Intensifying rotations increases soil carbon, fungi, and aggregation in semi-arid agroecosystems

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ABSTRACT

Increasing soil organic carbon (SOC) is a critical but daunting challenge in semi-arid agroecosystems. For dryland farmers, low levels of SOC and aggregation exacerbate the risks of farming in a water-limited environment − risks that will compound with climate change. Many dryland farmers in semi-arid climates use year long periods called summer fallow, where no crops are grown and weeds are controlled, to store rainwater and increase the yield of the following crop. In semi-arid climates around the world, dryland farmers are increasingly replacing summer fallow with a crop, a form of cropping system intensification. Cropping system intensification has the potential to increase SOC, but the drivers of this effect are unclear, and may change based on environmental conditions and management strategy. We quantified SOC, water-stable aggregates, and fungal and microbial biomass on 96 dryland, no-till fields in the semi-arid Great Plains, USA, representing three levels of cropping system intensity from wheat-fallow to continuous (no summer fallow) rotations along a potential evapotranspiration gradient. Cropping system intensity was positively associated with SOC, aggregation, and fungal biomass, and these effects were robust amidst variability in environmental and management factors. Continuous rotations averaged 1.28% SOC at 0–10 cm and had 17% and 12% higher SOC concentrations than wheat-fallow in 0–10 cm and 0–20 cm depths, respectively. Aggregate stability in continuous rotations was about twice that in wheat-fallow rotations. Fungal biomass was three times greater in continuous rotations than wheat-fallow, but was not significantly different from mid-intensity rotations. Using structural equation modeling, we observed that continuous cropping, potential evapotranspiration, % clay content, and fungal biomass together explained 50% of the variability in SOC, and that SOC appears to enhance aggregation directly and as mediated through increases in fungal biomass. Overall, the model suggests that cropping system intensity increases SOC both directly, through greater C inputs to soil, and indirectly, by increasing fungal biomass and aggregation. Our findings suggest that continuous cropping has the potential to provide gains in SOC and soil structure that will help offset C emissions and enhance the resilience of dryland agroecosystems.

1. Introduction

Increasing soil organic carbon (SOC) in semi-arid agroecosystems is a critical sustainability challenge for the 21st century. Semi-arid regions, defined as regions with a precipitation to potential evapotranspiration (PET) ratio of 0.2–0.5 (UN, 2011), constitute 20% of Earth's land surface and support a large agricultural population that is under increasing pressure from land degradation and desertification (Bot et al., 2000; Koohafkan and Stewart, 2008). Dryland farming in these regions depends solely on precipitation and uses no supplemental water, which presents a need for, and a challenge in increasing SOC. Warmer temperatures under future climate scenarios will further exacerbate water limitation in semi-arid climates (Ko et al., 2012;

USGCRP, 2014). Dryland agriculture contributes to climate change through energy use during its life cycle (e.g. fertilizer production) and emissions of greenhouse gases from soils, but agricultural soils can also sequester carbon dioxide from the atmosphere. Not only are dryland soils an underutilized resource for enhancing C sequestration to mitigate climate change (Lal, 2004), but increasing SOC is also a key climate change adaptation strategy for dryland farmers. Increasing SOC has the potential to mitigate the risks associated with increasing water limitation by enhancing water infiltration and storage (Franzluebbers, 2002). Greater SOC can also enhance soil functions like nutrient provision and retention, substrate provision for biodiversity, and erosion control (Wall, 2012), but increasing SOC in dryland systems is constrained by high erosion rates, low C inputs, and accelerated

mineralization from tillage (Plaza-Bonilla et al., 2015).

Environmental constraints on C inputs are further exacerbated by the common practice of a year-long period called summer fallow, where no crops are grown and weeds are controlled so that the soil can accumulate rainwater and increase the yield of the following crop. Summer fallow periods have historically helped stabilize wheat yields, but they are inefficient and management intensive. Precipitation storage efficiency is typically less than 35% under best management (Nielsen and Vigil, 2010), and fallow periods require frequent tillage and/or herbicides for weed control. No-till management (where weeds are controlled through herbicides instead of tillage) enhances water storage and enables dryland farmers to replace summer fallow periods with a crop, a form of cropping system intensification. Within no-till systems, cropping system intensification may increase SOC by increasing overall productivity relative to more traditional crop-fallow systems, where a crop is only grown once every two years (Sherrod et al., 2003; Peterson and Westfall, 2004). In semi-arid agroecosystems around the world, dryland farmers are undergoing transitions from crop-fallow to intensified cropping systems (Maaz et al., 2018), in what has been called a revolution in semi-arid cropping (Smith and Young, 2000). This widespread transformation in dryland agroecosystems may have significant implications for C sequestration and enhancing the resilience of dryland agriculture through gains in SOC. However, the mechanisms and extent to which cropping system intensity increases SOC independent of shifts in tillage practices are unclear and may be influenced by climate, soil type, and management strategy.

Given the limited productivity and associated amount of available C inputs to dryland soils, understanding the mechanisms and drivers of how C becomes stabilized is important to slow or reverse losses of SOC. Accrual of SOC can occur when C is protected from decomposition, either through adsorption on soil mineral surfaces, or when it is physically bound in soil aggregates (Jastrow, 1996). Protection of SOC in soil aggregates is a primary mechanism of SOC stabilization in agroecosystems and is highly sensitive to management (Tisdall and Oades, 1982). Several studies have observed the accumulation of SOC in aggregate pools as a significant driver of C accrual during the conversion from conventional till to no-till systems (Six et al., 1999). Similarly, cropping system intensification contributes greater C inputs to soil by replacing fallow periods with a growing crop, and has been associated with greater macroaggregation, microbial biomass, and SOC (Shaver et al., 2003; Peterson and Westfall, 2004; Sherrod et al., 2005; Mikha et al., 2010). Greater root biomass may enhance aggregation via root and associated rhizosphere microbial polysaccharides that contribute to aggregate formation and stabilization (Jastrow et al., 1998).

In addition to the direct influence of greater C inputs on SOC accrual, cropping system intensification may also indirectly enhance SOC through changes in the microbial community (Fig. 1). Fungi, in particular, can contribute to SOC stabilization by physically entangling soil particles in hyphae to form aggregates and by secreting cohesive substances like glycoproteins that enhance aggregation (Wilson et al., 2009). In addition to their role in aggregation, some evidence suggests that fungi may have a higher C use efficiency, and thus retain more C in the soil during the decomposition process relative to bacteria (Waring et al., 2013; Kallenbach et al., 2016; Malik et al., 2016). Due to the different potential functions provided by fungi and bacteria in ecosystem processes, the relatively coarse metric of the ratio of fungi to bacteria in soil is often related to its C sequestration potential (Strickland and Rousk, 2010), and others (Malik et al., 2016) suggest that fungi play a central role in SOC accrual (Fig. 1). Still, the functional importance of the fungi:bacteria ratio remains a point of controversy due to the wide range of functional diversity across both groups, and several lines of evidence have disputed the relationship between fungal dominance and C stabilization (Rousk and Frey, 2015).

Cropping system intensity also influences soil moisture and the availability of C substrates (Farahani et al., 1998b; Sherrod et al., 2003), both of which are strong determinants of microbial community
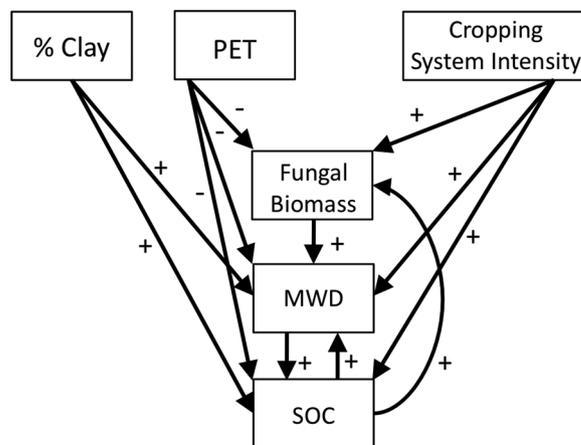

Fig. 1. Hypothesized relationship between cropping system intensity and the mechanistic drivers of SOC accrual as affected by climate, soil texture, and management. Plus and minus signs denote positive and negative relationships, respectively. MWD = Mean weight diameter of water-stable aggregates, PET = Potential evapotranspiration, SOC = Soil organic carbon.

dynamics (Drenovsky et al., 2004). For example, increasing the availability of C substrates by reducing the duration of fallow periods can increase populations of arbuscular mycorrhizal fungi (Thompson, 1987; Harinikumar and Bagyaraj, 1988). Additionally, cropping system intensification is often achieved by growing a greater diversity of crops, and previous studies have linked crop diversity to higher fungi:bacteria ratios and microbial biomass (Lange et al., 2014; McDaniel et al., 2014). However, Acosta-Martinez et al. (2007) found that cropping system intensity increased microbial biomass, but not always fungal biomass, and Stromberger et al. (2007) observed few differences between the microbial community structures of different dryland crop rotations. Further investigation into the effects of no-till crop rotations on microbial communities is needed to understand the potential role of microbes as mediators of C stabilization in dryland agroecosystems.

The effects of cropping system intensity on microbial communities and aggregation as drivers of C sequestration may change based on environmental factors like soil clay content and climate (Acosta-Martinez et al., 2003; Sherrod et al., 2003; Peterson and Westfall, 2004). As SOC accrual associated with cropping system intensity has primarily been observed in controlled experimental systems, and mainly considered in combination with reduced tillage (e.g. Norton et al., 2012), further exploration is needed into the extent that cropping system intensification impacts the mechanisms of SOC stabilization independent of tillage and across a range of environmental and management factors.

We conducted a study on dryland, no-till farms and long-term experiment stations in the semi-arid Great Plains, USA that captured a wide range of crop rotations, soil textures, PET rates, and management histories. This allowed us to quantify the potential for cropping system intensification to enhance SOC storage and aggregation relative to traditional crop-fallow systems and to evaluate the relative effects of management, texture, and climate on SOC levels. We hypothesized that increased cropping system intensity would be associated with greater SOC, fungal biomass, and aggregation, and that these trends would be robust across a range of environmental and management contexts (Fig. 1).

2. Materials and methods

2.1. Cropping systems

Wheat-fallow (WF) is one of the most common dryland cropping systems in the semi-arid Great Plains (Hansen et al., 2012). This system consists of growing winter wheat *(Triticum aestivum)* from September to
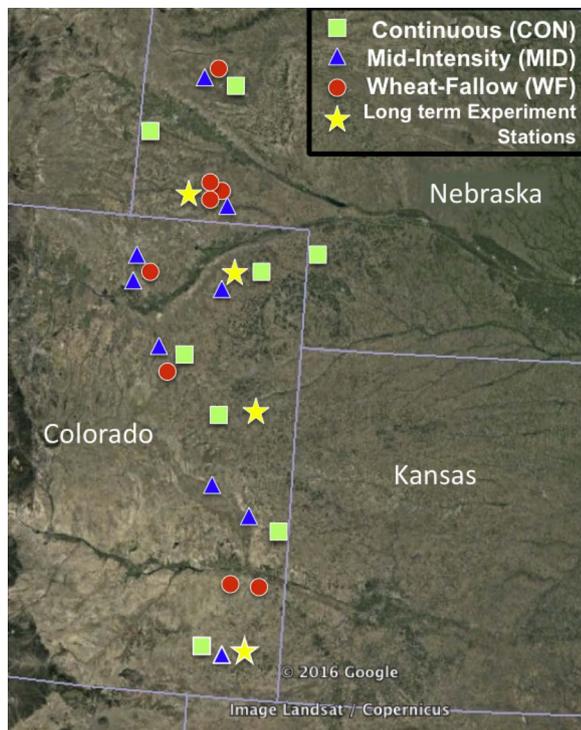
Fig. 2. Study locations color-coded by cropping system intensity. Multiple fields per location were sampled, and all three levels of cropping system intensity were present at each of the experiment stations.

July, then fallowing for 14 months until the next wheat planting. No-till farmers in this region often reduce summer fallow frequency from one out of two years (WF), to one out of three or four years (mid-intensity; MID), by rotating winter wheat with crops like corn (*Zea mays*), sorghum (*Sorghum bicolor*), proso millet (*Panicum miliaceum*), peas (*Pisum sativum*), or sunflowers (*Helianthus annuus*). They may also eliminate summer fallow altogether via continuous cropping (CON).

2.2. Study sites

Sampling was conducted in 2015 and 2016 on 96 dryland, no-till fields in eastern Colorado and western Nebraska, representing 54 fields from working farms and 42 fields from long-term experiment stations (Fig. 2). Each of three levels of cropping intensity – WF (n = 27), MID (n = 37) and CON (n = 26) – was represented along a potential evapotranspiration (PET) gradient that increased from 1368 mm yr^{-1} in northwestern Nebraska to 1975 mm yr^{-1} in southeastern Colorado (Fig. 2). Additionally, two 30-year old Conservation Reserve Program perennial grass plots (30-yr CRP) at the three long-term experiment stations in Colorado (Fig. 2) were sampled as a reference for comparison with the cropping systems (n = 6). To assign a value of PET to each site, a linear equation was used based on known PETs from 6 locations as measured by open-pan evaporation (Peterson et al., 2001) and the latitude of each site. We used climate data from 1980 to 2010 to assign a value of 30-yr average annual precipitation to each field. Average annual precipitation at the study sites ranged from 349 to 472 mm and means by cropping intensity were statistically equivalent (PRISM, 2017). Five-year field histories were collected for each field (Table 1). We collected N fertilizer use data from working farms for the years 2010–2014 to calculate annualized fertilizer use. No field received compost or manure. All fields were under tilled WF management for several decades prior to implementation of no-till and the current crop rotation. Every field was planted to winter wheat in the fall of 2015.

2.3. Soil sampling

In the fall of 2015, soil samples from the 0–20 cm depth were taken using a corer (2 cm dia.) at 4 locations within each field that represented corners of a 10 × 10 m square on each field and geo-referenced for later samplings. At each location, we composited 10 soil cores. Field replicates were analyzed separately for SOC and later averaged to obtain field-level means. Soil samples used to determine texture and pH were composited and analyzed by field. Soil texture was determined by hydrometer, and pH using a 1:1 slurry of soil and deionized water at Ward Laboratories in Kearney, NE. At the three long-term experiment stations in Colorado (see Fig. 2), samples were taken from both a summit and toeslope position in each field to examine if the differences in water availability at upland and lowland positions influenced SOC. Samples on all other fields were taken from a flat topographical position and labeled as a summit.

Additionally, soil samples were taken in spring of 2016 at the same locations as the fall sampling. The spring sampling was to a shallower 0–10 cm depth because the surface soil layers are more likely to be influenced by management practices, and surface soil physical properties, such as aggregation, can confer important functionality on water infiltration and storage (Mann, 1986; Shaver et al., 2002). A 5.5 cm slide-hammer corer was used to take one 0–10 cm depth soil sample per sampling location (4 cores per field) to assess water-stable aggregation, bulk density, SOC, total N, and PLFA. Bulk density, SOC, and total N were analyzed by sampling location (4 field replicates), and later averaged to obtain field-level means. Soils to determine water-stable aggregation and PLFA were composited and analyzed by field. Subsamples of field moist soils (20 g) were weighed, dried at 105 °C, and reweighed to determine gravimetric water content. Toeslope positions at the long-term experiment stations were excluded in the spring sampling. All samples were kept on ice in coolers for 4–36 h before being refrigerated at 4 °C.

2.4. Soil carbon & water-stable aggregates

We determined SOC and total N on spring and fall air-dried soils. Soils were ground on a roller grinder and analyzed for total C and N on a LECO CHN-1000 auto analyzer (St. Joseph, MI). Soil inorganic C was assessed using the modified pressure calcimeter method (Sherrod et al., 2002), and subtracted from total C to determine concentrations of SOC.

A wet sieving method adapted from Elliott (1986) was performed on 80 g air-dried subsamples to separate soils into large macroaggregate (> 2000 μm), small macroaggregate (250–2000 μm), free microaggregate (53–250 μm), and free silt and clay (< 52 μm) size fractions. Air-dried soils were submerged in water for 5 min prior to sieving for slaking. Sieves were manually moved up and down 50 times over a period of 2 min in a shallow pan of deionized water. Each size fraction was collected in pre-weighed aluminum pans, dried in a forced-air oven at 60 °C and weighed. Floating litter was decanted into a separate pan, dried, and weighed. Aggregate mean weight diameter (MWD) was calculated as an indicator of aggregate stability according to Van Bavel (1950). Very few large macroaggregates were present, so they were combined with small macroaggregates for subsequent sand correction and C analysis. Concentration of C of each size fraction was measured following similar methods as the bulk soil, described above.

A sand correction was performed on both the macroaggregate and microaggregate fractions to compare sand-free weights and C content between soils with different sand contents. Briefly, 5 g subsamples were mixed with 5% sodium hexametaphosphate and shaken to disperse aggregates. This solution was then passed through 53 μm and 250 μm sieves for microaggregate and macroaggregate fractions, respectively. Sand that remained on top of the sieve was dried and weighed. Sand-free C content of the aggregate fractions was calculated as:

Sand-free %C = % C × (1 − proportion of sand)$^{-1}$

Table 1

Soil properties and management histories of study sites. Means are reported for each variable, with the range of values presented below each mean in parentheses. Values for annualized N fertilizer use and soil C:N represent means ± standard error. Soils were sampled to 20-cm depth with the exception of values for bulk density and soil C:N, which are for the 0–10 cm depth. Letters represent significant differences between cropping systems (α = 0.05). Annualized N fertilizer use is the total amount of N fertilizer applied over the years 2010–2014 divided by 5. WF = wheat-fallow; MID = rotations with fallow every 3 or 4 years; CON = continuous rotations; 30-yr CRP = Conservation Reserve Program shortgrass prairie strips restored 30 years ago (n = 6).

Cropping system	# of Fields	Clay (%)	Silt (%)	Sand (%)	pH	Years no-till	Years in rotation	N fertilizer (kg N ha^{-1} yr^{-1})	Bulk Density (g cm^{-3})	Soil C:N
WF	27	22 (10–31)	39 (19–50)	41 (22–71)	7.4 (6.3–8.5)	20 (0–30)	23 (10–50)	31 ± 1.0a	1.0 (0.8–1.3)	8.7 ± 0.1b
MID	37	21 (8–36)	36 (15–60)	43 (22–76)	7.3 (6.3–8.3)	19 (1–30)	19 (3–30)	45 ± 1.6a	1.0 (0.8–1.2)	8.9 ± 0.1ab
CON	26	22 (8–40)	38 (17–53)	40 (14–75)	7.4 (6.3–8.3)	22 (4–30)	21 (5–30)	34 ± 1.4a	1.0 (0.8–1.2)	9.2 ± 0.1a
30–yr CRP	6	18 (8–25)	33 (21–46)	49 (29–71)	7.7 (7.2–8.2)	30	30	NA	0.9 (0.8–1.0)	10.3 ± 0.2

2.5. Phospholipid fatty acids (PLFA)

PLFA analyses were conducted on subsamples of the soils used to measure aggregation. Immediately upon passing through the 8 mm sieve, soils were further sieved to 2 mm and frozen at −20 °C within two days of sampling before being freeze-dried. PLFAs were extracted and separated at Ward Labs (Kearney, NE) as described in Hamel et al. (2006). Briefly, 2 g of lyophilized soil (dry weight equivalent) was extracted in 9.5 ml mixture of dichloromethane (DMC)/methanol/citrate buffer (1:2:0.8 v/v) for 1 h at 240 rpm. Then, 2.5 ml of DMC and 10 ml of a saturated KCl solution were added to each tube, shaken for 5 min, and centrifuged to separate the organic fraction. Soil lipid extracts were separated in silica gel columns, transmethylated, and PLFAs were quantified by gas chromatography on an Agilent 7890A GC. The fatty acid methyl ester 18:2ω6c was used to represent fungal biomass, and 10:0 2OH, 14:0 iso, 15:0 iso, 15:0 anteiso, 16:0 iso, 16:1ω7c, 17:0 iso, 17:0 anteiso, 17:0 cyclo, and 18:1ω7c were used to represent bacterial biomass (Frostegård and Bååth, 1996). Only bacterial and fungal PLFAs (65 total biomarkers) were added to represent microbial biomass (polyunsaturated and PLFA biomarkers longer than 20C chains were excluded from the analysis).

2.6. Statistical analysis

The relationships between cropping system intensity and SOC at 10 cm and 20 cm, aggregate MWD and C content, and microbial PLFA were tested using multiple linear regression. Models were selected using backwards selection with cropping system intensity as a categorical variable, and all management factors (# years in no-till, # years in rotation, and fertilizer use) and environmental factors (PET, % clay, pH, and slope) until all remaining terms were significant (α = 0.05). To account for environmental and management factors as covariates, least-squared means for each level of cropping system intensity were generated and tested for significant pairwise comparisons. Additionally, the proportion of variance explained by each of the predictors was estimated by dividing the sum of squares for each predictor by the total sum of squares. The relationships between aggregation and SOC, and between fungal biomass and macroaggregation were tested using linear regressions. Differences between C concentrations and C:N ratios of aggregate size classes were tested for significance using ANOVA, and pairwise comparisons were made using a Tukey post hoc analysis. P-values less than 0.05 were considered significant. We used R for all data analyses (R Team, 2013), and multiple linear regressions were generated and tested for significance using the packages lme4 (Bates et al., 2014), lsmeans (Lenth and Hervé, 2015), and lmerTest (Kuznetsova et al., 2015). Due to the small sample size, CRP fields were excluded from statistical analyses and are presented in figures for the purpose of a relative comparison only.

We used structural equation modeling (SEM) to test the fit of our hypothesized model (Fig. 1). SEM tests whether experimental data fit a proposed model using a covariance matrix (Kline, 2015). A non-

significant (p > 0.05) Chi-square test indicates that the model fits the data (Grace et al., 2010). SEM calculates path coefficients that represent the strength and directionality (positive or negative) of relationships between variables, and partitions variance when a response variable is connected by two or more explanatory variables. Because of this variance partitioning, removal of a path between two variables can impact path coefficients between other variables. A positive path coefficient for MID or CON reflects a positive effect of mid-intensity or continuous rotations relative to WF, respectively.

We began with the hypothesized model but found that it did not fit the data (Chi-square p-value < 0.001). We refined the model by adding significant paths (α = 0.05), identified by visualizing relationships between residuals of previously unconnected variables. We also removed insignificant paths. We compared the models that significantly fit the data using Akaike information criterion. The final model (Fig. 8) was significant (Chi-square p-value > 0.05) and had a lower AIC than the others we compared it to. Structural equation models were created and tested using the lavaan package in R (Rosseel, 2011).

3. Results

Intensified cropping systems had higher SOC, aggregation, and fungal and total microbial biomass, and these trends were robust amidst variability in environmental and management conditions.

3.1. SOC

We observed greater SOC concentrations in CON relative to MID and WF rotations at both the 0–10 and 0–20 cm depths (Fig. 3). Cropping system intensity (p = 0.02), PET (p < 0.001), % clay
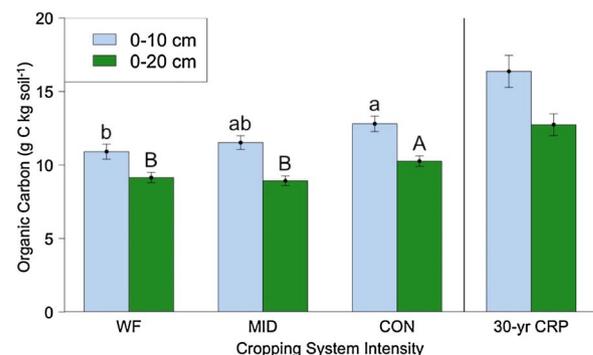

Fig. 3. Cropping system intensity effects on SOC concentration in the bulk soil. Bar heights and error bars represent model generated least-squared means ± standard error. Significant covariates in models at both depths were % clay, PET, and slope position. Lower case letters represent significant differences between treatments at the 0–10 cm depth (p < 0.05), and upper case letters represent significant differences between treatments at the 0–20 cm depth (p < 0.05). WF = wheat-fallow (n = 27); MID = rotations with fallow every 3 or 4 years (n = 37); CON = continuous rotations (n = 26); 30-yr CRP = Conservation Reserve Program shortgrass prairie strips restored 30 years ago (n = 6).

(p < 0.001), and slope position (p < 0.001) explained 54% of the variability in SOC at the 0–10 cm depth. Similar to the shallow depth, cropping system intensity (p < 0.01), PET (p < 0.001), % clay (p < 0.001), and slope position (p < 0.001) explained 54% of the variability in SOC at the 0–20 cm depth. After accounting for PET, % clay, and slope as covariates, SOC concentrations in WF, MID, and CON averaged 1.09%, 1.15%, and 1.28% at 0–10 cm, and 0.92%, 0.89%, and 1.03% at 0–20 cm, respectively (Fig. 3). SOC levels were 17% higher in CON rotations than WF at the 0–10 cm depth, but CON was not significantly different from MID (Fig. 3). However, SOC concentrations in CON rotations were 16% greater than MID, and 12% greater than WF to a depth of 20 cm. SOC concentrations in CON and the less intensified rotations were about 80% and 70% of those in the 30-yr old CRP at both depths, respectively. SOC concentrations in MID rotations were similar to that of WF at both 0–10 cm and 0–20 cm depths (Fig. 3). Cropping system intensity explained 4% of the variability in SOC at 0–10 cm and 0–20 cm depths. Soil% clay content explained 13% and 17%, and PET explained 15% and 14% of the variability in SOC at 0–10 cm and 0–20 cm depths. Slope position explained 12% of the variability in SOC at both depths. There were no significant cropping intensity effects on bulk density (Table 1).

3.2. Aggregate stability and aggregate-associated C

Aggregate MWD and C content increased with cropping system intensity (Figs. 4 and 5). Cropping system intensity (p > 0.01), PET (p = 0.03), and % clay (p < 0.01) explained 30% of the variability in MWD of water-stable aggregates in the 0–10 cm depth. After accounting for PET and % clay as covariates, aggregate MWD in CON rotations was about twice as large as those in WF, and aggregate MWD in MID rotations was intermediate of the two (Fig. 4). Aggregate MWD in the 30-yr CRP was 4 times greater than CON rotations, and 8 times greater than WF (Fig. 4). Cropping system intensity explained 12%, soil clay content explained 9%, and PET explained 6% of the variability in aggregate MWD.

Cropping system intensity was unrelated to the sand-corrected C concentration across size classes. The C concentrations of macro-aggregates were the highest, and C concentrations of the free silt and clay fraction were the lowest, regardless of cropping system intensity (Table 2). There were few differences in C:N ratio between aggregate size classes and ratios varied from 9 to 14 (data not shown), but the C:N ratio of the bulk soil was higher in CON compared to WF rotations (Table 1). Clay% was a significant covariate in the models of C in each aggregate size class, and # years no-till was also a covariate in the
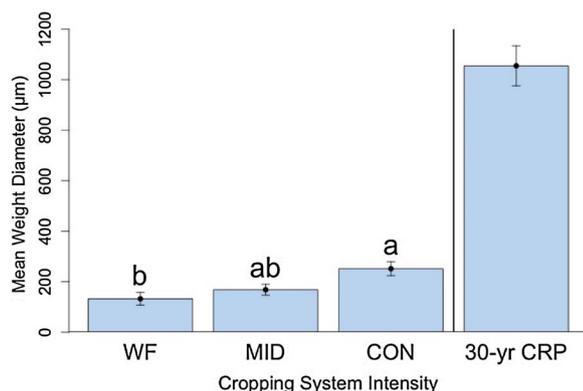
model of free silt and clay C. Total C content of the free silt and clay fraction was lower in MID rotations compared to WF, but was no different than CON rotations (Fig. 5A). There were no significant differences in C content of free microaggregates (Fig. 5B).

3.3. Microbial PLFA

Total PLFA concentration (a proxy for microbial biomass), the fungi:bacteria ratio, and total fungal PLFA concentration increased with cropping system intensity (Fig. 6). There was no relationship between cropping system intensity and bacterial PLFA concentration (data not shown). Cropping system intensity (p = 0.04), % clay (p < 0.01), and pH (p < 0.01) explained 31% of the variability in microbial biomass. Total PLFA in CON rotations was 35% greater than that of WF, and MID rotations were intermediate between the two. Total PLFA in 30-yr CRP was 1.5, 1.8, and 2.1 times greater than CON, MID, and WF rotations, respectively (Fig. 6A). Cropping system intensity explained 7%, soil clay content explained 9%, and pH explained 10% of the variability in total PLFA.

Cropping system intensity was the only significant predictor of the fungi:bacteria ratio (p < 0.01, $R^2 = 0.18$) and total fungal PLFAs (p < 0.01, $R^2 = 0.15$). CON rotations had three times higher fungi:bacteria ratios than WF and MID rotations were intermediate of the two (Fig. 6B). Total fungal PLFA was 3 times greater in CON rotations compared to WF, but was not significantly different from MID rotations (Fig. 6C).

3.4. Relationships between aggregation, fungi, and SOC

Aggregate MWD in dryland cropping systems increased linearly with fungal biomass ($MWD = 119.8 + 4.0 \times fungal\ PLFA$, F = 15.82, p < 0.001, $R^2 = 0.20$, Fig. 7A). SOC increased linearly with aggregate MWD ($SOC = 0.828 + 0.001 \times MWD$, p < 0.001, $R^2 = 0.23$, Fig. 7B).

3.5. Structural equation model

Cropping system intensity had positive direct and indirect effects on fungal biomass, SOC, and aggregate MWD in the final structural equation model (Fig. 8). CON rotations had positive effects on fungal biomass, which was also positively affected by SOC. CON, but not MID rotations, indirectly influenced aggregate MWD as mediated through increases in SOC. The positive effects of CON on fungal biomass also mediated positive effects on SOC and aggregate MWD. Soil clay content positively affected fungal biomass and SOC, and PET negatively affected SOC. Overall, the structural equation model explained 30 and 50% of the variability in aggregate MWD and SOC, respectively.

4. Discussion

We examined the relationship between cropping system intensity and soil properties under no-till management. Our findings suggest that cropping system intensity was positively associated with SOC and aggregation, and that these trends were potentially mediated by greater fungal biomass. The management effects were present despite the inclusion of wide ranges in soil texture, climate, and management history. While the observational nature of this study prevents us from drawing causal links between management and outcomes, detecting a management signal within the noise of variability present when sampling on working farms suggests that continuous cropping is a suitable strategy for increasing SOC, even in higher PET climates.

4.1. Cropping system intensity and SOC

Even with no-till management, summer fallow periods in WF and MID rotations can only store a maximum of 40% of total precipitation to use for the next crop, as weeds and evaporation result in significant
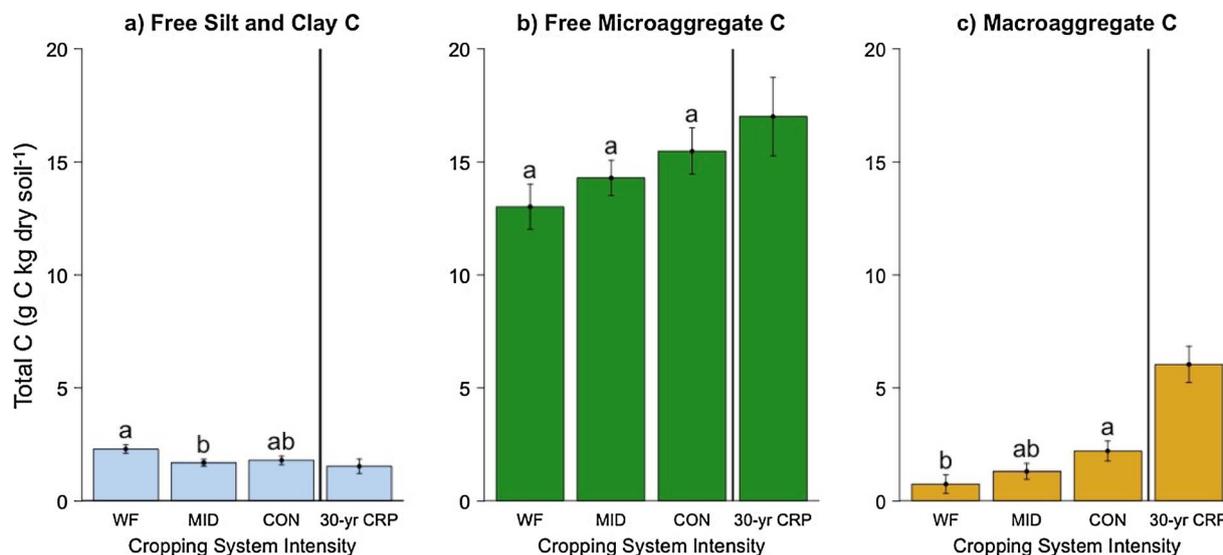

Fig. 4. Cropping system intensity effects on water stable aggregation assessed via mean weight diameter in surface soils (0–10 cm depth). Bar heights and error bars represent model generated least-squared means ± standard error. PET and % clay were significant covariates in the model. Lower case letters represent significant differences between treatments (p < 0.05). WF = wheat-fallow (n = 20); MID = rotations with fallow every 3 or 4 years (n = 29); CON = continuous rotations (n = 18); 30-yr CRP = Conservation Reserve Program shortgrass prairie strips restored 30 years ago (n = 6).

Fig. 5. Total C content of the: a) free silt and clay, b) free microaggregate, and c) macroaggregate fractions for surface soils (0–10 cm depth). Bar heights and error bars represent model-generated least-squared means ± standard error. Lowercase letters represent significant differences in C between cropping system intensities. Clay% was a significant covariate in the models for each of the size classes, and years no-till was also a covariate in the model of the free silt and clay fraction. WF = wheat-fallow (n = 20); MID = rotations with fallow every 3 or 4 years (n = 29); CON = continuous rotations (n = 18); 30-yr CRP = Conservation Reserve Program shortgrass prairie strips restored 30 years ago (n = 6).

water losses during this time (Peterson et al., 1996). Replacing summer fallow periods with crops increases the overall precipitation use efficiency of cropping systems (Farahani et al., 1998a), and as a result, cropping system intensification can potentially double the total amount of crop residue production relative to WF (Peterson and Westfall, 2004). Although we did not measure C input, others have found that SOC concentrations often mirror the gradient of C inputs associated with cropping system intensity and perennial grasslands (Sherrod et al., 2005; Engel et al., 2017). However, we observed that differences in SOC were only observed when summer fallow was completely eliminated, as there were no significant differences in SOC in MID rotations compared to WF (Fig. 3).

The structural equation model offers one possible mechanistic explanation for the observed differences in SOC between the cropping systems. The final model suggested that the effects of PET and clay more strongly influenced SOC than the additional C inputs associated with MID rotations relative to WF, but that the combined direct and indirect effects of CON rotations on SOC were enough to overcome these environmental factors (Fig. 8). Additionally, greater precipitation use efficiency in CON systems may also contribute to more SOC by maintaining soil water content at lower levels throughout the year relative to less intense rotations, thereby reducing organic matter decomposition (Paustian et al., 2000).

Assuming that all fields started at similar levels of SOC at the initiation of the present crop rotation, continuous cropping was associated with an average increase of $0.08\,Mg\,C\,ha^{-1}\,yr^{-1}$ relative to WF at the 0–10 cm depth. This is consistent with prior estimates of C accrual (0.07–$0.16\,Mg\,C\,ha^{-1}\,yr^{-1}$) associated with dryland cropping system intensification (Peterson and Westfall, 2004; Engel et al., 2017). In addition to the host of agronomic benefits associated with greater

SOC, the total C emissions associated with the life cycle of dryland no-till grain production in the U.S. is on average $0.1\,Mg\,C\,ha^{-1}\,yr^{-1}$ (Nelson et al., 2009), and thus the conversion to no-till continuous cropping from no-till wheat-fallow has the potential to offset the C footprint of grain production in these systems through enhanced soil C sequestration. We also observed 0.11% higher SOC concentrations to a depth of 20 cm in CON compared to MID rotations. Relative to less intensified rotations, CON systems more closely mimic natural regional ecosystems by supporting a growing crop every year, and this similarity is evident in SOC and other soil properties that are closer to the levels of the 30-yr CRP in continuously cropped soils. However, we note that levels of SOC in CON soils are still much lower than the grassland soils, suggesting that significant constraints to SOC accumulation exist in annual cropping systems. Overall, SOC was influenced by site factors such as soil texture and PET with smaller relative effects of management. However, the small increases in SOC associated with cropping system intensity likely contributed to the larger relative management system impacts on properties such as aggregation and soil fungi that have functional importance for water and nutrient cycling in these systems.

4.2. Aggregates

Cropping system intensity was associated with higher water-stable aggregation and macroaggregate-associated C (Figs. 4 and 5), and explained more variance in aggregate MWD than either soil clay content or PET. Higher intensity rotations may contribute to aggregation through enhanced above and belowground C inputs, and greater residue cover on the soil surface protects aggregates from the destructive forces of wind and rain (Kong et al., 2005; Mulumba and Lal, 2008).

Table 2
Sand-corrected C concentration (%) of water-stable aggregate and mineral size fractions. Values represent means ± standard error. Letters represent significant differences between size fractions within cropping system intensity. No significant cropping system differences were observed. 30-yr CRP data were not included in the statistical analysis. WF = wheat-fallow (n = 20); MID = rotations with fallow every 3 or 4 years (n = 29); CON = continuous rotations (n = 18); 30-yr CRP = Conservation Reserve Program shortgrass prairie strips restored 30 years ago (n = 6).

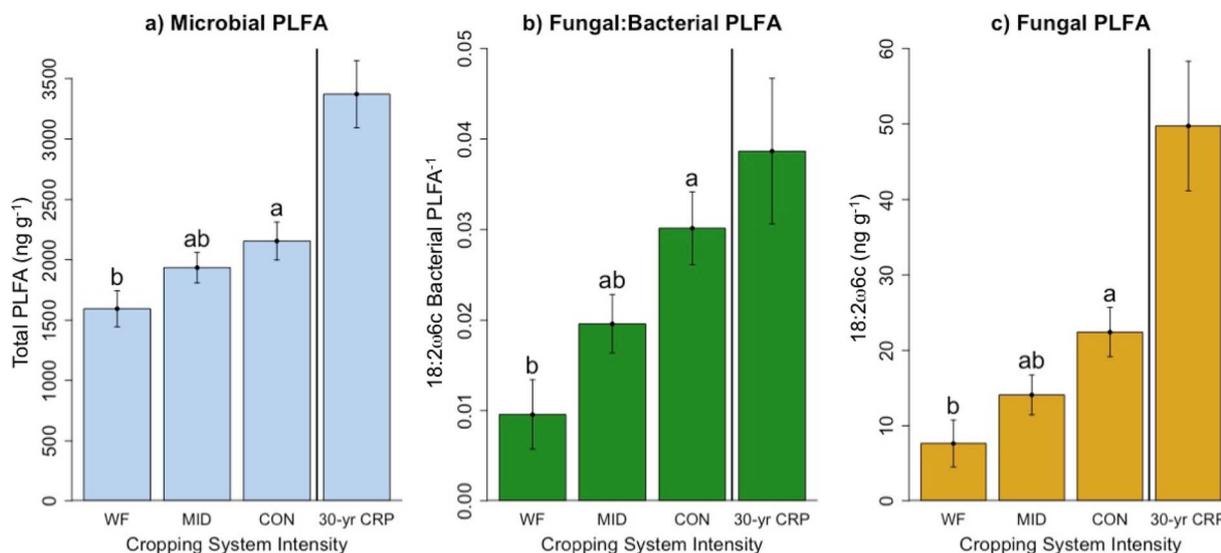|	WF	MID	CON	30-yr CRP
Macroaggregates (> 250 μm)	2.40 ± 0.03a	2.46 ± 0.03a	2.24 ± 0.05a	2.23 ± 0.08
Microaggregates (53–250 μm)	1.65 ± 0.02b	1.86 ± 0.02b	2.12 ± 0.04ab	2.92 ± 0.07
Silt and Clay (0–53 μm)	1.13 ± 0.02c	1.09 ± 0.01c	1.17 ± 0.02b	0.97 ± 0.02

Fig. 6. Cropping system intensity effects on a) Microbial PLFA, b) Fungal:bacterial PLFA ratio, and c) Fungal PLFA. Bar heights and error bars represent model generated least-squared means ± standard error. Clay% and pH were significant covariates in the model of total PLFA abundance. Lower case letters represent significant differences between treatments ($p < 0.05$). WF = wheat-fallow (n = 20); MID = rotations with fallow every 3 or 4 years (n = 29); CON = continuous rotations (n = 18); 30-yr CRP = Conservation Reserve Program shortgrass prairie strips restored 30 years ago (n = 6).

Annually cropped semi-arid agroecosystems are particularly susceptible to erosion due to constraints on plant production and residue cover, and the greater amount of aggregation in the 30-yr CRP relative to the cropping systems reflects the contributions of perennial roots and constant plant cover to enhancing soil structure.

We predicted a co-increase in both SOC and aggregate MWD in intensified rotations as the greater level of C inputs become physically protected in aggregates, which would contribute to the accumulation of SOC (Fig. 1). Additionally, as SOC can also enhance soil aggregation, we predicted and observed a similar positive effect of SOC on aggregate MWD (Tisdall and Oades, 1982; Figs. 1 and 8). We were surprised to find that removing the direct effect of aggregate MWD on SOC improved the fit of the structural equation model, but we found that SOC

directly and indirectly increases MWD as mediated through soil fungi, as is discussed in Section 4.3 (Fig. 8). A more sensitive indicator of aggregate-associated C may have revealed a more direct influence of aggregation on SOC in the structural equation model. Others have suggested that increases in microaggregates within macroaggregates are responsible for a majority of the difference in SOC between differently managed cropping systems (Six and Paustian, 2014). We did not isolate microaggregates within macroaggregates here due to low overall aggregation across our study sites.

We note that analyzing the relationship between SOC and aggregate MWD independent of environmental and management factors revealed a positive relationship, as expected (Fig. 7B). This is in agreement with others who have examined the relationship between SOC and aggregate
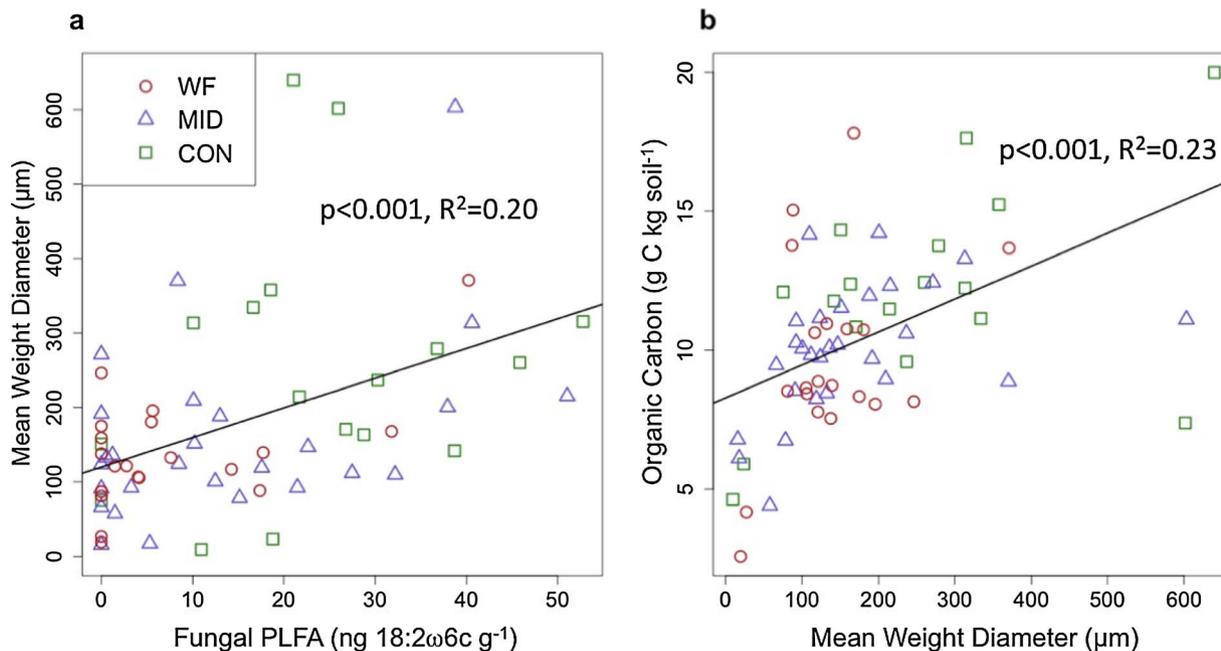

Fig. 7. a) Relationship between fungal biomass and MWD of water-stable aggregates. MWD = 119.78 + 3.99*fungal PLFA ($p < 0.001$, $R^2 = 0.20$), and b) relationship between MWD of water-stable aggregates and SOC concentrations to 10 cm depth. SOC = 8.28 + 0.01*MWD ($p < 0.001$, $R^2 = 0.23$). WF = wheat-fallow (n = 20); MID = rotations with fallow every 3 or 4 years (n = 29); CON = continuous rotations (n = 18); 30-yr CRP = Conservation Reserve Program shortgrass prairie strips restored 30 years ago (n = 6).
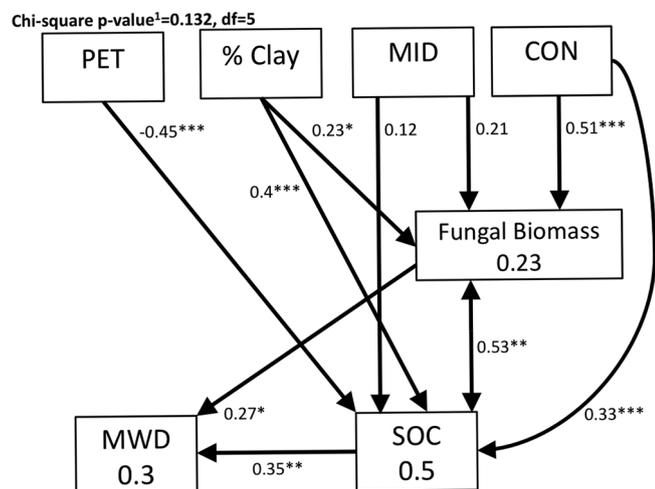
Chi-square p-value[1]=0.132, df=5

Fig. 8. Structural equation model. PET = Potential evapotranspiration, MID = rotations with fallow every 3 or 4 years, CON = continuous rotations, Fungal Biomass = Abundance of the fungal PLFA 18:2ω6c, MWD = Mean weight diameter of water-stable aggregates, SOC = Soil organic C concentration. Magnitudes of MID and CON effects are relative to WF as the intercept. Numbers in boxes represent R^2 values and numbers along the arrows are standardized path coefficients, which represent the magnitude of the effect. Significance of each pathway is denoted by ***p < 0.001, **p < 0.01, *p < 0.05, p < 0.1. [1]Chi-square test P > 0.05 indicates that the model and data structure are not significantly different.

MWD, highlighting aggregation as an important C stabilization mechanism in dryland soils (Kemper and Koch, 1966; Shaver et al., 2003). Greater proportions of C-rich macroaggregates in CON rotations contributed to higher SOC concentrations in the bulk soil relative to WF (Figs. 3, 5C, Table 2). The C:N ratio was similar across aggregate size classes and mineral fractions, and generally ranged from 9 to 14. These low values relative to fresh inputs suggest that much of the occluded C in macroaggregates is likely derived from more highly processed C (Elliott, 1986; Jastrow, 1996). Plant C inputs can become stabilized as microbial byproducts of decomposition and tightly bind to soil mineral surfaces (Cotrufo et al., 2013). An accumulation of this microbially-processed C in macroaggregates (and possibly in microaggregates within macroaggregates) is potentially responsible for much of the observed difference in SOC between different cropping systems.

4.3. Microbial communities

We found that both fungal biomass and fungi:bacteria ratio increased with cropping system intensity (Fig. 6), lending support for the interpretation of fungi:bacteria as a soil property that influences C dynamics and is sensitive to management (De Vries et al., 2012; Waring et al., 2013). Rotation intensity likely influenced the fungal community through changes in the soil C:N ratio, and overall greater SOC (Waring et al., 2013; Malik et al., 2016). Past studies have drawn links between greater N fertilizer use, lower soil C:N, and lower fungal dominance in soils (Bardgett and McAlister, 1999; Waring et al., 2013). Total N fertilizer use from 2010 to 2014 was no greater in intensified systems (Table 1) despite achieving greater total crop production compared to WF (Rosenzweig et al., in review), and this likely contributed to the observed increase in soil C:N with cropping system intensity (Table 1). Thus, it is possible that lower nutrient availability in intensified systems may be contributing to the observed increase in fungi:bacteria (Strickland and Rousk, 2010). Additionally, intensification is most often achieved through growing a greater diversity of crops, and crop diversity, independent of intensity, can enhance microbial biomass, fungal dominance, and ultimately SOC (Lange et al., 2014; McDaniel et al., 2014). We did not observe a relationship between pH and fungi:bacteria, possibly due to a lack of variability in pH across sites (Table 1). We also found little influence of the number of years in no-till

on microbial communities, possibly because most sites had at least 5 years of no-till management, which is long enough to exert a considerable effect relative to conventional tillage (Rosenzweig et al., 2016).

The influence of cropping system intensity on SOC and aggregation may be attributed to the role of fungi in mediating the processes that control these properties. The relationship between SOC and fungi is circular, as fungi contribute to C sequestration, and soils with more SOC also tend have more fungi (Strickland and Rousk, 2010). Our findings from the structural equation model suggest that SOC and fungi positively influenced each other, supporting the idea of a positive feedback loop (Fig. 8). While the link between fungi, C use efficiency, and SOC remains controversial (Strickland and Rousk, 2010), it is generally accepted that fungi contribute to SOC accrual by enhancing the physical protection of organic matter in aggregates (Six et al., 2006). The positive linear relationship between fungal biomass and aggregate MWD corroborates past work examining the link between them (Fig. 7A). Aggregation also has important feedbacks with overall agroecosystem performance in semi-arid climates, as aggregates create pore space and improve the soil's ability to reduce surface runoff (and erosion) and capture water (Shaver et al., 2003), which is the most limiting factor to crop production in dryland systems.

4.4. Conclusions

While WF remains one of the most common cropping systems in the semi-arid High Plains, this and other semi-arid regions around the world are undergoing a profound transition to intensified dryland cropping systems, and thus it is critical to understand the implications of this transformation (Hansen et al., 2012; Maaz et al., 2018). We found different levels of SOC, aggregation, and fungal biomass between different levels of cropping system intensity and tested hypothesized links between them. Overall, our results suggest that cropping system intensity, independent of tillage, increases SOC both directly, through greater C inputs to soil, and indirectly, through effects on microbial communities and aggregation. We observed these relationships to be remarkably robust across a wide climatic gradient, and amidst variability in soil texture and management history. These results corroborate others who have found greater aggregation and SOC in more intensely cropped systems, but also shed new light on the central role that fungi may play in C storage in dryland agroecosystems. We found that the elimination of summer fallow in semi-arid cropping systems has the potential to offset the C emissions associated with no-till grain production, and provide gains in SOC that will contribute to the long-term success of dryland agriculture.

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