in soil health condition among the seven reconstruction groups were evaluated using PerMANOVA ($n = 999$) followed by pairwise comparison (*multiconstrained* function in *BiodiversityR* package). In the dbRDA ordination, vector analysis was conducted using the *envfit* function in the *vegan* package to determine the relationship between post-reconstruction age groups with all 20 soil health indicators involved in the dbRDA ordination plus soil sand, silt, and clay content. In the ordination biplot, the vector arrow points in the direction of the most rapid change in the vector variables (Oksanen et al., 2017). In addition, multiple regression was conducted for the scores of soil samples on the first constrained eigenvector to explore the overall soil health condition changes with increasing post-reconstruction years for both depths.

2.4.3. Relationships among soil health indicators

Relationships among the 23 measured soil health indicators across all 14 sites were explored with Pearson correlation analysis, combining the results from both depths (0–5 cm and 5–15 cm). Two variable selection methods, both-direction stepwise multiple regression [*stepAIC* function in *MASS* package (Venables and Ripley, 2002)] and best subsets regression [*regsubsets* function in *leaps* package (Lumley and Miller, 2017) and *train* function in *caret* package (Kuhn et al., 2019)], were used to identify the best regression models for predicting soil biological indicators (SOC, TN, AC and AN, MC and MN, and enzyme activities) by prairie reconstruction age (prairie reconstruction age and square of prairie reconstruction age) and other soil physical and chemical indicators (pH, water content, WAS, and sand, silt, and clay content). The best subset model selection was identified using k-fold cross-validation (*train* function in *caret* package). The k-fold cross-validation consisted of first dividing the data into k subsets, where k was set to 10. Each subset (10%) served successively as a test data set and the remaining subset (90%) as training data. The average cross-validation error, root mean square error (RMSE), was computed as the model prediction error, which was used to select the optimal model with the smallest value. The main purpose of conducting the variable selection procedures is not to run multiple regression, but to explore the importance of prairie reconstruction age and soil physical and chemical properties for soil biological properties.

3. Results

3.1. Soil health indicator response to prairie reconstruction

Soil depth significantly influenced all soil health indicators except for soil particle size distribution and the AC: SOC ratio. At each depth, at least 13 out of 20 soil health indicators had quadratic relationships with post-reconstruction age (Table 1). For the quadratic relationships, the average optimum years (values closest to the remnant prairie) were 9-yr (0 to 5-cm) and 8-yr (5- to 15-cm). The corresponding optimum values, independent of soil health indicator, did not achieve levels equivalent to RP except for β-glucosidase at 0 to 5-cm and AC at 5- to 15-cm (Table 1).

There was no significant difference among the R2–13 sites in terms of clay content but there were significant quadratic relationships with post-reconstruction age for sand and silt content (Table 1; Fig. 1A and 1B). In comparison with the reference sites, RP at 5- to 15-cm ($\bar{x}$ 67 g kg^{-1}, sd = 7.6 g kg^{-1}) had less clay content than R2–6 ($\bar{x}$ 178 g kg^{-1}, sd = 64.2 g kg^{-1}), while clay content in the R0 ($\bar{x}$ 130 g kg^{-1}, sd = 5.3 g kg^{-1}), BF9 ($\bar{x}$ 103 g kg^{-1}, sd = 43.2 g kg^{-1}), LT25 ($\bar{x}$ 132 g kg^{-1}, sd = 40.1 g kg^{-1}), and LT57 ($\bar{x}$ 117 g kg^{-1}, sd = 40.4 g kg^{-1}) were not significantly different from R2–6 or RP.

Soil pH linearly declined with reconstruction age at both soil depths (Table 1; Fig. 1C). The same trend was applicable to the two long-term reconstructed prairies as R2–13 < LT25 < LT57. Among all sites, RP exhibited the lowest soil pH independent of soil depth (Table 1). WAS increased from 0 to 8-yr post-reconstruction and tended to decrease thereafter [$R^2 = 0.79$ (at 0 to 5-cm) and 0.71 (at 5- to 15-cm); Table 1; Fig. 1D]. The average WAS across reconstructed prairie sites with ages 2- to 13-yr was 76.3% (0 to 5-cm) and 62.7% (5- to 15-cm), which represents a five to six-fold increase over the R0. The optimum value of WAS in the R2–13 sites (88%) at 8.4-yr was comparable to RP at 0 to 5-cm (95%). In LT25 and LT57, WAS was greater than R0, but less than RP at both depths. As expected, WAS in the 0 to 5-cm depth was greater than in 5- to 15-cm soil depth overall (Fig. 1D).

Soil organic carbon increased with increasing yr post-reconstruction until 8-yr and decreased afterward (Fig. 2A). Optimum SOC content in the PFCA sites was only half that of RP, greater than LT25, but still less than LT57. Although TN (Fig. 2B) followed a similar trend as SOC, the C:N ratio (SOC to TN ratio on a mass basis) was not stable over time, but followed similar parabolic curves with reconstruction age.The C:N ratios at R2–13 were lower than at LT25, L57, and RP at both depths (Table 1).

Models for AC, AN, MC, and MN were concave at both depths except AN at 5–15 cm, which did not significantly change with the post-reconstruction time (Table 1; Fig. 2C to 2F). Compared with RP, the R2–13, BF9, LT25, and LT57 have not returned to native levels of AC, MC, AN, or MN in the 0 to 5-cm depth. Independent of soil depth, the AC: SOC ratio linearly decreased with increasing post-reconstruction years (Table 1). The model for the MC:SOC ratio was concave at 0 to 5-cm and did not change at 5- to 15-cm over time and also did not significantly differ among the reconstruction age groups (R0, R2–6, R9–13, BF9, LT25, LT57, and RP). At the 0 to 5-cm depth, the AC:MC ratio model exhibited a convex shape, but decreased linearly at 5- to 15-cm. At the 5- to 15-cm depth, AN:TN linearly decreased over time and the AN:MN ratio model was convex, but the MN:TN model was concave with increasing post-reconstruction years. In this depth layer, R2–13 demonstrated greater average AC content relative to RP. Compared with RP, all reconstructed sites had reduced levels of TN, AN, and MN.

At both depths, β-glucosidase activity reached RP levels at *ca.* 7-yr post-reconstruction (Table1 and Fig. 3A). β-glucosaminidase activity showed a similar trend; however, the greatest β-glucosaminidase

Table 1
Linear models of soil health indicators across the chronosequence of prairie reconstruction at Prairie Fork Conservation Area (R0 and R2–13), and the comparative reconstructed (BF9, LT25 and LT57) and remnant prairie site (RP).

Soil Health Indicators (SHI)	Model[a]	Adj-R^2	*P*-value	R0 SHI	R1–13 optimum year	R1–13 optimum SHI[b]	BF9 SHI	LT25 SHI	LT57 SHI	RP SHI
0–5 & 5-15 cm together										
Sand	$y = -2.056*x^2 + 32.756x + 110.38$	0.195	0.0008	66.7	6.3	213.8	101.6	116.8	270.6	252.6
Silt	$y = 3.29*x^2–40.87x + 760$	0.215	0.0004	800.4	6.2	633.3	786.5	760.1	619.6	675.4
AC:SOC	$y = -0.0007x + 0.0387$	0.261	<0.0001	0.035	13	0.030	0.030	0.035	0.026	0.022
0–5 cm										
SOC[c]	$y = -0.020*x^2 + 0.326x + 1.484$	0.642	<0.0001	1.71	8.2	2.81	2.86	2.53	3.06	4.89
TN	$y = -0.0014*x^2 + 0.023x + 0.135$	0.604	<0.0001	0.14	8.2	0.23	0.23	0.19	0.22	0.36
C:N ratio	$y = -0.0227*x^2 + 0.353x + 11.016$	0.512	<0.0001	11.1	7.8	12.4	12.6	13.6	14.1	13.5
AC	$y = -0.0055*x^2 + 0.077x + 0.648$	0.257	0.0069	0.61	7.0	0.92	0.88	0.97	0.90	1.22
AN	$y = -0.047*x^2 + 0.83x + 6.23$	0.437	0.0002	6.88	8.8	9.89	11.02	10.7	10.5	17.0
AN: TN ratio	Not significant	na	na	4.88	na	4.52	4.84	5.72	4.88	4.67
MC	$y = -0.014*x^2 + 0.22x + 0.62$	0.720	<0.0001	0.60	7.9	1.48	1.40	1.39	1.71	2.40
MC: SOC ratio	$y = -0.0002*x^2 + 0.003x + 0.042$	0.290	0.0037	0.04	7.5	0.05	0.05	0.06	0.06	0.05
AC: MC ratio	$y = 0.0057*x^2–0.106x + 1.039$	0.524	<0.0001	1.07	9.3	0.55	0.63	0.70	0.53	0.51
MN	$y = -1.16*x^2 + 17.75x + 78.31$	0.324	0.0019	88.0	7.6	146	113	140	135	247
MN:TN ratio	Not significant	na	na	0.06	na	0.06	0.05	0.08	0.06	0.07
AN: MN ratio	Not significant	na	na	78.9	na	77.0	101.7	75.5	80.6	69.7
C-EA	$y = -2.86*x^2 + 42.33x + 108.15$	0.661	<0.0001	120	7.4	265	251	198	180.	245
N-EA	$y = -0.85*x^2 + 13.1x + 35.41$	0.627	<0.0001	41.0	7.7	85.9	71.5	62.6	80.7	95.7
P-EA	$y = 20.71*x + 433$	0.262	0.0023	442	13	702	531	464	578	769
S-EA	$y = -3.76*x^2 + 56.68x + 51.32$	0.800	<0.0001	40.0	7.5	265	193	183	211	395
pH	$y = -0.036x + 6.76$	0.142	0.0230	6.21	13	6.30	6.59	6.20	6.12	5.89
WAS	$y = -0.9714*x^2 + 16.25x + 20.40$	0.791	0.0001	13.7	8.4	88	87	80	90	95
Clay	Not significant	na	na	135.7	na	124.2	120.4	114.3	102.6	77.4
WC	Not significant	na	na	29.6	na	30.9	27.4	21.7	26.0	23.8
5-15 cm										
SOC	$y = -0.009*x^2 + 0.137x + 0.987$	0.387	0.0005	1.01	7.6	1.51	1.63	1.04	1.70	2.43
TN	$y = -0.0006*x^2 + 0.009x + 0.096$	0.256	0.0071	0.10	7.5	0.13	0.15	0.09	0.14	0.21
C:N ratio	$y = -0.023*x^2 + 0.308x + 10.29$	0.274	0.0051	10.1	6.7	11.3	10.8	11.8	12.6	11.7
AC	$y = -0.004*x^2 + 0.048x + 0.358$	0.365	0.0008	0.31	6.0	0.50	0.47	0.32	0.36	0.47
AN	Not significant	na	na	4.13	na	4.96	5.38	3.35	4.79	7.04
AN: TN ratio	$y = -0.032x + 4.066$	0.124	0.0317	4.16	8.4	3.60	3.59	3.79	3.56	3.36
MC	$y = -0.006*x^2 + 0.087x + 0.384$	0.235	0.0102	0.38	7.0	0.70	0.69	0.37	0.87	1.29
MC: SOC ratio	Not significant	na	na	0.04	na	0.05	0.04	0.04	0.05	0.05
AC: MC ratio	$y = -0.028x + 0.988$	0.155	0.0181	1.14	13	0.62	0.69	0.87	0.42	0.37
MN	$y = -0.60*x^2 + 7.56x + 36.78$	0.367	0.0008	32.0	6.3	60.6	48.0	23.8	35.0	74.5
MN:TN ratio	$y = -0.0003x^2 + 0.0038x + 0.038$	0.405	0.0003	0.03	5.5	0.05	0.03	0.03	0.03	0.03
AN: MN ratio	$y = 1.4661*x^2–17.75x + 126.14$	0.385	0.0005	132.6	6.1	72	116	141	140	111
C-EA	$y = -1.13*x^2 + 15.49x + 40.81$	0.575	<0.0001	38.2	6.9	96.0	100.7	46.8	66.1	83.7
N-EA	$y = -0.56*x^2 + 8.18x + 12.29$	0.444	0.0001	12.0	7.3	42.16	29.6	22.4	49.0	47.9
P-EA	$y = -2.47*x^2 + 38.61x + 155.93$	0.228	0.0115	170	7.8	307	289	131	299	356
S-EA	$y = -2.01*x^2 + 26.46x + 39.01$	0.560	<0.0001	20.7	6.4	126	110.6	36.1	109	225
pH	$y = -0.05\times + 7.12$	0.160	0.0101	6.91	13	6.47	6.77	6.83	6.19	5.71
WAS	$y = -1.06*x^2 + 16.12x + 16.97$	0.706	<0.0001	9.61	7.9	78.3	67.9	53.2	89.4	90.0
Clay	Not significant	na	na	130.2	na	157.6	103.4	131.9	116.9	66.7
WC	Not significant	na	na	24.1	na	24.5	21.3	18.7	17.8	19.9

[a] Y: soil health indicator, X: time post-reconstruction (years).
[b] Optinum SHI was the SHI values closest to the remnant prairie in the regression, or the means of 0–13 yr reconstructed prairies if the model was not significant.
[c] Abbreviations and units: SOC: soil organic carbon (%), TN: total nitrogen (%), AC: active carbon (mg g^{-1}), AN: active N (total protein, mg g^{-1}), MC: mineralizable C (soil respiration, CO_2 mg g^{-1}), MN: mineralizable N (potentially mineralizable nitrogen, NH_4-N mg kg^{-1}), C-EA:β-glucosidase (mg *p*-nitrophenol kg^{-1} soil h^{-1}), N-EA:

β-glucosaminidase (mg *p*-nitrophenol kg^{-1} soil h^{-1}), S-EA: arylsulfatase (mg *p*-nitrophenol kg^{-1} soil h^{-1}), P-EA: acid phosphatase (mg *p*-nitrophenol kg^{-1} soil h^{-1}), WAS: wet aggregate stability (%), WC: water content (%), Sand/Silt/Clay (g kg^{-1}).

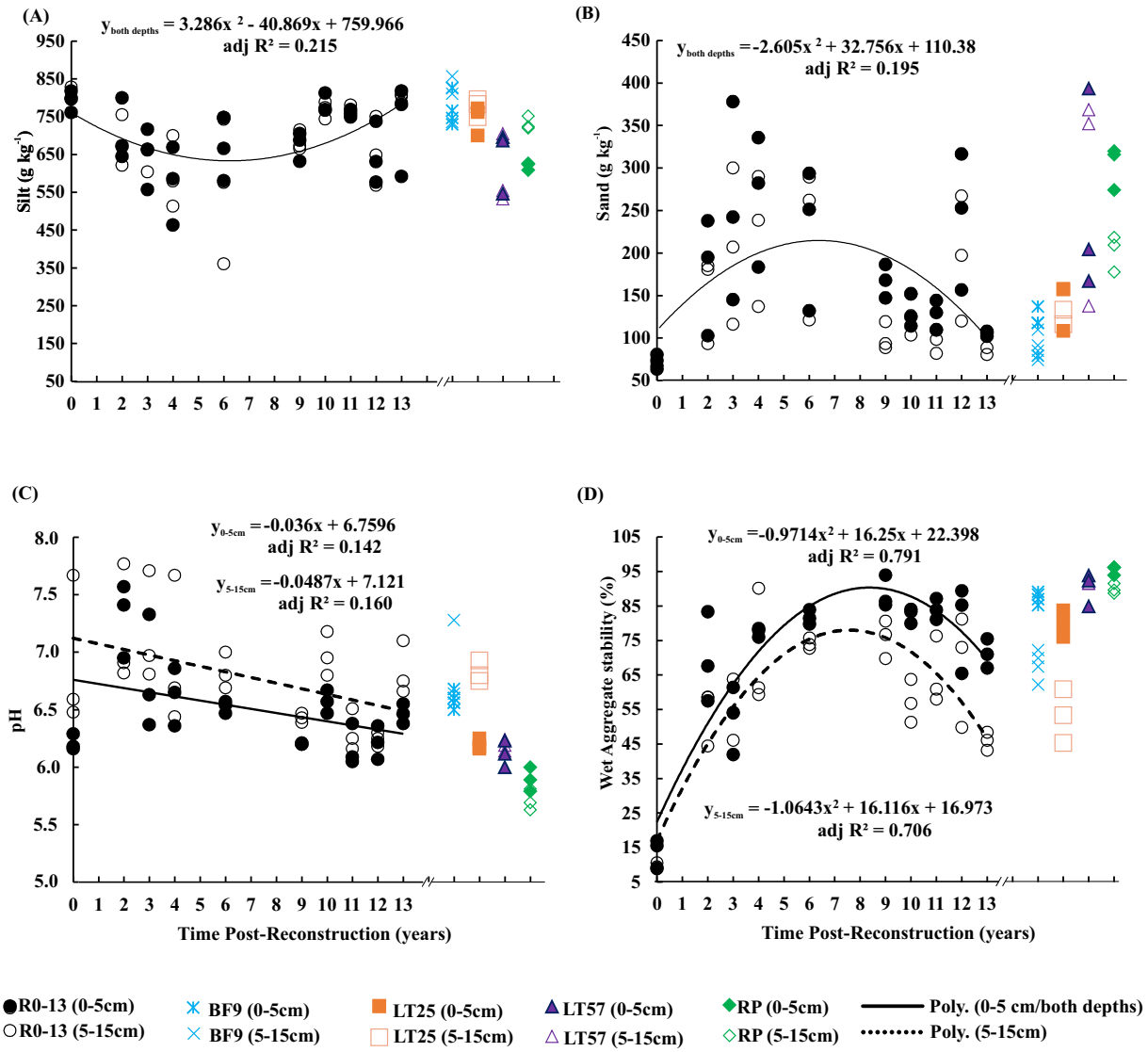

Fig. 1. Regression of soil silt content (A), sand content (B), pH (C), wet aggregate stability (D) against prairie post-reconstruction years at depths of 0–5 cm and 5–15 cm. Abbreviations: R0–13, 0- to 13-yr post-reconstruction sites; BF9, biofuel prairie 9-yr post-reconstruction site; LT25, ~25-yr post-reconstruction site; LT57: ~57-yr post-reconstruction site; RP: remnant prairie; and Poly, regression line.

activity in the reconstructed sites was still less than that in RP (Table1 and Fig. 3B). LT25 had less β-glucosaminidase activity than optimum values in the R2–13 at both depths. The best model for acid phosphatase activity at 0 to 5-cm showed a linear increase with reconstruction time (Table1 and Fig. 3C). At 5- to 15-cm, acid phosphatase activity followed a quadratic curve with time after reconstruction. Arylsulfatase activity followed quadratic curves at both depths, and optimum values were only half that observed at RP (Table1 and Fig. 3D).

The constrained ordinations in Fig. 4 A1 (0–5 cm) and B1 (5–15 cm) display the overall soil health condition that is characterized by all the measured soil health indicators influenced by the post-reconstruction age group. Only CAP1 was significant and explained 27.7% at 0–5 cm and 43.2% of variances at 5–15 cm, respectively. At both depths, soil health under R0 was different from R2–6, R9–13, and BF9 according to the pairwise comparison and R0 was also dissimilar from RP according to the CAP1. R0 was associated with a greater AC:MC ratio; but other groups, particularly RP, were associated with greater values of soil biological indicators, including SOC, TN, AC, MC, AN, MN, enzyme activities, C:N ratio, MC: SOC ratio, as well as sand content. R2–6, BF9, and R9–13 were different from RP. At 0–5 cm, R2–6 was different from R9–13, and LT25 was different from R2–6 and R9–13. At 5–15 cm, LT25 was different from R9–13, and LT57 was different from R2–6. In addition, the overall soil health illustrated by the changes of site (soil sample) scores in the dbRDA ordination with increasing years after reconstruction demonstrated similar quadratic curves for the majority of soil health indicators (Fig. 4A2 and B2). At both depths, higher scores were associated with greater values of the biological indicators. RP had the highest scores at both depths, indicating the greatest C and N contents in various pools, as well as greater enzyme activities.

3.2. *Relationships among soil health indicators*

The maximum, mean, minimum, and standard error for all measured soil health indicators were calculated for R0, R2–6, R9–13, BF9, LT25,

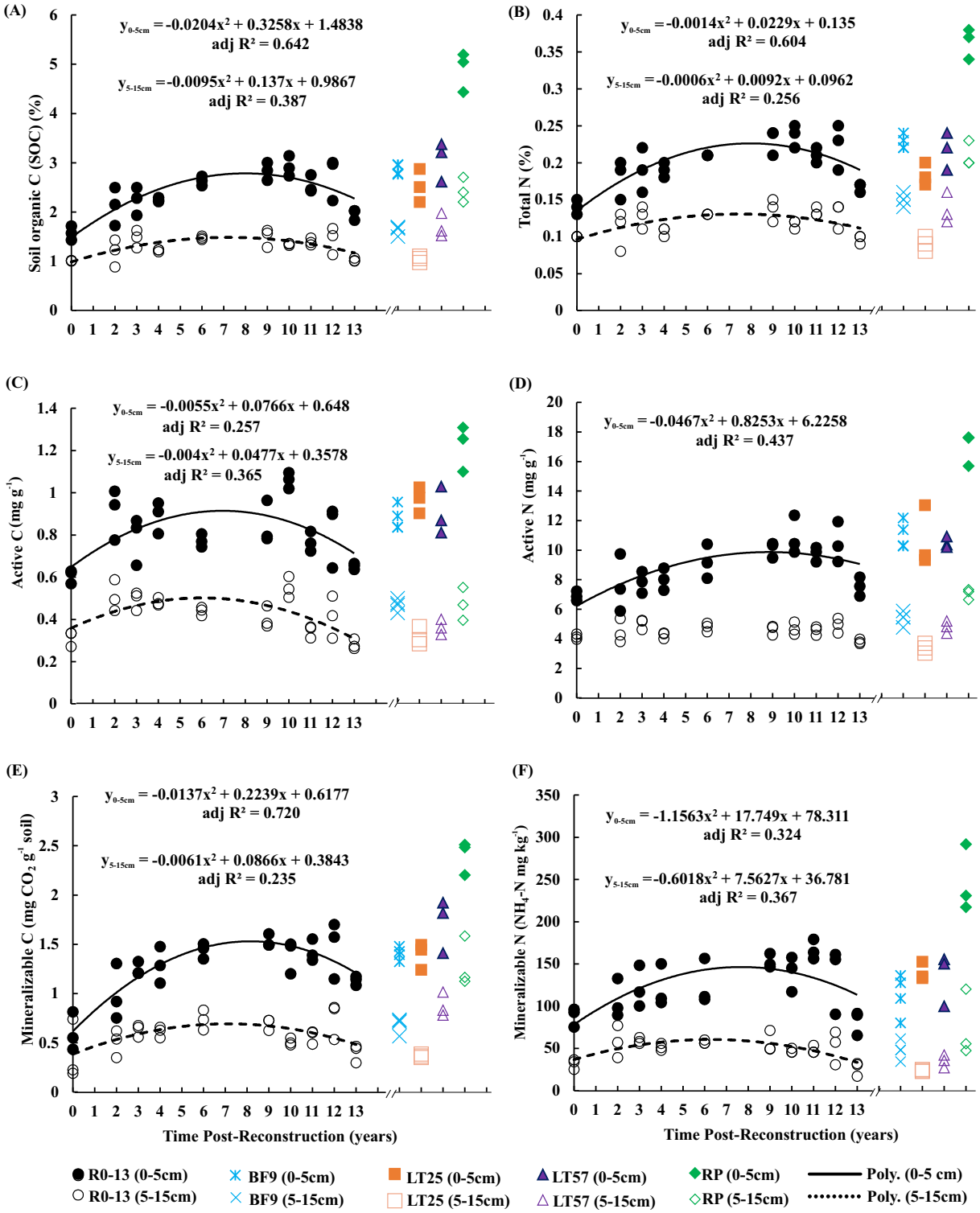

Fig. 2. Regression of soil organic carbon (A), total nitrogen (B), active carbon (C), total protein (D), mineralizable carbon (E), mineralizable nitrogen (F) against prairie post-reconstruction years at depths of 0–5 cm and 5–15 cm. Abbreviations: R0–13, 0- to 13-yr post-reconstruction sites; BF9, biofuel prairie 9-yr post-reconstruction site; LT25, ~25-yr post-reconstruction site; LT57: ~57-yr post-reconstruction site; RP: remnant prairie; and Poly, regression line.

LT57, and RP (Table S2). Several soil health indicators were significantly correlated with each other ($p < 0.05$) (Fig. 5). Notable high correlations ($r = 0.59$ to 0.99) were found among soil biological indicators (SOC, TN, AC, AN, MC, MN, and enzyme activities). Except for particle size distribution and soil pH, soil water content at sampling time was positively related to all soil biological indicators ($r = 0.30$ to 0.59). Soil pH was positively related to clay content, AC: SOC and AC: MC ratios, but negatively correlated with all other soil biological indicators. Soil WAS was positively correlated with the majority of soil biological properties. Sand content was more highly correlated with soil health indicators compared with clay and silt content.

Overall, post-reconstruction years was the most important factor influencing soil biological properties at 0–5 cm, but WAS was the most important variable for predicting soil biological properties independent

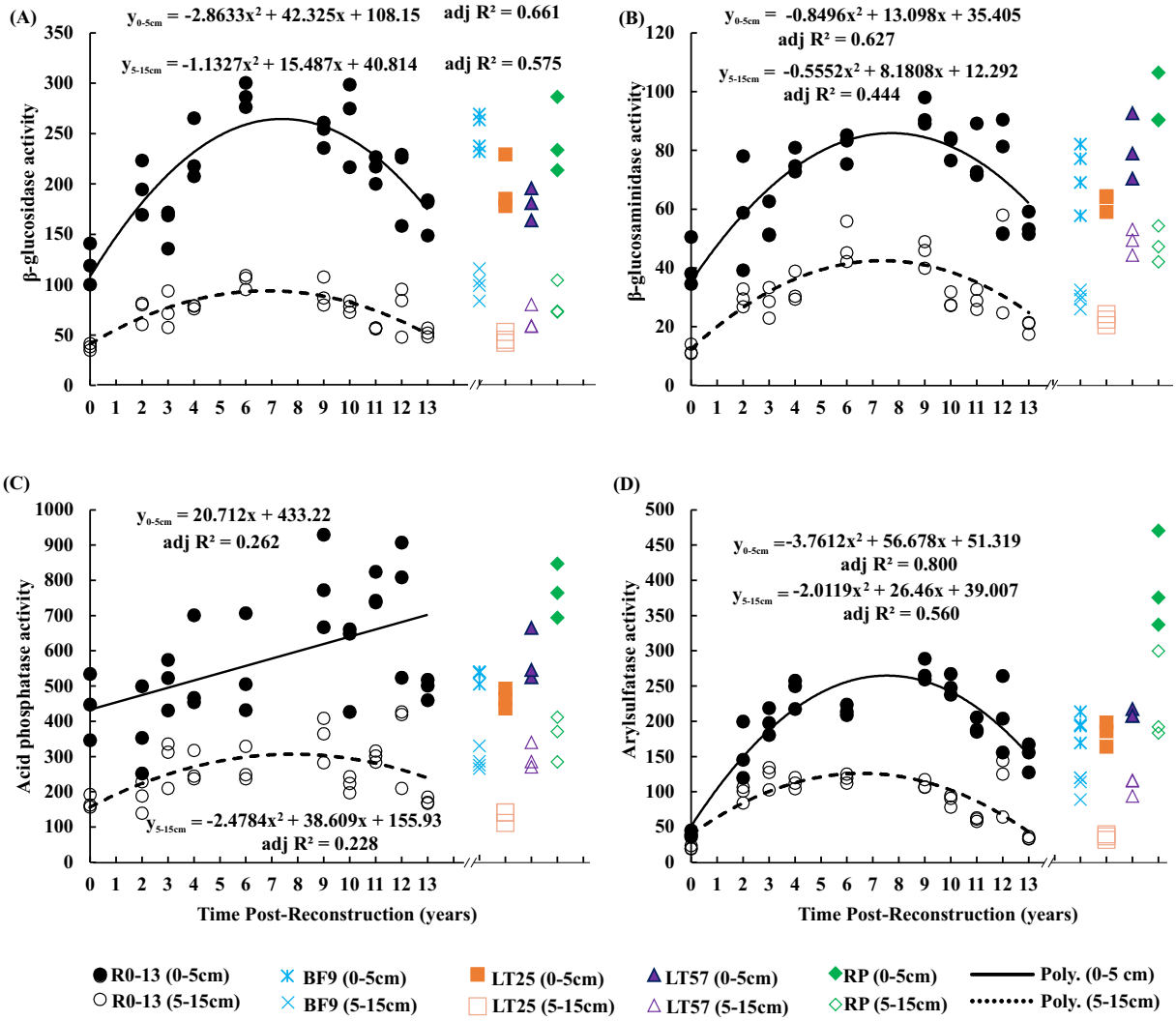

Fig. 3. Regression of soil enzyme activities (mg *p*-nitrophenol kg^{-1} soil h^{-1}): β-glucosidase (A), β-glucosaminidase (B), acid phosphatase (C) and arylsulfatase (D) against prairie post-reconstruction years at depths of 0–5 cm and 5–15 cm. Abbreviations: R0–13, 0- to 13-yr post-reconstruction sites; BF9, biofuel prairie 9-yr post-reconstruction site; LT25, ~25-yr post-reconstruction site; LT57: ~57-yr post-reconstruction site; RP: remnant prairie; and Poly, regression line.

of the method or model selection criterion used at 5–15 cm (Table 2). Specifically, square of time post-reconstruction (years) and time post-reconstruction (years) were selected for predicting at least 8 out of 10 soil health indicators at 0–5 cm. WAS was selected for all 10 soil biological indicators at both depths. Furthermore, if only one variable was selected to predict soil biological indicators (best subset regression), WAS was selected, except where post-reconstruction years was selected for acid phosphatase at 0–5 cm. Soil water content and WAS at 0 to 5-cm and the square of the post-reconstruction years at 5- to 15-cm were the next most nominated variables. Soil particle size distribution showed less importance compared with others (Table 2).

4. Discussion

It has been assumed that converting from agricultural production systems to perennial systems, such as reconstructed prairie, can improve soil health in degraded soils (*e.g.*, Veum et al., 2015). However, few studies evaluating land use conversion over time have included claypan soils, which present challenges due to inherently greater surface erodibility and reduced subsurface drainage (Blanco-Canqui et al., 2002). In this study, we found significant improvements in soil health within 8-yr of tallgrass prairie reconstruction in the Central Claypan Region of Missouri.

4.1. Response of soil health indicators to prairie reconstruction

Over time, prairie reconstruction led to a decline in soil pH (Fig. 1C; Table 1). More acidic pH under prairie soils compared with agricultural land was also reported by Brye and Pirani (2005). Under prairie systems, the oxidation of nitrogen and sulfur from year-round organic matter residues combined with increased uptake of base cations and release of H^+ from roots by perennial prairie plants relative to row crops results in soil acidification (Brye et al., 2008). Increased soil acidity post-reconstruction is important because pH is a master variable in environmental chemistry and can influence the diversity of the microbial community and its functions (Husson, 2013; Fierer and Jackson, 2006).

Prairie reconstruction increased SOC, TN (Fig. 2), and the C:N ratio, with remnant prairie demonstrating the greatest SOC and TN content and the highest C:N ratio (Table 1). Improvement in SOC and TN content following discontinuation of cultivation have previously been reported (*e.g.*, Knops and Tilman, 2000; Nunes et al., 2020b) and attributed to the suppression of tillage, which in turn slows decomposition and leads to higher SOC and TN content. Furthermore, prairie systems have longer growing seasons and greater above-and below-ground biomass than annual crops, which results in greater inputs of plant litter, plant roots, and root exudates, favoring organic matter accumulation and soil biological activity. The greatest SOC and TN concentrations were found in

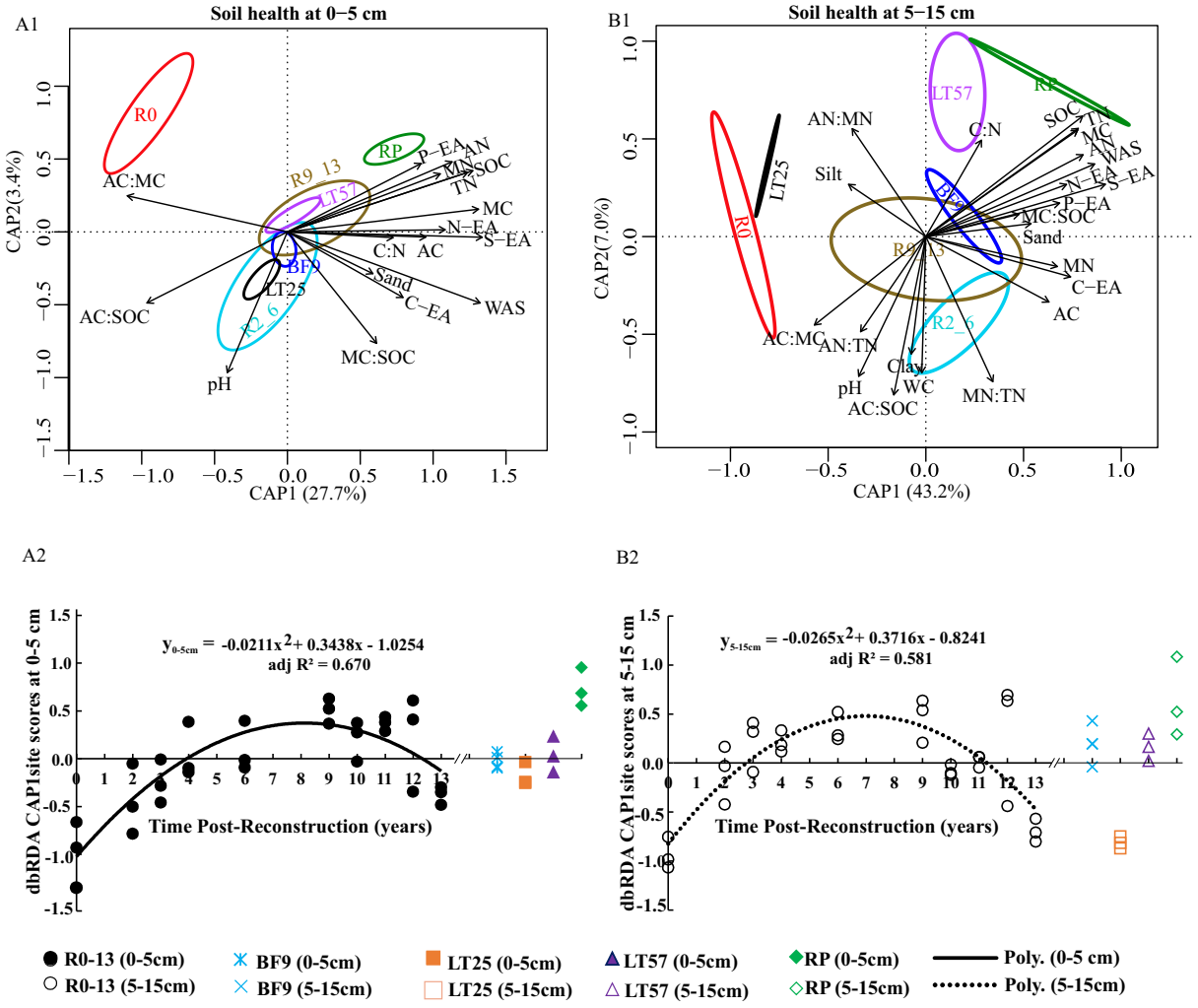

Fig. 4. Constrained ordination Distance-based redundancy analysis (dbRDA) of 20 soil health indicators at 0–5 cm (A1) and 5–15 cm (B1) from all the research sites, including seven reconstruction groups (R0, R2–6, R9–13, BF9, LT25, LT57, and RP). Ellipses illustrated the confident areas for R0 (red), R2–6 (sky blue), R9–13 (brown), BF9 (blue), LT25 (black), LT57 (purple), and RP (green). Vectors analysis includes all the 20 soil health indicators [(water content (WC), wet aggregate stability (WAS), pH, soil organic carbon (SOC), total nitrogen (TN), active carbon (AC), total protein (AN), mineralizable carbon (MC), mineralizable nitrogen (MN), β-glucosidase (C-EA), β-glucosaminidase (N-EA), arylsulfatase (S-EA), acid phosphatase (P-EA), and ratios of C:N, AC:SOC, MC:SOC, AC:MC, AN:TN, MN:TN, and AN:MN) and soil particle size distribution (sand, silt, and clay content)]. Only significant vectors are shown in the plots ($p < 0.05$). Fig. A2 and B2 are the regressions of the site (soil sample) scores on the CAP1 against the prairie post-reconstruction year at depths of 0–5 cm and 5–15 cm, respectively.

the remnant prairie (Table 1; Fig. 2), indicating that the reconstructed prairies may not be at equilibrium and may still have the potential for more C and N accumulation, including the labile pools of AC, AN, MC, and MN. However, another study conducted in southern Wisconsin found that a 65-yr-old reconstructed prairie still contained 37% less SOC in the top 25-cm than the remnant prairie (Kucharik et al., 2007). Our research demonstrated that converting from agricultural land use back to prairie can increase the C:N ratio even for highly degraded, claypan soils. These changes in C dynamics also have potential long-term ecological implications. For example, Prober et al. (2005) suggested that the greater C:N ratio found in remnant prairies favored native prairie plants over invasive annual plants.

Active C, AN, MC, and MN represent labile C and N pools that are ready for microbes to decompose to acquire energy and nitrogen under a suitable environment (Blair et al., 1995; Weil et al., 2003; Ros et al., 2011; Hurisso et al., 2016; Hurisso et al., 2018). It has been suggested that AC is more closely related to processed and stabilized soil C, while MC is more related to long-term mineralizable C (Culman et al., 2012; Hurisso et al., 2016). Effective C management involves balancing two ecological processes: mineralization of C and N for short-term plant uptake, and sequestering C and N for long-term maintenance of soil health, including structure and fertility (Lehmann and Kleber, 2015); however, a limited number of studies have examined the relationships between AC and MC or AN and MN. Within the native prairie system, fresh biomass inputs from the year-round living and actively growing roots results in more labile organic residues for microbes to utilize and transform for plant uptake. The increased MC promotes greater microbial activities, which benefits nutrient cycling and C sequestration (Li et al., 2017). In this study, the increase in AC at both depths and decrease in the AC:SOC ratio following prairie reconstruction indicate that more labile C has been incorporated into the soil and, simultaneously, more recalcitrant SOC has accumulated. The lack of an effect of prairie reconstruction on N ratios at 0 to 5-cm suggests that the relative abundance of these N pools was stable. In the 5–15 cm depth, however, the decrease in the MN:TN and AN:TN ratios in conjunction with an increase in AN, MN, and TN content indicate more stable N accumulation following prairie reconstruction.

Soil health improvement from 0 to 8-yr of prairie reconstruction was also evident in the soil enzyme activities involved in C, N, P, and S cycling, the increases of which ranged from 1.6 to 6.6-fold and 1.8 to 6.1-fold at 0–5 and 5–15 cm, respectively. However, relative to the remnant prairie, there was still potential for improvement, especially for

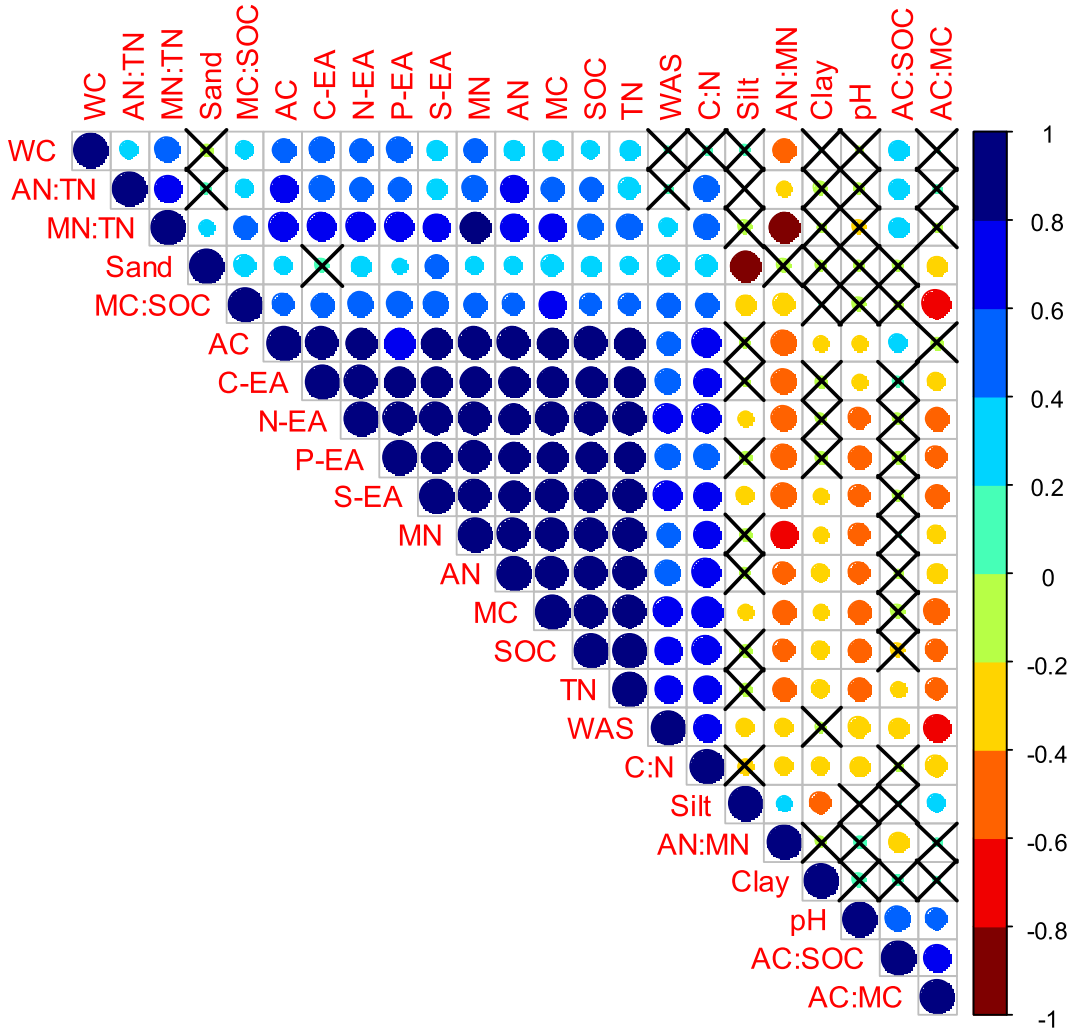

Fig. 5. Pearson correlation coefficients for all soil health indicators. Abbreviations and units: SOC, soil organic carbon (%); TN, total nitrogen (%); AC, active carbon (mg g^{-1}); AN, active N (total protein, mg g^{-1}); MC, mineralizable C (soil respiration, CO_2 mg g^{-1}); MN, mineralizable N (potentially mineralizable nitrogen, NH_4-N mg kg^{-1}); C-EA, β-glucosidase (mg *p*-nitrophenol kg^{-1} soil h^{-1}); N-EA, β-glucosaminidase (mg *p*-nitrophenol kg^{-1} soil h^{-1}); S-EA, arylsulfatase (mg *p*-nitrophenol kg^{-1} soil h^{-1}); P-EA, acid phosphatase (mg *p*-nitrophenol kg^{-1} soil h^{-1}); WAS, wet aggregate stability (%); WC, water content (%), and "X", not significant ($p > 0.05$).

sulfatase activity which was still 1.62 times greater in RP than the LT57 site. Similarly, Acosta-Martinez et al. (2003, 2004) observed trends in enzyme activities reflecting lower values in cultivated soils compared with reconstructed or native prairie soils within 5 to 10 years of establishment in Texas. The observed increase in enzyme activities suggests an improved biogeochemical function in terms of nutrient cycling. The fact these different enzymes have been impacted to different extents confirms the complex interaction of organic inputs with microbial activity, since enzymes are produced when substrate concentrations are sufficient for a positive return on resource investment (Allison et al., 2010; Acosta-Martinez et al., 2003).

The correlation between WAS and enzyme activities can be linked to the stabilization of soil aggregates by the products of the reactions that enzymes catalyze, such as polysaccharides (Buks and Kaupenjohann, 2016). Greater WAS indicates the presence of larger and expanded root systems under prairie soils. This root biomass ensures a continuous supply of organic materials, root exudates, nutrients, and oxygen to the microbial community and impacts other biological processes known to affect soil structure (Martin et al., 1995; Jastrow et al., 1998; Six et al., 2004). Furthermore, prairie systems provide continuous soil cover compared with cropped land while also avoiding mechanical disruption of soil aggregates (Nunes et al., 2020a). Improved soil structure under reconstructed prairies increases gaseous exchange, water retention and infiltration, and root penetration, and decreases soil susceptibility to erosion (Jastrow et al., 1998; Amézketa, 1999; Six et al., 2000), which is particularly important for claypan soils.

4.2. *Apparent decline in soil health 8-yr post-reconstruction*

The apparent decline in soil health following 8-yr of prairie reconstruction was not expected. However, similar results have been observed in other ecosystem restoration projects using the chronosequence approach (Li et al., 2018). Four primary factors likely contributed to the observed trend: 1) prairie restoration programs initially targeted highly degraded soils, and thus older sites may represent more degraded soils; 2) historical agricultural land use varied across the chronosequence, with older sites under pasture or grass and newer sites under row-crop production; 3) prairie reconstruction methods and management practices have improved over time – namely the more recent inclusion of mixed forbs and legumes with warm-season grasses; and 4) ecological processes such as nucleation survivability of seeded native forbs where small patches of shrubs and/or grasses serve as focal areas for recovery (Grygiel et al., 2009). As a result, the impact of prairie reconstruction on soil processes and ecosystem function can be variable.

Management considerations, such as previous land use, establishment procedures, and subsequent management practices, play an

Table 2
Optimal model selections using both-direction stepwise multiple regression (St. reg) and best subsets regression (BSR).

		0-5 cm								5-15 cm							
		Yrsq	Yrs	pH	WC	WAS	Sand	Silt	Clay	Yrsq	Yrs	pH	WC	WAS	Sand	Silt	Clay
SOC	St. reg	x	x											x			
	BSR	x	x		x					x		x	x	x			
TN	St. reg	x	x		x							x		x			
	BSR	x	x		x			x		x		x		x	x		
AC	St. reg	x			x	x				x				x			
	BSR		x			x				x				x			
AN	St. reg	x	x											x			
	BSR	x	x	x	x					x				x			
MC	St. reg	x	x											x			
	BSR	x	x							x	x		x	x	x	x	
MN	St. reg	x	x		x	x					x			x			
	BSR	x		x	x	x					x			x			
C-EA	St. reg	x	x			x	x							x			
	BSR	x	x			x	x			x	x			x			
N-EA	St. reg	x		x		x								x			
	BSR	x	x	x	x	x			x	x	x	x	x	x	x	x	
S-EA	St. reg	x	x		x			x		x				x			
	BSR	x	x							x				x	x		
P-EA	St. reg	x	x	x								x	x	x			
	BSR	x	x	x	x							x	x	x			
Number of times selected by variable selection methods to predict the above 10 soil health indicators																	
St. reg		10	8	2	4	4	1	1	0	2	1	2	1	10	0	0	0
BSR		9	9	4	6	4	1	1	1	8	4	4	4	10	4	2	0

Abbreviations: Yrsq, square of time post-reconstruction (years); Yrs, time post-reconstruction (years); WAS, wet aggregate stability; WC, water content; SOC, soil organic carbon; TN, total nitrogen; AC, active C; AN, active N; MC, mineralizable C; MN, mineralizable N; C-EA, β-glucosidase; N-EA, β-glucosaminidase; S-EA, arylsulfatase; P-EA, acid phosphatase.

important role in soil health restoration (Kucharik, 2007). The decline of soil health in the older sites (11-, 12-, and 13-yr post-reconstruction) may show severe soil degradation from long-term agricultural land use (Veum et al., 2015) and the interaction of soil conditions at the initiation of reconstruction activities with ecosystem age (Post et al., 2004; Li et al., 2018). It is possible that the natural recovery rate at PFCA may have slowed 8-yr after reconstruction. In many ecosystem reconstruction projects, parameters increase rapidly during the first several years then level off in late successional conditions (Brown, 1991; Baer et al., 2002). A plant community study conducted at PFCA in July 2017 found that native plant community indices (floristic quality and species richness) initially increased with prairie reconstruction, but plateaued after 4-yr and did not decline (Newbold et al., 2019). Other studies have reported declines in older reconstruction sites (Sluis, 2002; Camill et al., 2004; Hansen and Gibson, 2014). However, management at PFCA for older sites (>7-yr) included periodic prescribed fires in the late growing season to limit the dominance of C4 grasses and maintain plant diversity (Newbold et al., 2019), which may explain why the decline in soil health was not mirrored in the study of floristic quality. Long-term continued monitoring of soil health at PFCA may unravel the role of management history and reconstruction practices on soil health recovery.

4.3. Reconstructed sites compared with native prairie

Our results suggest that there is still potential for improved soil health and ecological function in the reconstructed prairie sites when compared with the remnant, never cultivated reference prairie site (Tucker Prairie; RP). Newbold et al. (2019) showed plant diversity was still below that of the remnant prairie when the PFCA reconstruction sites plateaued. This suggests that after intensive cultivation, soil health may never reach the same level of functioning as the native ecosystem. Furthermore, these results suggest that the reconstructed prairie sites at PFCA have not yet reached soil health equilibrium and further studies are needed to determine the long-term potential of prairie reconstruction practices to reclaim soil function.

The LT25 site (Sears Prairie) was donated to the Missouri Department of Conservation (MDC) as a fescue pasture in 1980. It was converted to big bluestem in about 1995 and managed for mixed-native grasses and forbs since the early 2000s with less than 50 species (personal communication, MDC). Therefore, this site was out of production for over 37 yr but under native prairie for approximately 17 yr as of 2017. The LT57 located in Redman Conservation Area was taken out of cultivation and converted to mixed grasses in 1960. However, the seeding plan at that time did not include a diverse mix of native grasses and forbs. Improved floristic diversity has the potential to accelerate soil health recovery and complicates the comparison between PFCA and early restoration sites based only on the year of reconstruction. These sites illustrate the potential influence of specific management practices on soil health restoration.

4.4. Synergistic evolution of soil health indicators with prairie reconstruction

Our prairie reconstruction study showed how the biological soil properties are correlated with soil physical and chemical properties. Prairie reconstruction provided lower soil disturbance and more organic inputs than in agricultural systems which encouraged microbial growth, promoted soil nutrient cycling as reflected in enzyme activities, and released more labile nutrients as reflected by the MC/MN and AC/AN ratios and WAS (Table 1). Additionally, stable soil C and N pools are an outcome of microbially-driven decomposition processes mediated by enzyme activity and increased labile C and N pools (Cotrufo et al., 2013; Lehmann and Kleber, 2015). The microbially-driven formation of soil organic matter is influenced by many factors that control organic material decomposition. For instance, soil structure can influence microbial access to organic materials (Gougoulias et al., 2014), while soil pH can influence soil enzyme activities, especially phosphatase (Dick et al., 2000). Additionally, this study emphasized the importance of WAS as a physical soil health indicator and its utility as part of a minimum soil health dataset when resources and labor are limited for soil health assessment.

Integration of multiple aspects of soil science is required to understand complex ecological outcomes in soil health restoration (Heneghan et al., 2008). Soil health restoration is a long-term process resulting from

complex interactions among soil physical, chemical, and biological processes. Individual soil properties may be restored following prairie reconstruction; however, understanding the interaction of historical management, restoration practices, and multiple soil functions is critical for optimizing ecological function. Do soil properties respond similarly to plant species restoration (Corbin and Holl, 2012) and follow a "nucleation" pattern where one or a few soil properties lead the restoration process and trigger the improvement and restoration of other properties later on? If yes, which soil properties are the nuclei in the soil health restoration?

Soil biological properties have strong influences on soil physical and chemical properties. Physically, more organic matter improves soil structure and associated soil properties (Tisdall and Oades, 1982). Chemically, soil organic matter affects cation exchange capacity, the capacity for buffering changes in soil pH, through the decomposition of organic materials (McCauley et al., 2009). Organic matter accumulation with prairie reconstruction can also lead to soil acidification due to the nitrogen cycling process (Bolan et al., 1991; Helyar, 1976) and the removal of greater amounts of inorganic cations than anions in prairie growth (Riley and Barber, 1969). Reconstruction or restoration in the sense of returning an ecosystem to a specified reference condition requires a sophisticated understanding of plant-soil-microbe-climate interactions. An integrated strategy involving soil physical, chemical, and biological properties is essential for soil health restoration, and the observed changes in soil health indicators across the chronosequence of reconstruction in this study demonstrated the core role of biological soil properties in the recovery of soil health.

5. Conclusions

Our study showed that prairie reconstruction not only serves an important role in the Midwestern U.S. to improve wildlife habitat and sustain native vegetation, but also to recover soil health. The soil health condition along a chronosequence of post-reconstruction years (up to 13-yr) was evaluated through a suite of soil physical, chemical, and biological properties. In general, soil health indicators followed a "bell-shaped" curve from 0 to 13-yr, with an optimum at ~8-yr. Overall, the optimum levels of most soil health indicators were still lower than the remnant prairie, suggesting that the reconstructed prairie sites had not yet reached equilibrium. The decline of soil health indicators in sites >8-yr post-reconstruction likely resulted from a combination of historical agricultural degradation, improvement in prairie reconstruction practices, or natural reconstruction succession. The relationships among soil health indicators also emphasized the core role of aggregate stability and biological properties in soil health restoration. Overall, this study highlights the potential to reclaim ecological function in degraded agricultural lands through well-managed prairie reconstruction.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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