Ecological Indicators 142 (2022) 109280

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

Links of microbial and vegetation communities with soil physical and chemical factors for a broad range of management of tallgrass prairie

Richard Teague [a,b,1], Steve Dowhower [a,*]

[a] Texas A&M AgriLife Research Center, Vernon, TX, USA
[b] Department of Rangeland, Wildlife, and Fisheries Management, Texas A&M University, College Station, TX 77843, USA

ARTICLE INFO

Keywords:
Rotation grazing
Heavy grazing
Exclosures
Tree subcanopy
Fire
Hay

ABSTRACT

Identifying ecological indicators and management factors that influence sustainability and resilience, both ecologically and economically, is key to restoring grassland landscapes' ecological function. We examine soil and vegetation responses to different combinations of adaptive multi-paddock grazing (AMP) managed to improve soil and ecological function as the foundation to improve the provision of ecosystem services and economic benefits, relative to heavy continuous grazing (HCG) and moderate continuous grazing (MCG).We used multi-dimensional scaling (MDS) and analysis of similarities (ANOSIM) to indicate associations among soil, soil biota and vegetation parameters to indicate associations in response to the different grazing management strategies. AMP grazing improved total herbaceous biomass, C_4 tallgrasses, native perennial summer growing forbs, and vegetation cover while decreasing bare ground cover and less productive or invasive herbaceous species. AMP also had higher biomass of total soil microbes, actinomycetes, and gram-positive and gram-negative bacteria associated with improved soil aggregation and nutrient cycling than HCG, with MCG having intermediate responses. Arbuscular mycorrhizal fungi crucial for enhanced water and nutrient acquisition by plants were higher with AMP and were lower with HCG, with MCG intermediate between the two. AMP also outperformed HCG and usually MCG in the critical soil physical elements such as soil aggregation fostering improved ecological function. These are substantive improvements, achieved despite AMP having double the stocking rate of MCG. These positive outcomes were generally not compromised with the BURN and HAY treatments as both were managed with AMP grazing. The exception was HAY, which showed increased soil penetration resistance compared to AMP but less than with HCG or MCG. AMP grazing also compared favorably with the grazing Exclosures for most parameters measured. The presence of low densities of trees had predominantly positive results relative to treeless AMP and MCG, particular for soil temperature, soil organic matter and cation exchange capacity. These findings provide evidence that AMP grazing is a powerful management strategy to positively alter plant composition and soil physical, chemical, and microbial properties relative to season-long continuous grazing to enhance the provision of ecosystem services and economic benefits in Southern Tallgrass prairie.

1. Introduction

Rangelands are seminatural ecosystems in which natural plant communities support domestic livestock or wildlife pastoral enterprises to support people living in them. They are diverse ecosystems covering about 40 % of the globe's terrestrial area and are not suitable for agriculture or forestry because of climatic, topographic, or edaphic limitations. Maintaining or enhancing the productive capacity and resilience of rangeland ecosystems is critical for rural and urban populations who live in them (Millennium Ecosystem Assessment, 2005; Walker et al., 2002). These ecosystems have evolved since the late Mesozoic era under periodic grazing by large ungulates, fire and fluctuating climatic regimes to be highly productive, biodiverse and resilient communities (Frank et al., 1998).

Land-use changes after the European settlement of the Great Plains contributed to the most substantial decline of native species, biodiversity, and ecological function of any significant ecosystem in North America (Risser et al., 1981). Tallgrass prairie is one of the most endangered ecosystems in North America, where 82 % has been lost (Risser et al., 1981; Diggs et al., 1999; Samson and Knopf, 1994). Fire has been

* Corresponding author at: Texas A&M AgriLife Research, P.O. Box 1658, Vernon, TX 76385-1658, USA.
E-mail address: sdowhower@ag.tamu.edu (S. Dowhower).
[1] Present address: 4600 Cottonwood Lane, Vernon, TX 76384, USA.

https://doi.org/10.1016/j.ecolind.2022.109280
Received 21 January 2022; Received in revised form 1 August 2022; Accepted 3 August 2022

virtually eliminated from most prairies, and much of the original biodiverse prairie grasslands have been replaced by row crop production or introduced forage grasses. The remaining acreage is mostly degraded ecologically due to neglect and mismanagement of livestock.

Native tallgrass prairie is the most productive native grass ecosystem in North America and one of the most biodiverse, providing essential habitat for many of our most endangered plant, animal, bird and insect species (Risser et al., 1981; Diamond and Smeins, 1993). It is characterized by the dominance of the native tallgrass grasses big bluestem (*Andropogon gerardii)*, little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) and when these species dominate, the prairie is at its most diverse and productive. These and associated plants are the most productive, palatable, and important forage grasses found in tallgrass prairie, and they contribute significantly to ecosystem biodiversity, function, and wildlife habitat (Wallace and Dyer, 1995; Diggs et al., 1999).

Grassland and savanna ecosystems evolved synergistic interactions among soil fungi and microbes, plants, and various associated animal life forms. These interactions resulted in the sequestration of large amounts of atmospheric carbon into stable soil carbon pools. As carbon sequestration rates exceeded oxidation rates in these evolved ecosystems, the high levels of soil organic carbon enhanced the productivity, resilience, hydrology and carbon capture capacity of these soils (Frank and Groffman, 1998; Altieri, 1999; Van der Heijden et al., 2008; de Vries et al., 2012; Morriën et al., 2017). The high carbon soils that developed in these perennial grassland ecosystems have high infiltration rates, water holding capacity, fertility and biodiversity that enhances primary production, and extends the amount and longevity of green photosynthesizing leaves to elevate evapotranspiration providing terrestrial hydrological cooling that governs 95 % of the earth's natural cooling (Ferguson and Veizer, 2007). While these integrated biophysical systems resulted in enhanced soil organic carbon, human agricultural activities, including repeated tilling, overgrazing, and burning have led to the reversal of the soil carbon dynamic and the depletion of accumulated soil carbon.

Efforts at restoring biodiversity and ecological function on degraded land often involve cessation of all agricultural and grazing practices to allow succession processes to restore late-succession soil microbial and plant composition and function (Levine et al., 2011; Morriën et al., 2017). However, disturbance ecology theory postulates that periodic disturbance is integral to the persistence of functional prairie ecosystems and requisite species diversity (Pickett and White, 1985). Soil microbial and associated plant communities in grazing ecosystems developed as complex, dynamic communities comprising herbaceous plants, soil biota, the grazers, and their predators (Frank et al., 1998; Retallack, 2013). Periodic defoliation via intermittent grazing, fire, or mowing is necessary to ensure essential ecosystem functions including energy capture via photosynthesis, maintenance of hydrological function, and nutrient cycling facilitated by high biodiversity among soil, plant, grazing animals, and insects essential for ecosystem function. Without these coevolved elements, natural succession processes proceed incompletely and slowly.

Changes in these ecological functions and plant species alter the composition of soil biota and function, providing feedback that can be positive or negative (Coleman and Crossley, 1996). Decomposition of organic matter, which provides nutrients for plants, is performed primarily by bacteria and fungi (De Vries et al., 2006). Plant and soil biota associations provide major structuring forces in plant communities and are important drivers of ecosystem function, composition and productivity (Bardgett, 2005). These interactions include: (1) soil microbe alteration of the physical structure of the soil affecting habitat for other soil fauna and microbes and influencing rainfall infiltration and the movement of water and nutrients through the soil; (2) fungal associations with plant roots enhancing nutrient and moisture availability for plants; (3) microbial breakdown of organic matter making nutrients available for plants; and (4) plant root exudates providing nutrition for microbes.

Mid and tall grass communities thrive and remain competitive under infrequent moderate defoliation but deteriorate in the absence of disturbance of infrequent grazing, fire or mowing followed by adequate recovery (Vogl, 1974; Rice and Parenti, 1978; Knapp, 1985; Seastedt, 1995; Seastedt and Knapp, 1993; Blair, 1997; Dyer et al., 1993; Turner et al., 1993; Teague et al., 2011). The absence of disturbance results in a decline in productivity by as much as 83 % due to reduction of light capture by photosynthesis, soil surface water infiltration and nutrient cycling and acquisition (Curtis and Partch, 1950; Weaver and Roland, 1952; Engle et al., 1987; Smith and Stubbendieck, 1990). This is readily reversed using appropriately managed intermittent pulse grazing followed by adequate post-grazing recovery (Teague et al., 2013) and leaving sufficient plant residue and litter cover to facilitate enhanced soil microbial function that is the foundation of ecosystem function (Thurow, 1991; Bardgett, 2005; De Vries et al., 2012).

In the absence of restorative grazing management, burning or mowing are possible management alternatives (Kelting, 1957; Penfound and Kelting, 1950; Penfound, 1964). In tallgrass prairie a critical factor that can determine productivity decline in the absence of fire is low soil temperature early in the growing season (Rice and Parenti, 1978). In the case of burning and mowing, it is crucial to remove sufficient mown material to avoid thatch build-up that causes soil temperatures to remain too low in early spring, delaying growth, and shading from excessive dead plant material, that reduce productivity for that year. The dominant high seral prairie grasses have the C_4 photosynthetic pathway, an adaptation to hot conditions and operate optimally at relatively high temperatures, so the earlier soil temperatures are elevated, the sooner growth begins (Osborne and Beerling, 2006). Also, fire alone has been shown to benefit big bluestem more than litter removal and the addition of ash associated with burning (Petersen, 1994).

Excessive litter covering the soil and plant standing cover both negatively influence the recruitment of big bluestem and other tall grasses, but neither have an impact on the growth of established tall grass plants (Foster and Gross, 1997). Burning in late winter increases soil temperatures and lowers soil moisture relative to unburnt areas, and big bluestem is a superior competitor under these conditions (Knapp, 1985). Removal of spring standing biomass favors C_4 grasses but raking to remove litter in the spring had a less positive effect than burning for these plants (Hulbert, 1969; 1988; Old, 1969). The benefits to C_4 grasses from periodic and timely pulsed grazing and appropriate burning increase sunlight penetration, which increases light availability and warms the soil for the early season growing shoots of the grasses (Svejcar, 1990). Fires early in the growing season extend the period of active growth for C_4 plants (Kucera and Ehrenreich, 1962). Also, since many undesirable grass species have C_3 photosynthesis and emerge early in the growing season, prescribed burns in the spring can be used to control them (Ehrenreich and Aikman, 1963).

Fire removes aboveground biomass, but it may not promote plant diversity when it is the only removal process in a prairie (Collins et al., 1998). Fires damage many heat-sensitive seeds (Whelan, 1995) and, when performed in the spring, harm plants that emerge before the fire (Briggs and Knapp, 2001). In the absence of large grazers, which prefer grass forage, burning can lead to prairies composed mainly of C_4 grasses (Collins et al., 1998) that grow more rapidly than C_3 herbaceous plants in hot, open conditions after a recent burn (Knapp and Medino, 1999). Overabundance of C_4 grasses is common in many ungrazed, restored prairies even several decades after restoration (Kindsher and Tieszen, 1998). A lack of forbs in restorations is problematic because forbs are the most diverse plant group present in the prairie (Freeman, 1998), and they supply food and habitat for many other organisms. Thus, prescribed spring burning is useful for controlling many unwanted species and favors many prairie endemics (Ehrenreich and Aikmann, 1963; Towne and Knapp,1996).

In unburnt tallgrass prairie, during the growing season, bison and cattle select patches with low forb cover dominated by big bluestem

(Vinton et al., 1993). The grass patches grazed by bison or cattle early in the season are returned to throughout the rest of the season while those not grazed early are avoided the rest of the season. This decreases tiller productivity and survival, and rooting depth on the selected patches in subsequent seasons (Weaver, 1954; Vinton and Hartnett, 1992; Teague et al., 2013). To ensure the sustainability and resilience of grazed ecosystems, so they continue to provide essential ecosystem services, native prairie ecosystems need to be managed using grazing management protocols that avoid overstocking and overgrazing (Teague, 2018). This is achieved first, by ensuring that livestock numbers do not exceed the amount of forage available while retaining enough ungrazed herbaceous material to ensure maintenance of essential soil microbial and ecosystem functions. Second, it is necessary to graze for short periods followed by provision of adequate recovery, and distribution of livestock impacts over the entire management unit. This has been achieved by farmers around the world using adaptive multi-paddock (AMP) grazing following holistic planned grazing protocols (Provenza et al., 2013; Savory and Butterfield, 2016; Teague et al., 2015; Teague and Kreuter, 2020).

In contrast, grazing livestock in large paddocks under continuous grazing without recovery after grazing or burning results in repetitive use of preferred plants and patches. Even at low stocking rates, these patches persist and expand, progressively degrading the landscape (Fuls, 1992; O'Connor, 1992; Teague et al., 2004). Consequently, an appropriate stocking rate alone does not avoid rangeland degradation (Norton, 1998; 2003; Barnes et al., 2008; Teague et al., 2013). To facilitate recovery of degraded ecosystem function, biodiversity, and productivity we need to restore high seral herbaceous species composition and essential ecological and watershed functions on commercial ranches.

This study examines what factors and management will cause big bluestem and associated desirable tallgrass plants to be restored to their former abundance in southern tallgrass prairie ecosystems. We hypothesize that appropriately managed adaptive multi-paddock grazing (AMP), alone or with the use of prescribed fire or mowing, will achieve changes in plant composition towards dominance by high seral herbaceous species and result in improved soil physical, chemical, and microbial properties and biodiversity relative to season-long continuous grazing.

2. Methods

2.1. Study site

The study was conducted in North Central Texas in Cooke County south of Muenster, Texas (31.9686° N, 99.9018° W). The climate is continental with an average 220 frost-free growing days. Mean annual precipitation is 820 mm with a bimodal distribution peaking in May-June and September. Mean annual temperature is 18 °C. Elevation ranges from 300 m to 330 m. The vegetation in the area is dominated by rolling tallgrass prairie rangeland on the upland and midslope catenal positions (71 %) with native mixed oak forest along the larger watercourses (14 %), with agricultural land (10 %), and other land uses (5 %) making up the balance. The uplands and midslopes make up the major portion of the landscape and are dominated by the original native vegetation as they are too shallow for agriculture and generally have not been previously tilled. Consequently, they are still used primarily for livestock grazing and recreational hunting (Diggs et al., 1999).

On the experimental sites the vegetation was native tallgrass prairie that had not previously been tilled or fertilized. Native tall prairie grasses dominated the upland and midslope catenal positions and are comprised of C_4 tallgrasses *Schizachyrium scoparius*, *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum* and mid-grasses *Bouteloua curtipendula* and *Sporobolus compositus* in association with the perennial forbs *Ambrosia psilostachya*, *Aster ericoides* and *Gutierrezia texana*. Heavy continuous grazing pressure has resulted in a switch to the grasses *Buchloe dactyloides*, *Bothriochloa laguroides*, *Bouteloua hirsuta*, *Nassella leucotricha* and annual forbs, particularly *Gutierrezia dracunculoides*, are more common (Dyksterhuis, 1946; Dyksterhuis, 1948; Diggs et al., 1999).

Soils of the uplands and midslopes are predominantly clay-loams derived from limestone and have high permeability and relatively high soil organic matter (Teague et al., 2011). The upland catenal positions are of the shallow Aledo clay-loam series, and the midslope catenal positions that made up the larger portion of the landscape are dominated by deeper clay-loam soils of the Sanger clay series (USDA, 2009). All sites sampled on all three ranches were of the Sanger clay series. The grazing management history on each of the ranches involved in the study has been the same for 15 years prior to the beginning of this study in 2008. Consequently, the soil and plant biology had likely adjusted to the very different grazing protocols being studied as indicated by Teague et al. (2011) working on these neighboring ranches.

2.2. Experimental design and treatments

The study was conducted on three neighboring ranches in Cooke County, Texas. The ranches had been managed using: (1) heavily stocked continuous grazing (HCG) on the Mitchell ranch; (2) moderately stocked continuous grazing (MCG) on the Danglemayr ranch; and (3) adaptive multi-paddock rotational grazing (AMP) on the Pittman ranch. All three ranches were managed for commercial objectives and represented the range in ranch sizes for the area described in detail in Park et al., (2017). The management prior to and during the study at each location was:

1. The HCG ranch was the control and represented the management prevalent on most ranches in the area. It was stocked for most of each year with stocker steers at a high stocking rate of approximately 27 AU 100 ha^{-1} $year^{-1}$. Numbers were rarely adjusted from year to year. Replicates were from 3 locations.
2. The MCG ranch was stocked year-round with beef cows and calves at NRCS recommended levels to average 14 AU 100 ha^{-1} $year^{-1}$. Numbers were adjusted in drought years to assure forage on offer always exceeded the requirements of the livestock and left enough residual to support basic ecological function. Replicates were from 3 pastures
3. The AMP ranch was stocked year-round with replacement beef heifers using holistic planned grazing protocols (Savory and Butterfield, 2016). Grazing was for periods of 1 day followed by recovery periods of 30 to 45 days in fast growth periods and 80 to 100 days in slow growth periods. Grazing and recovery periods were adjusted according to existing conditions to achieve the most favorable outcomes for forage plants and animal nutrition. At any one time the entire number of cattle grazed in one of 41 paddocks before moving to the next to allow enough recovery. Stocking rates averaged 27 AU 100 ha^{-1} $year^{-1}$ and were adjusted when necessary to make sure forage on offer always exceeded the requirements of the livestock leaving enough residual to cover the soil from insolation and desiccation to facilitate optimal soil microbial function. Replicates were 3 for additional treatments within AMP grazing but were 4 for AMP in 6 paddocks.

To determine what grazing, resting and fire management will increase big bluestem and other dominant tallgrasses of high seral prairie communities, dominance in tallgrass prairie implemented the treatments listed below.

1. HCG on a neighbor ranch.
2. MCG on a neighbor ranch.

3.1 AMP grazing as practiced by Dixon ranches, with 1- to 2-day grazing periods followed by ± 40-day recovery-rest in the warm season growing months and approximately 80 days during periods of slow growth.

3.2 Longer periods of recovery between grazing (2 × Recovery) with moderate pulse grazing with a ± 80-day recovery-rest after warm season grazing (cf. 3a above) and a ± 100-day recovery-rest during periods of slow growth.
3.3 Late winter fires conducted in 2010 and 2013 with moderate infrequent pulse grazing as per 3a above.
3.4 Late summer fire conducted in 2009 and 2012 then graze as per 3a above, when recovered.
3.5 Ultra-high-density graze in late winter conducted in 2009, 2011, and 2013 then graze as per 3a above, when recovered.
3.6 Ultra-high-density graze in summer conducted in 2009, 2010, and 2012 then graze as per 3a above, when recovered.
3.7 Cutting for hay once at the end of summer with removal of cut herbage conducted in 2009, 2010, 2012, and 2013.
3.8 Mowing once at the end of summer with cut herbage left in situ conducted in 2009, 2010, 2012, and 2013.

4. Tree understory (TREE) in MCG (2 above, 1 site) and AMP (3a above, 2sites).
5. 5.Grazing excluded (EXCL).

When analyzing the results from these treatments there were no differences in response between late winter fire and summer fire so the data from these two treatments was analyzed together and labelled as BURN (3c and 3d above). Similarly, the ultra-high-density graze in late winter and in summer were analyzed together as AmpH (3e and 3f above) and cutting for hay and mowing were combined as HAY (3 g and 3 h above).

Vegetation was sampled for MCG and AMP with other practices applied within AMP paddocks from 2009 to 2016. EXCL and HCG were sampled from 2011 to 2016. Site availability, sampling effort (time), and cost constrained ability to have balance in sampling. Thus, Soil physical and Soil chemical samples were collected in 2017. Also, imbalance in site numbers was a function of combining similar treatments that had minor, short-term differences (ca. winter burn and summer burn to BURN).

An array of variables over the course of study were collected. Biotic variables were vegetation species biomass, vegetation functional group biomass, species presence/absence, and microbial biomass. The environmental variables were soil/surface physical properties, soil chemical components, and soil temperature. For multivariate comparisons of vegetation in relation to environmental and biotic factors, trees were assigned biomass based on vegetation of the 2 nearest grazed plots (within 50 m) multiplied by 0.2 for warm season herbs and multiplied by 2 for cool season herbs resulting in trees having about 75 %, warm season herbs 18 %, and cool season herbs 8 % of biomass.

Microbes were sampled in 2016 and 2017 but only for HCG, MCG, and AMP for both years. BURN, HAY, EXCL, and TREE were sampled 1 year so multivariate comparisons amongst sampling types were based on adjusted means related to the 3 grazing treatments sampled both years. Soil physical and soil nutrient samples were collected in 2017. Soil temperature sampling was initiated in 2010 and extended to 2016. Temperature averages for 2-months at 8 times of day were compared. For multivariate comparisons of soil temperatures, the unsampled tree was assigned values between the other two tree's soil temperatures.

2.3. *Vegetation measurements*

Herbaceous biomass and species composition, bare ground and litter cover were measured at each 30-m × 30-m experimental site. The sites were divided into rectangular quarters with 5 flag tosses within each quarter determining the 20 × 0.5 m^2 random quadrat locations. Grass and forb weights were estimated with 1 in 10 quadrats harvested and dried to a constant weight to arrive at double sampling biomass dry weights for each quadrat (as described by Dowhower et al., 2001). Visual estimates were made of non-herbaceous vegetation cover of bare ground and litter cover within quadrats as were proportions of grass species and forb species. To simplify interpretation, we analyzed herbaceous biomass by functional group using the following 11 groups: perennial C_4 tallgrasses, perennial old-field C_4 grasses, perennial C_4 midgrasses, perennial C_4 short grasses, annual C_4 grasses, perennial C_3 grasses, annual C_3 grasses, perennial early forbs, perennial late forbs, annual early spring forbs, and annual late forbs that grow and flower through summer and fall.

2.4. *Soil measurements*

To determine treatment effects on soil parameters we measured soil microbial composition and nutrient status. For soil microbial composition, soil samples were collected for living microbial biomass using phospholipid fatty acid (PLFA) analysis at each site with ten randomly located soil cores 16 mm in diameter. They were collected at a depth of 0–10 cm on each treatment plot. Samples were placed in insulated containers with cold packs and shipped over-night to the Ward Laboratory (Ward Laboratories, Inc., Kearney, NE) for PLFA analysis.

At each site referenced above we measured the following soil parameters: bulk density, penetration resistance, soil organic matter and nutrient status to determine the accumulated grazing management effects on the soil. Soil bulk density was measured at 15 subsampling points using 19-mm diameter × 70-mm long soil sampling tubes and gravimetric analysis. Soil penetration resistance was measured at 5 cm, 10 cm and 15 cm depths using an impact penetrometer described by Herrick and Jones (2002), and Herrick et al. (1999).

Soil sampling for organic matter analyses was at two depths (0–15 cm and 15–30 cm) and at 0–15 cm for all other nutrients. Visible organic

Table 1
Vegetation biomass (g/m^{-2}(−|-)) for grazing management treatments averaged for 2011 to 2016 in tallgrass prairie at Muenster, Texas. Sites are 3 for HCG, MCG, and EXCL, 8 for AMP, and 6 sites for AmpH, BURN, and Hay.

Herbaceous group	se range	HCG	MCG	AMP	AmpH	BURN	HAY	EXCL
Total herbage	20–34	242^{d}	364^{bc}	473^{ab}	433^{b}	470^{ab}	452^{b}	534^{a}
Grass	23–40	111^{c}	291^{b}	360^{ab}	301^{b}	335^{ab}	336^{ab}	385^{a}
Forb	16–29	131^{ab}	73^{b}	112^{ab}	132^{a}	135^{a}	116^{ab}	149^{a}
C_4 Tallgrass	30–54	2^{b}	108^{a}	196^{a}	144^{a}	185^{a}	170^{a}	174^{a}
C_4 Old-field grass	26–47	24^{b}	114^{ab}	111^{a}	104^{ab}	99^{ab}	108^{a}	186^{a}
C_4 Midgrass	9–16	29	39	33	30	31	15	9
C_4 Shortgrass	0.5–1	6^{a}	1^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}
C_4 Annual grass	1–2	8^{a}	2^{b}	0^{b}	0^{b}	1^{b}	1^{b}	1^{b}
C_3 Perennial grass	2–4	26^{a}	18^{ab}	12^{bc}	13^{b}	12^{bc}	10^{bc}	4^{c}
C_3 Annual grass	3–4	15^{a}	6^{b}	8^{ab}	6	5^{b}	7^{b}	11^{ab}
Perennial cool forb	1–1	1	1	2	2	2	2	0
Perennial warm forb	13–23	29^{c}	15^{c}	69^{b}	89^{ab}	93^{ab}	73^{ab}	117^{a}
Annual cool forb	1–2	10^{a}	3^{b}	2^{b}	3^{b}	4^{b}	4^{b}	3^{b}
Annual warm forb	8–13	85^{a}	54^{b}	35^{bc}	28^{bc}	31^{bc}	30^{bc}	23^{c}

Same letters within rows indicate no difference between treatments ($p > 0.10$).

matter above mineral earth was carefully removed before taking sample cores. We sampled at 10 randomly located sub-sample points (cores) at each site. These were bulked, homogenized and air-dried. A composite sample for each soil depth was analyzed at Ward Laboratories, Inc., Kearney, NE. Nitrate (NO3 −) and ammonium (NH4 +) according to Kenney and Nelson (1982). Total N (NO3 − and NH4 +) was determined according to McGeehan and Naylor (1988). Soil organic carbon (SOC) was analyzed using the loss on ignition (LOI) described by Combs and Nathan (1998).

Continuous monitoring of temperature (hourly) was made at each site with automatic data loggers. Temperature loggers recorded air temperature at 2 locations and soil temperature at 3 cm depth for each replicate.

2.5. Statistical models

Univariate biological and environmental variables were analyzed with the Mixed model (SAS, 2016) testing the main effect treatment with treatment × site as the error term. Some variables were associated with other class variables *ie.* year, soil depth, and season with time-of-day. These class variables and their interactions were tested with residual error. The 8-diurnal and 6-seasonal periods summarize temperatures well for the grazing treatment interactions, but there was no 3-way interaction ($F = 0.2$, $p = 0.99$). Environmental data was not transformed. Biological data means were presented but probabilities between means are based on square root transformed data.

Multivariate analysis was performed in three manners: ordination using MDS, ANOSIM comparing treatment group's dissimilarity, and correlations of variables to the triangular correlation matrix (non-metric MDS, Anosim, and Best procedures, Primer package, Clarke and Warwick, 2001). For multivariate comparisons of soil temperatures of 6 2-month periods, and 8 3-hour periods equaling 48 time periods for each site with the unsampled TREE assigned values between the other two tree's soil temperatures. Biological data was square root transformed with the triangular matrix based on Bray-Cutis similarity. Environmental data was normalized, and the similarity index was based on Euclidian distance. The MDS ordinations presented were based on mean vegetation treatment values by year and mean treatment site values averaged over years. ANOSIM dissimilarity of vegetation-only comparisons was based on ordered years as a factor. Vegetation comparisons to abiotic data was of mean data over years. Best variable combinations correlated to the multivariate groupings were identified.

3. Results

3.1. Precipitation

Precipitation was highly variable within and among years with a 3-fold difference for extremes in annual precipitation (Fig. 1). Precipitation was 127 % to 170 % of the long-term mean (LTM) in three years, two years were within 5 % of LTM, two years had about 80 % of LTM, and one year had 54 % of LTM. Precipitation amounts compared to drought condition ratings of the U.S. Drought Monitor appear in disagreement, likely because streamflow, crop and planting conditions, and recovery periods are factored into the drought monitor index. Severe drought occurred over 3 of 8 years. Precipitation in 2012 was 95 % of LTM with at least moderate drought conditions 41 % of the year from winter and spring. Rainfall in 2015 was 157 % of LTM but showed drought conditions 63 % of the year, with the previous fall at 76 % of LTM and summer at 40 % of LTM.

3.2. Vegetation biomass

Vegetation biomass varied considerably by grazing treatment (Table 1, d.f. 6 & 33, $F = 11$, $p < 0.01$) and greatly by year (d.f. 6 & 139, $F = 134$, $p < 0.01$) with a grazing × year interaction (d.f. 30 & 139, $F = 4.3$, $p < 0.01$). The interaction indicates differences in magnitude, not sign of the slope allowing direct comparisons of treatment means (Schabenberger and Pierce, 2001). Vegetation biomass was almost as variable at 2.5-fold as precipitation and was correlated with precipitation. Biomass was harvested in fall, to coincide with peak standing crop most years and was most correlated to the water year precipitation (October through September; $r = 0.89$), decreased for the calendar year precipitation ($r = 0.71$), and was more poorly correlated for drought monitor indices of DSCI ($r = -0.56$), percent of time with abnormally dry to worse conditions ($r = -0.59$), and with drought conditions ($r = -0.49$). Drought indices were similarly, negatively correlated to water year precipitation.

EXCL averaged the greatest biomass (534 g m^{-2}, se = 34 g m^{-2}, Table 1) and HCG least (242 g m^{-2}, se = 34 g m^{-2}). AMP and BURN had similar biomass to EXCL, while MCG, AmpH, and HAY had significantly less biomass than EXCL ($P < 0.10$). A similar pattern occurred for Total grasses. Total forb biomass was similar for treatments except for MCG, which had less biomass but were chemically treated for weed control on this ranch at least twice over the study period. For herbaceous functional

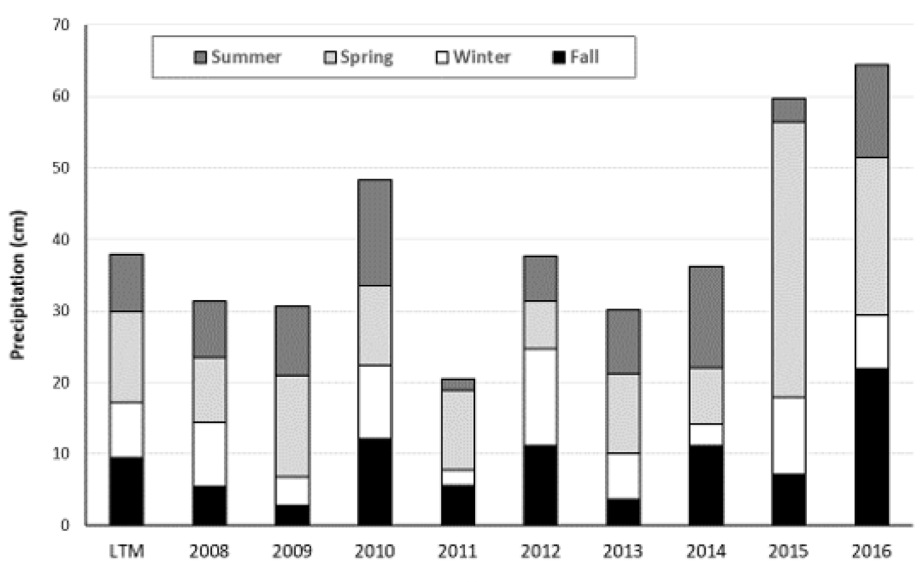

Fig. 1. Precipitation by season and water year (Oct -Sep) and the Long-Term Mean (LTM).

groups, differences were primarily between HCG and the other grazing and management practices. HCG was associated with very little C_4 Tallgrass and low C_4 Old-field grass. HCG had decreased Perennial warm forb biomass, but greater Annual warm forb, Annual cool forb, C_3 Midgrass, C_4 Annual grass, and C_4 Short grass biomass. For MCG intermediate levels of C3 Midgrass and Annual warm forb biomass and decreased Perennial warm forb biomass occurred.

HCG, AmpH, and MCG had the greatest species richness while EXCL had the least (Table 2). BURN, HAY, and AMP had moderate species numbers. EXCL sample plots were smaller in area and had a much thicker litter layer than other treatments that would limit particular species from establishing. HCG had more annual species than other treatments except MCG.

The Non-metric MDS associated with multivariate analysis of vegetation species over the years of the study indicated the differences in species composition and biomass between grazing treatments from wide variations of precipitation over the study years (Fig. 2).

Analysis of Similarities (ANOSIM R, Table 3) indicated considerable dissimilarity of vegetation composition between EXCL, AMP, MCG, and HCG with average dissimilarity $R = 0.72$. Moderate dissimilarity occurred between AMP and MCG ($R = 0.43$, $p = 0.001$). Minor to no dissimilarity occurred among AMP, BURN, HAY, and AmpH (1 of 6 comparisons indicated $R = 0.11$, $p = 0.014$ the others $R < 0.02$, $p > 0.28$). Considerable dissimilarity occurred between years ranging from dissimilarity of $R = 0.23$, $p = 0.014$ to $R = 0.71$, $p = 0.001$ averaging $R = 0.50$. ANOSIM dissimilarities for means over years presented differed little compared to by year comparisons, with AMP vegetation comparisons to BURN, HAY, and AmpH indicated for only 2 of 23 comparisons with minor differences ($R = 0.21$, $p = 0.048$ and $R = 0.18$, $p = 0.032$). Multivariate analysis of this square root transformed species biomass was more sensitive than square root transformed functional group biomass or species presence/absence analysis. Average of the 6 possible comparisons of HCG, MCG, AMP, and EXCL had dissimilarity (R) of 0.72, 0.60, and 0.60, for species biomass, group biomass, and presence/absence, respectively.

Vegetation sites were reduced, and yearly data were averaged and aligned to the same sites of microbe and environmental variables collection sites to enable multivariate comparisons of biotic and environmental data (Table 4, Appendix 1). The one-way vegetation ANOSIM of year means and two-way analysis with years was similar (Table 3). The species most correlated the multivariate matrix of species biomass were Little bluestem, Tall dropseed, Ragweed, and Heath aster (Table 4, corr. = 0.93). Vegetation functional groups most correlated to the multivariate pattern for vegetation functional groups were Tallgrass, Old-field grass, and Perennial warm forbs (corr. = 0.96).

3.3. Soil microbes

PFLA analysis of soil samples collected during two active growing periods indicated high variability between replications and different responses among grazing treatments between years. Total microbial biomass was greater in June 2016 on AMP than HCG, while other treatments were not differentiated (Table 5). In 2016 PFLA comparisons were made among BURN, HAY, HCG, MCG, and AMP. Microbial portions were correlated to total microbial biomass with the only difference being AMP having greater biomass than HCG for Total microbe biomass ($p = 0.05$, Table 5), Total bacteria ($p = 0.05$), Gram-positive bacteria ($p = 0.03$), Gram-negative bacteria ($p = 0.07$), Actinomycetes (gram-positive mycelial bacteria, $p = 0.02$), and Mycorrhizal fungi ($p = 0.08$) in 2016.

Total fungi, rhizobial bacteria, saprophytic fungi, and protozoa were highly variable and not differentiated among grazing treatments. In 2017, PFLA's were collected earlier, in April, with soil microbes comparable for EXCL, TREE, HCG, MCG, and AMP. Analysis indicated more Mycorrhizal fungi associated with EXCL than TREE (Table 5, $p = 0.07$) and EXCL than MCG ($p = 0.10$). For both 2016 and 2017, only soils of HCG, MCG, and AMP were analyzed, with only AMP having greater biomass of mycorrhizal fungi than HCG. The year interaction with grazing treatment indicates that Microbial biomass, Total bacteria, Gram-positive bacteria, Gram-negative bacteria, and Actinomycetes sampled in April 2017 on HCG soils were much greater than those sampled in June 2016 while values for MCG and AMP soils were no different. These differences were associated with all bacterial groups, while decreased fungi groups occurred for the three grazing treatments for April 2017 sampling. The seasonal or yearly differences were a more significant factor than grazing treatments in microbial populations. Microbial respiration occurred earlier and later in the year on HCG sites (Dowhower et al., 2020).

For multivariate analysis, HCG, MCG, and AMP values for the two years were averaged. The other treatments (BURN, HAY, EXCL, and TREE) were adjusted to a mean value based on their relationship to HCG, MCG, and AMP. The multivariate analysis of the seven unique microbial groups (non-combined portions) identified with PFLA measures had small differences between microbial communities associated with EXCL and MCG (Table 4, $R = 0.33$, $p = 0.1$), EXCL and AMP ($R = 0.28$, $p = 0.098$), and AMP and TREE ($R = 0.33$, $p = 0.052$). Actinomycete, mycorrhizal and saprophytic fungi biomass accounted for much of the multivariate pattern (corr. = 0.89).

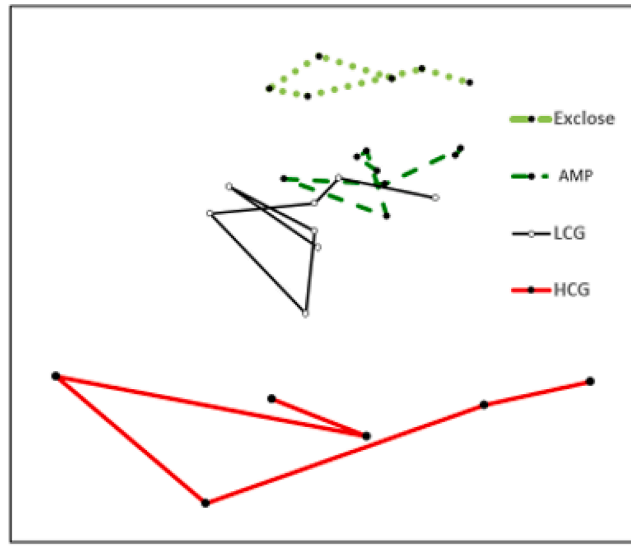

Fig. 2. Non-metric MDS of EXCL and grazing treatments of vegetation biomass^{-2} over years ending in 2016 at right. AMP values were the average of 4 sites vs 3 sites for others.

Table 2
Species richness per plot over 6 years of the study for perennial, annual, and all herbs in tallgrass prairie at Muenster, Texas. Sites are 3 for HCG, MCG, and EXCL, 8 for AMP, and 6 sites for AmpH, BURN, and Hay.

Herbaceous group	SE range	HCG	MCG	AMP	AmpH	BURN	HAY	EXCL
Perennial herbs	1.3–2.2	30 ^{ab}	29 ^{ab}	30 ^{a}	33 ^{a}	28^{b}	29 ^{bc}	21^{c}
Annual herbs	0.6–1.1	16 ^{a}	15 ^{ab}	11 ^{cd}	13^{b}	10 ^{cd}	12 ^{bc}	12 ^{bc}
All Herbs	1.5–2.6	46 ^{a}	43 ^{ab}	41 ^{bc}	46 ^{a}	38 ^{cd}	41 ^{bc}	33 ^{d}

Same letters within rows indicates no differences between treatments ($p < 0.05$).

Table 3
Dissimilarity R of pairwise test values between grazing treatments from multivariate analysis (two-way ANOSIM Grazing × ordered Years) of square root transformed vegetation species biomass from 2009 to 2016. Sites are 3 for HCG, MCG, and EXCL 6 for AmpH, BURN, and Hay, and 7 for AMP.

	Pairwise Tests (R)								
Graze	HCG	MCG	AmpH	BURN	HAY	AMP	Year vs	Year	R	P < R
MCG	**0.87**						2009	2010	**0.71**	0.001
AmpH	**0.98**	**0.70**					2010	2011	**0.49**	0.001
BURN	**0.99**	**0.66**	0.01				2011	2012	**0.54**	0.001
HAY	**1.00**	**0.70**	0.11	−0.04			2012	2013	**0.56**	0.001
AMP	**0.81**	**0.43**	0.02	−0.08	0.00		2013	2014	**0.54**	0.001
EXCL	**0.55**	**0.52**	**0.63**	**0.63**	**0.67**	**0.47**	2014	2015	**0.44**	0.001
							2015	2016	**0.23**	0.001

Significance: **bold underline** $p < 0.05$; Non-bold are treatments comparisons within AMP grazing ($p > 0.28$).

Table 4
Multivariate discrimination (dissimilarity R) of prairie treatments based on environmental or biological variables and the major factors in tallgrass prairie at Muenster, Texas Sites are 4 for AMP and 3 for other sites.

Multivariate	HCG	HCG	HCG	HCG	MCG	MCG	MCG	AMP	AMP	Excl	
Groupings vs	MCG	AMP	Excl	Tree	AMP	Excl	Tree	Excl	Tree	Tree	Major factors of resemblance matrix and corr.
Soil Temperature	0.85	**0.83**	1.00	1.00	0.02	0.11	0.93	0.19	**0.87**	0.74	Jun13:00, Aug19:00, Oct13:00 0.98
Soil Physical	1.00	**1.00**	1.00	1.00	0.04	0.26	0.70	−0.02	**0.82**	0.63	Litter, OM top, Penetrometer top 0.93
Soil Nutrients	0.82	0.50	0.78	0.85	0.13	0.56	0.37	**0.72**	0.30	0.33	K, Zn 0.77
Environmental	0.96	**0.96**	1.00	1.00	0.19	0.70	0.78	**0.70**	**1.00**	0.82	Bare ground, K, Jun13:00 0.91 Mycorrhiza, Sage, Rose, Cocklebur 0.81
Soil Microbes	0.04	−0.07	0.22	−0.07	0.07	0.33	0.22	−0.02	0.19	−0.07	Actinomycete, Mycorrhiza, Saprophyte 0.92
Herb Groups	1.00	**1.00**	0.33		**0.80**	0.33		0.09			Tallgrass Oldfield grass Perennial warm forb 0.96
Species biomass	1.00	**1.00**	0.33		**0.72**	0.56		**0.48**			Little bluestem, Dropseed, Ragweed, Aster 0.93
Species pres/abs	1.00	0.80	0.82		0.33	0.74		0.24			Big bluestem, Indian, Signal grass, Evax 0.77
Herb & Microbe	1.00	**0.96**	0.70	1.00	0.54	0.56	0.63	0.33	**0.82**	0.63	Microbes, Tallgrass, Ragweed, Aster 0.96 Bare ground, Litter, Penetrometer 0.80

Significance: **bold underline** $p < 0.05$ possible for only AMP comparisons; underline $p < 0.101$; Significant differences are generally at $p = 0.10$ when only 10 permutations could be generated comparing treatments with 3 replicates each.

Table 5
Soil microbial biomass (ug/g) for grazing treatments and sites in tallgrass prairie at Muenster, Texas. Sites are 4 for AMP and 3 for other treatments.

Parameter	se	HCG	MCG	AMP	BURN	HAY	EXCL	Tree
Total Microbe 2016	1376, 1589	2877^{b}	4958 ^{ab}	7594 ^{a}	5288 ^{ab}	5865 ^{ab}		
2017	939, 1084	4645	2965	4016			4732	2722
2016 & 2017	751, 867	3761↑	3961↓	5805		↓		
Bacteria 2016	643, 742	1457^{b}	2702 ^{ab}	3860 ^{a}	2553 ^{ab}	2793 ^{ab}		
2017	544, 628	2653	1621	2115			2512	1525
2016 & 2017	384, 444	2055↑	2162↓	2988				
Fungi 2016	215, 248	311	562	698	448	816		
2017	92, 107	221	133	270			347	169
2016 & 2017	104, 120	266	348	484				
Gram -ve 2016	288, 333	567^{b}	1043 ^{ab}	1465 ^{a}	982 ^{ab}	1229 ^{ab}		
2017	200, 231	941	433	655			696	432
2016 & 2017	156, 180	754↑	738↓	1060↓				
Gram + ve 2016	361, 417	889^{b}	1659 ^{ab}	2395 ^{a}	1571 ^{ab}	1563 ^{ab}		
2017	349, 403	1712	1188	1460			1816	1093
2016 & 2017	210, 277	1301↑	1424↓	1928↓				
Actinomycete 2016	132, 153	325^{b}	632 ^{ab}	851 ^{a}	553 ^{ab}	563 ^{ab}		
2017	145, 168	852	498	617			642	461
2016 & 2017	104, 120	589↑	565↓	734↓				
Rhizobia 2016	58, 67	20	122	60	10	176		
2017	14, 17	13	15	42			14	22
2016 & 2017	33, 38	17	68	51				
Mycorrhiza 2016	52, 60	91^{b}	171 ^{ab}	454 ^{a}	149 ^{ab}	195 ^{ab}		
2017	31, 36	75 ^{ab}	46^{b}	87			138 ^{a}	36^{b}
2016 & 2017	28, 33	83	109	165				
Saprophyte 2016	165, 190	220	392	454	300	622		
2017	62, 72	146	88	184			209	133
2016 & 2017	77, 89	183	240	319				
Protozoa 2016	34, 39	34	65	80	44	95		
2017	9, 10	5	5	16			25	19
2016 & 2017	17, 20	30	35	48				

Same letters within rows indicate no treatment difference ($p < 0.05$).

3.4. Soil surface physical interface

Factors associated with soil health include SOM, soil structure measures, soil pH, salts and cations, bare ground, and litter cover of the soil surface (Table 6) as outlined by Aguilera et al. (2013), Altieri (1999), and Teague et al. (2011). Soil texture certainly affects physical properties, but as sampling was conducted on the same soil series and catenal positions for all treatments, this is unlikely a factor except with localized erosion, which was not evident at sampling sites. Vegetation cover, which is highly correlated to herbaceous biomass, was estimated as 100 % - bare ground - litter cover. Cover factors all had Grazing × Year interactions (F 4.0–4.6, $p = 0.0001$) that, like biomass measures, expanded and contracted with precipitation. Bare ground % was greater with HCG, moderate with MCG, and least on AMP and EXCL. EXCL and AmpH had greater litter cover than BURN, HAY, and AMP.

Penetration resistance was least near the surface and increased with depth in all treatments except with HCG with greater penetration resistance at the surface (Grazing × Depth interaction, $F = 2.0$, $p = 0.047$, Table 6). HCG and HAY had the greatest overall penetration resistance and EXCL the least, while other grazing treatments were intermediate. Bulk density among treatments showed a similar pattern. Increased Trampling and Bare ground and decreased SOC reduce aggregate stability (Van der Heijden et al., 2008; Bardgett, 2005; Coleman and Crossley, 1996). TREE and HCG had lower Aggregate stability than other treatments, except MCG was intermediate.

Soil organic matter decreased with depth with no interactions among grazing treatments (Grazing × Depth, $F = 0.7$, $p = 0.75$). TREE had the greatest SOM, HCG the least, and other treatments had intermediate levels (Table 6). Soil pH was somewhat lower for TREE than other treatments. Cation exchange capacity was greater for TREE, MCG, and EXCL than HAY and HCG, while BURN sites were intermediate. Soil salts were greatest with TREE and EXCL, least with BURN and HCG, and intermediate for MCG, AMP, and HAY treatments.

Multivariate analysis of these soil physical variables indicated HCG had very high dissimilarity to TREE, EXCL, MCG, and AMP (Table 4). TREE differed from all other management treatments while MCG, AMP and EXCL were similar. Factors most correlated with the multivariate pattern are Vegetation cover, OM, aggregate stability, and Penetration resistance 0–15 cm (Table 4, corr. = 0.89). Anosim analysis indicated considerable differences of HCG from other treatments ($R > 0.82$, $p < 0.10$) as well as TREE differences from other treatments (Table 6, $R > 0.66$, $p < 0.10$). Litter cover of EXCL, MCG, and HCG exceeded that of AMP ($p < 0.07$), but in this study, litter cover was the portion that was not bare ground or standing vegetation; thus, AMP had the most combined vegetative cover while HCG had the least (Table 6).

3.5. Soil nutrients and chemistry

Soil chemistry includes macro-nutrients, micronutrients, and those that, though essential nutrients, behave much as salts being mobile within the soil profile, often accumulating near the soil surface through evapotranspiration processes. Although sites being compared comprised the same soil, parent materials deposited in shallow seas over eons can potentially have different concentrations of chemicals due to geographical separation not related to grazing treatment. For a particular soil, several soil chemical concentrations were more similar for grazing treatments and an associated soil within 8 km in a county than for the same soil in a different county at about 120 km distance (Teague et al., 2011). In the current study, HCG was separated the furthest from other treatments at 3 km.

The most variable chemical constituent among grazing treatments was Total N varying 4.6-fold (Table 7), while the macro-nutrient P varied 1.4-fold, and K varied 1.6-fold. The Micro-nutrients Zn, Cu, and Mn varied 2.7 to 1.9-fold among grazing treatments while Na, Ca, Fe, S, and Mn varied 1.6 to 1.2-fold. EXCL soils had the greatest concentration of N and TREE had a greater concentration of N than BURN, HAY, and AMP (Table 7). Concentrations of P were greater for HCG and HAY than MCG, BURN, and AMP, while concentrations of K were less for HCG and HAY than other treatments. TREE MCG and EXCL had greater Ca concentrations than other treatments. EXCL had greatest Mg and Zn concentrations, while TREE had greatest S and Mn levels. HCG had greatest Cu levels and lowest Mn levels. Multivariate analysis of soil chemistry indicated that AMP and MCG were similar (Table 4, $R = 0.07$, $p = 0.5$) as were EXCL and TREE ($R = 0.37$, $p = 0.20$). Best correlated factors were K and Zn (corr. = 0.79).

3.6. Soil temperature

Soil temperatures lagged behind air temperature. Only soil temperature associated with HCG had high soil temperatures that were similar to that of air temperatures, with all other management practices having lower soil temperatures (Fig. 3a, $p < 0.05$). Overnight, soil temperatures remained higher than air temperatures. The greatest extremes in soil temperatures among grazing treatments occurred in the warmest period of the year and the warmest time of day. The coolest soils temperatures were those in the shade of trees, then EXCL, then AMP and MCG, while HCG had the highest soil temperatures ($p < 0.05$).

Except for November and December, tree soil temperature was lower than air and grassland soil temperatures (Fig. 3b). Soil temperatures on grass-dominated EXCL averaged 0.8 °C higher in May-Dec. ($p = 0.01$ to 0.15) and 1.3 °C higher 9:00 – 18:00 ($p < 0.05$) than TREE soil. Soil temperatures of MCG grassland averaged 1.3 °C greater than TREE soil ($p < 0.02$) throughout the year, peaking at 2.0 °C greater during July through August ($p < 0.03$). Additionally, MCG soil temperatures averaged 1.5 °C greater throughout the day peaking at 2.5 °C greater from 12:00 to 18:00 h than TREE soils. Temperature profiles of MCG and AMP were similar with 1 of 8 periods of the day and 1 of 6 2-month periods varying by 0.8 °C and 0.7 °C, respectively ($p > 0.3$). HCG soils average

Table 6
Soil physical parameters associated with grazing treatments in tallgrass prairie at Muenster, Texas. Sites are 4 for AMP and 3 for other treatments.

Parameter Units se	HCG	MCG	AMP	ampH	BURN	HAY	EXCL	Tree
Vegetation cover % 2.0	52.3 ^{d}	66.1^{c}	74.4 ^{a}	68.9 ^{bc}	71.8 ^{ab}	73.8 ^{a}	71.3 ^{abc}	
Bare ground cover % 1.5	20.5 ^{a}	8.1^{b}	2.7^{c}	4.4 ^{bc}	4.7 ^{bc}	3.4^{c}	1.4^{c}	
Litter cover % 1.5	23.3 ^{ab}	25.9 ^{ab}	23.5^{b}	26.7 ^{a}	23.1^{b}	23.4^{b}	27.3 ^{a}	
Bulk Density g cm^{-3} 0.33	1.10 ^{a}	0.97^{b}	0.89 ^{cd}		0.99^{b}	0.95 ^{bc}	0.83 ^{d}	0.91 ^{bc}
Penetration all joules 1.3	163 ^{a}	111 ^{cd}	118^{c}	118^{c}	136 ^{bc}	146 ^{ab}	89 ^{d}	
Penetration −5 J 0.5	↑ 59 ^{a}	33 ^{cd}	37^{c}	37^{c}	43 ^{bc}	46 ^{ab}	24 ^{d}	
Penetration-10 J 0.5	52 ^{a}	37 ^{cd}	39^{c}	40^{c}	46 ^{bc}	49 ^{ab}	31 ^{d}	
Penetration-15 J 0.5	53 ^{a}	42 ^{bc}	42 ^{bc}	41 ^{bc}	46 ^{ab}	51 ^{a}	35^{c}	
Aggregate stabile % 1.0	95.9^{c}	97.9 ^{ab}	99.3 ^{a}	99.1 ^{a}	99.3 ^{a}	99.1 ^{a}	99.1 ^{a}	94.3^{c}
Organic matter LOI% 0.5	6.2^{c}	7.8^{b}	8.7^{b}		8.9 ^{ab}	8.1^{b}	8.2^{b}	9.8 ^{a}
Soil pH 1:1 0.07	8.0 ^{a}	8.0 ^{a}	7.9 ^{a}		7.9 ^{a}	7.9 ^{a}	7.9 ^{a}	7.7 ^{a}
Cations me/100 g 1.4	34.0^{c}	38.8 ^{a}	36.6 ^{abc}		35.0^{b}	31.6^{c}	37.8 ^{ab}	39.6 ^{a}
Salts mho/cm 0.04	0.4^{c}	0.5^{b}	0.5^{b}		0.3^{c}	0.5^{b}	0.6 ^{a}	0.6 ^{a}

Different letters within rows indicate differences between treatments ($p < 0.05$).

Table 7
Soil nutrients and chemistry of grazing treatments and lone trees in tallgrass prairie at Muenster, Texas. Means are based on 4 sites for AMP and 3 sites for other treatments.

Parameter	Units	se	HCG	MCG	AMP	BURN	HAY	EXCL	TREE
Nitrogen	ppm N	2.0	6.7 ^{bc}	5.7 ^{bc}	5.0^{c}	3.3^{c}	4.3^{c}	15.3 ^{a}	9.3^{b}
Mehlich P-III	ppm P	0.4	3.7 ^{a}	2.7^{b}	2.8^{b}	2.7^{b}	3.7 ^{a}	3.3 ^{ab}	3.3 ^{ab}
Potassium	ppm K	15	180 ^{cd}	249 ^{ab}	221 ^{bc}	209^{c}	166 ^{d}	257 ^{a}	269 ^{a}
Calcium	ppm Ca	270	6461 ^{cd}	7317 ^{ab}	6909 ^{abc}	6566 ^{cd}	5964 ^{d}	7055 ^{ab}	7463 ^{a}
Magnesium	ppm Mg	14	141^{c}	173 ^{bc}	164 ^{bc}	182 ^{ab}	154 ^{bc}	214 ^{a}	181 ^{ab}
Iron	ppm Fe	2.3	19.7 ^{a}	21.7 ^{a}	21.1 ^{a}	19.4 ^{a}	19.6 ^{a}	18.2 ^{a}	16.5 ^{a}
Sodium	ppm Na	1.3	22 ^{a}	19^{b}	15^{c}	17 ^{bc}	24 ^{a}	17 ^{bc}	19^{b}
Sulfur	ppm S	0.43	9.3 ^{ab}	8.5^{b}	9.9 ^{a}	9.5 ^{ab}	9.6 ^{ab}	8.6^{b}	10.2 ^{a}
Manganese	ppm Mn	0.7	3.8^{c}	5.7 ^{ab}	5.3 ^{bc}	4.9 ^{bc}	4.1 ^{bc}	5.6 ^{ab}	7.1 ^{a}
Copper	ppm Cu	0.21	1.82 ^{a}	0.74^{b}	0.90^{b}	0.72^{b}	0.80^{b}	0.88^{b}	0.93^{b}
Zinc	ppm Zn	0.17	1.05 ^{ab}	0.50^{c}	0.83 ^{bc}	0.71 ^{bc}	0.91^{bc}	1.37 ^{a}	0.77 ^{bc}

Comparisons with the same letter within rows are similar (P > 0.05).

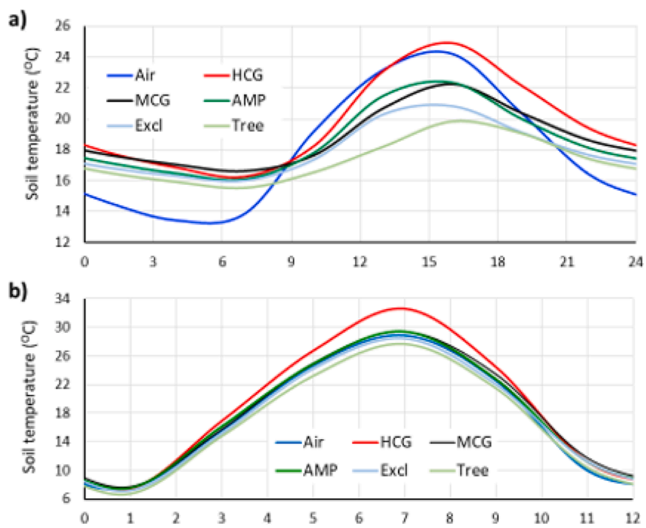

Fig. 3. Soil Temperature of grazing treatments and air temperature for a) time of day and b) month.. Means based on 2 sites for Air and Tree soil, on 4 sites for AMP, and 3 sites for other treatments.

1.8 °C warmer from 12:00 – 24:00 ($p < 0.01$) and 1.8 °C warmer July through December ($p < 0.01$) than soil temperatures of MCG and AMP treatments.

A full assessment of seasonal and diurnal differences in soil temperatures among grazing treatments is unnecessary for identifying treatment differences. Multivariate analysis of soil temperatures with the six 2-month periods and eight 3-hour periods totaling 48 variables for each of the five treatments and their replicates indicated that two variables, May/June 13:00 and Jul/Aug 19:00, account for the major portion (corr. = 0.96) of the multivariate pattern. ANOSIM analysis indicated considerable differences among HCG and the other treatments (Table 4; $R > 0.77$, $p < 0.10$) and between TREE and other treatments ($R > 0.75$, $p < 0.10$). The exception was for TREE and EXCL ($R = 0.75$, $p = 0.20$). Soil temperature patterns for EXCL, MCG, and AMP were more similar ($R < 0.29$, $p > 0.06$).

Warmer soil temperatures early and late in the year would likely promote vegetation growth and microbial activity unless soil moisture was limiting. Warmer soil temperatures in summer with greater transpiration rates of plants and soil evaporation would reduce soil moisture, but with adequate moisture, greater microbial activity would occur. Seasonal temperature differences would be a factor differentially favoring germination or growth of some plant species or functional groups. Greater microbial activity without increased vegetative productivity would result in decreased OM. At these sites soil moisture of HCG averaged 26 % compared to 29 % for MCG and 30 % for AMP ($p = 0.069$ and $p = 0.005$, respectively) (Dowhower et al., 2020).

3.7. Factor combinations influencing grazing practice differences

Assessment of biota included vegetation species and soil microbe biomass. Analysis of Similarities of square root transformed vegetation and microbe data combined indicated dissimilarity among all combinations of HCG, MCG, AMP, EXCL, and TREE (Table 4, $R = 0.54$ to 1.00, $p < 0.10$) except for AMP and EXCL ($R = 0.33$, $p = 0.06$). The selection of 'best' correlated variables included a subset of common vegetation species and functional groups and microbe groups and microbe subgroups. Selection of species or subgroups within a major group was avoided. The best correlated variables to the Biotic community were C4 shortgrass, Big bluestem, Bundleflower, and Ground rose (corr. = 0.897). Combinations of 11 other species or functional groups are well correlated (corr. > 0.893).

To determine which environmental variables are correlated to the multivariate biological pattern, environmental factors were standardized and combined to provide more concise descriptive variables associated with land management practices evaluated in this study. The environmental matrix, based on Euclidian distances of standardized values, consisted of 14 physical soil interface factors (including marginal factors: vegetation cover, OM, pH, salts, and cation exchange capacity), 12 soil chemical and nutrient concentrations, and the 12 most correlated of 48 soil temperature measurement periods chosen to reduce temperature dominance. The multivariate analysis of these environmental variables indicated dissimilarity of all combinations of HCG, MCG, AMP, EXCL, and TREE (Table 4, $R = 0.70$ to 1.00, $p < 0.10$) except MCG vs AMP ($R = 0.19$, $p = 0.30$). The multivariate pattern of environmental factors was correlated with Litter cover, K, Mar-Apr 16:00, and Jul-Aug 22:00 h soil temperature (corr. = 0.91). Additional combinations include Vegetation cover, Penetration resistance, and 5 other soil temperature periods (corr. > 0.894).

To emphasize treatments managed with grazing, EXCL and TREE were excluded. The degree to which biological and environmental factors have commonality is displayed with Non-metric MDS graphs of HCG, MCG, AMP, BURN, and MOW (Fig. 4). The 2 MDS's are moderately related (relate Rho = 0.74, P = 0.001). Both the Biotic and Environmental MDS's indicate that HCG differs considerably from the other Grazing treatments (ANOSIM dissimilarity $R > 0.92$, $p <= 0.10$). For Biotic composition, MCG differed from BURN, MOW, and AMP (dissimilarity $R > 0.54$, $p <= 0.10$) but the 3 treatments within rotations were similar (dissimilarity $R < 0.17$, $p > 0.31$). For multivariate Environmental data, the 3 treatments within rotations were similar (dissimilarity $R < 0.36$, $p > 0.11$). Environmental data of MCG differed from MOW and BURN (dissimilarity $R > 0.63$, $p = 0.10$) but was more similar for MCG and AMP (dissimilarity $R = 0.19$, $p = 0.23$).

The ultimate objective was to identify environmental factors most associated with the biotic communities under different management that correspond to superior qualities in terms of productivity and

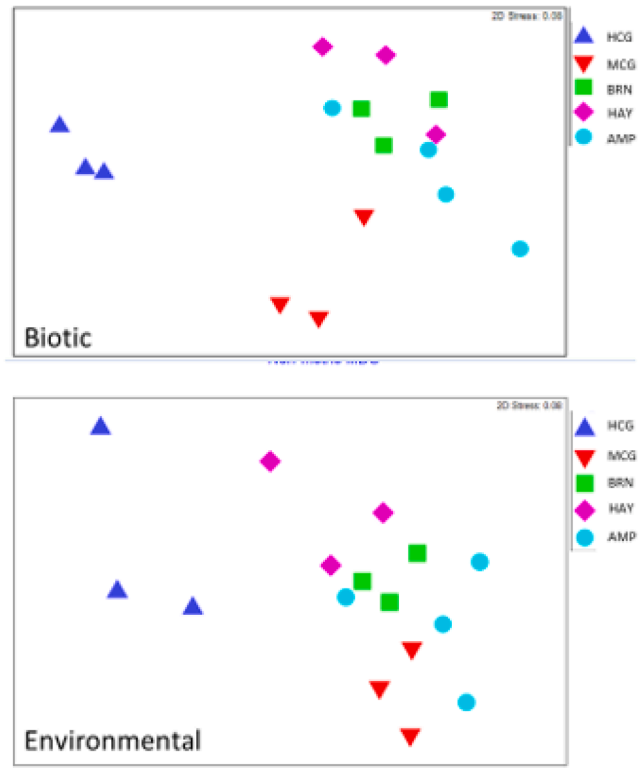

Fig. 4. Non-metric MDS aligned graphs of grazing treatments for a) biotic and b) environmental variables. +

recycling of nutrients. Regarding the grazing treatments C4 tallgrass, Annual warm forbs, Cyperus, and Heath aster were most correlated to the 'biological' multivariate pattern (corr. = 0.929). Dropping Cyperus, the 3 'best' variables have a corr. = 0.919. Another 9 species or vegetation functional groups and Actinomycetes can be combined in groups of 3 to correlate well to the biotic pattern (corr. > 0.906). The 2 variables, C4 tallgrass and Annual warm forb, were well correlated to the biotic community (corr. = 0.879) and the combination of 3 to 4 variables was well correlated (corr. = 0.879 to 0.897). However, the multivariate assemblage of vegetation functional groups was not as sensitive at detecting differences between EXCL and AMP or MCG (Table 4). Environmental variables most correlated to the biotic community were Bare ground, Vegetation cover, Penetration resistance, and Mn (corr. = 0.852). Additionally, combinations of Aggregate stability, S, and any 1 of 4 Soil temperature periods are almost as well correlated (corr. > 0.830). At least 7 combinations of environment factors excluding soil temperatures and soil chemistry are almost as well correlated (corr. > 0.800).

The environmental variables most correlated to the environmental matrix were Bare ground, K, and soil temperature (Mar-Apr 13:00, and May-Jun 16:00) (corr. = 0.954). Excluding soil temperatures results in Bare ground, OM, Penetration resistance, and K being the most correlated with environmental variables (corr. = 0.908). Eliminating soil chemical variables resulted in Bare ground, OM, Penetration resistance, and K being most correlated (corr. = 0.870). Best correlation of biotic factors to the abiotic matrix included Little bluestem, Heath aster, Ground rose, and Silver nightshade (corr. = 0.827). Additionally, the Legume group and 5 species combinations are almost as correlated (corr. > 0.819 to 0.824). Best 4 vegetation functional group variables correlation to environmental data was even lower (corr. = 0.736).

4. Discussion

To restore long-term sustainability and ecological resilience in grazed ecosystems requires management that regenerates soil and ecosystem function. While the greatest limiting factor in grazing land ecosystems is the infiltration and retention of surface water in the soil (Thurow, 1991), optimal ecosystem function also requires soil organic matter accumulation, efficient nutrient cycling, high levels of below and above ground biodiversity, and efficient solar energy capture for the greatest number of days each year (Savory and Butterfield, 2016; Teague et al., 2013). Soil function is predominantly mediated by the interdependence of soil microbes, fungi, insects, plants and animals. Plants support microbial life by supplying carbohydrates in the form of root exudates and detritus that feed microbes. In return, plants prosper from nutrient release resulting from interactions among soil archaea, bacteria, fungi, and other microbial and eukaryotic species (Morriën et al., 2017; De Vries et al., 2006; Coleman and Crossley, 1996). Therefore, how plants are managed directly affects the associated soil biota as the energy driving ecological functions are derived predominantly through the conversions of solar energy to carbohydrates by photosynthesizing plants.

As a preferred forage plant, big bluestem and other associated desirable tallgrass species decrease and disappear under continuous grazing as they are frequently and often severely grazed and not allowed adequate recovery after defoliation (Vinton and Hartnett, 1992). Grazing too severely reduces soil cover, plant vigor and root biomass and depth, reducing community productivity and resilience (Weaver, 1954; Weaver and Roland, 1952). Another factor contributing to the decline of high seral herbaceous plants in tallgrass prairie includes a lack of periodic defoliation that causes a buildup of too much litter that decreases light interception unless periodically removed. In undefoliated or lightly defoliated prairie, light is the primary limiting factor. Competition for light quickly favors the tallest herbaceous plants, and self-shading results in a reduction in plant growth due to a decrease in photosynthesis and nutrient cycling, reducing ecosystem productivity and biodiversity. Under these conditions, water and nitrogen accumulate (Seastedt 1995), as occurred in this study, and big bluestem is more competitive at lower levels of nitrogen (Jumpponen et al., 2005). Consequently, herbaceous prairie communities deteriorate in the absence of disturbance and thrive under periodic, moderate defoliation followed by adequate recovery (Knapp, 1985).

Grazing removes light as a limiting factor and enhances nutrient cycling and biodiversity as other plants can compete, and nitrogen becomes the limiting factor (Seastedt and Knapp, 1993; Blair, 1997). Consequently, periodic defoliation in the form of infrequent grazing, mowing or fire, followed by planned recovery such as using AMP grazing management, can result in compensatory growth in tall grass and mixed-grass prairie ecosystems (Teague et al., 2011; Dyer et al., 1993; Turner et al., 1993).

There is a symbiotic relationship among many tallgrass graminoids, including big bluestem and mycorrhizal fungal endophytes. These relationships can vary from strong dependency to lack of dependency according to soil fertility and plant host-fungal endophyte specificity (Anderson et al., 1994). The absence of mycorrhizal colonization of roots has been shown to decrease plant growth in big bluestem, which would reduce the competitiveness and proportion of this species in a diverse community. Managing to improve soil microbial composition enhances soil carbon and nitrogen cycling to increase ecological function and biological fertility (Van der Heijden et al., 2008; Nielsen et al., 2011; de Vries et al., 2012).

Grazing management that increases microbial densities and diversity expands below ground microbial networks and diversifies other beneficial biota composition and activities. Other beneficial soil biota would include arthropods, such as dung beetles and earthworms, leading to increased nutrient cycling efficiency and carbon uptake to enhance biological outcomes (Pecenka and Lundgren, 2019). Management strategies that increase herbaceous production and biodiversity restore soil function, expand below ground microbial networks, and increase the efficiency of nutrient cycling and carbon uptake by diversifying fungal and bacterial composition and activities to strongly benefit soil structure ecological functions (Morriën et al., 2017). Conversely, management practices that result in inadequate post-herbivory recovery, residual herbaceous biomass and ground cover lead to impaired microbial interactions and functions, herbaceous plant productivity and biodiversity to reduce ecosystem services (LaCanne and Lundgren, 2018).

In this study, the management that resulted in the greatest total herbage, C_4 tallgrasses, and native perennial summer growing forbs was AMP and the least HCG, with MCG being intermediate. This even though AMP was stocked twice as heavily as MCG. Native tallgrasses are the dominants in high seral prairie, and native summer growing forbs add essential biodiversity attesting to the importance of domination by these plant groups when aiming to restore the highly productive and diverse original tallgrass prairie. Plant groups that indicate degraded ecosystem function in this region are C_4 annual grass, C_4 shortgrass, C_3 grasses, and annual forbs that were most prevalent with HCG management. The other treatments that included AMP grazing management, AmpH, BURN, and HAY, had broadly similar vegetation responses to AMP.

Regarding the importance of soil microbial responses to management treatments, total microbial biomass was higher in AMP than HCG and intermediate in MCG. High soil microbial biomass is an essential indicator of soil function. It contributes to improved soil aggregation, porosity, water infiltration rates and water holding capacity, and more rapid soil carbon and nutrient turnover (Coleman and Crossley, 1996). Our study's key response was that arbuscular mycorrhizal fungi (AMF) were higher with AMP and lowest with HCG and intermediate with MCG. AMF fungi are keystone species in grasslands and many terrestrial ecosystems as they enhance plant access to nutrients, mediate interactions among plants and other microbes, and enhance plant diversity (Averill et al., 2014; McHugh and Dighton, 2004). Consequently, the symbiosis between AMF and plants enhances photosynthesis by 50 %, and AMF contributes directly to the soil organic matter and increases soil aggregate stability (Rellig, 2004).

Actinomycetes, and Gram-positive (GP) and Gram-negative (GN) bacteria improve soil structure and soil aggregation, nutrient recycling, and water retention (Fanin et al., 2019). Our data indicate that actinomycetes and GP and GN bacteria were higher in AMP than HCG and intermediate in MCG. GP and GN abundance and their ratio dynamics have utility as indicators of the relative carbon availability for soil bacterial communities in organic soils and soil function in natural ecosystem soils (Fanin et al., 2019). Overall, GN bacteria are associated with simple labile carbon and plant-derived carbon compounds, while GP bacteria are more strongly associated with more complex carbon forms. There were no differences in the GP:GN ratio among HCG, MCG, and AMP.

Different grazing and cropping management practices profoundly impact soil physical parameters and function (Lal, 2004). We recorded substantive differences in soil physical parameters among the management treatments we studied. In grassland ecosystems, good plant and litter cover is needed to protect soil loss and maintain normal soil function (Bardgett, 2005; Rietkerk et al., 2000; Thurow, 1991). Bare ground is not covered from solar irradiance, causing elevation of soil temperatures and desiccation, decreasing microbial activity, accelerating loss of organic matter, and elevating erosion risk (Thurow, 1991). Elevated soil temperature has a direct negative effect on factors that contribute to ecosystem function, including infiltration rates, soil evaporation, nutrient retention, and biodiversity (Neary et al., 1999; Whelan, 1995, Wright and Bailey, 1982).

Regarding the soil cover parameters in our study, vegetation cover and bare ground were more favorable with AMP than HCG and MCG, contributing to superior soil bulk density and penetration resistance with AMP than both HCG and MCG. Bulk density with AMP was not different from that in EXCL plots, and aggregate stability was better with AMP than HCG with MCG intermediate. Regarding the three treatments that used AMP, AmpH, BURN, and HAY, they mostly had the same AMP responses. The exception was HAY that had higher soil penetration resistance than AMP. Soil organic matter was greater with AMP than HCG, intermediate with MCG, while BURN, HAY, and EXCL were no different to AMP. Cation exchange capacity was essentially the same with all treatments. In summary, AMP outperformed HCG and usually MCG in the critical soil physical elements fostering improved ecological function, the basis for delivery of improved ecosystem services, and ranching profitability.

The multivariate analyses aimed to identify the leading associations among management treatments and important soil and vegetation parameters and indicated dissimilarity of all HCG combinations with MCG, AMP, EXCL, and TREE, except MCG vs AMP. Environmental factors most associated with the multivariate matrix of plant species were Sulfur, mid-summer evening soil temperatures, and vegetation cover. The biotic pattern of HCG, MCG, and AMP alone were correlated with bare ground, soil penetration resistance, and herbaceous cover. Litter cover, Bulk density, Penetration resistance, and vegetation cover most correlated with the vegetation. Other correlates with HCG, MCG and AMP were Bare ground, Penetration resistance, and Herbaceous cover. Negative correlations with the environmental pattern of TREE and EXCL were mycorrhizal fungi and invasive non-graminoid plants.

5. Conclusions

Effective soil management provides the most significant potential for achieving sustainable use of grassland ecosystems with a variable, uncertain, and rapidly changing climate. Substantial degradation and desertification of grasslands have occurred globally due to human mismanagement and neglect. To ensure long-term sustainability and ecological and economic resilience in these ecosystems requires determining what factors and management will effectively restore ecological function in grassland landscapes. As microbes mediate 90 % of soil and ecosystem function, and soil microbes depend largely on plant-derived energy sources, how we manage plants is critical to regenerating long-term rangeland sustainability and environmental resilience. Consequently, we examine soil and vegetation responses to the most commonly used heavy continuous grazing (HCG) relative to moderately stocked continuous grazing (MCG) and different combinations of AMP grazing managed adaptively to improve soil and ecological function as the foundation to improve the provision of ecosystem services and economic benefits.

AMP grazing results from this study indicate improved total herbaceous biomass, proportions of C_4 tallgrasses, native perennial summer growing forbs, vegetation cover, less exposed bare ground, and less unproductive and invasive herbaceous species. AMP also had higher biomass of total soil microbes, actinomycetes, gram-positive and gram-negative bacteria associated with improved soil aggregation and nutrient cycling than HCG, with MCG having intermediate responses. The crucial arbuscular mycorrhizal fungal component, related to enhanced water and nutrient acquisition by plants and soil aggregation, was also higher with AMP, lowest with HCG, and intermediate with MCG. AMP also outperformed HCG and usually MCG in the critical soil physical elements fostering improved ecological function, the basis for delivery of improved ecosystem services, ranching profitability, and socio-ecological resilience. These are substantive improvements, despite AMP having double the stocking rate of MCG since the ability to carry more animals while improving ecological function has substantial economic value.

We did not refute the hypothesis that appropriately managed AMP grazing will achieve changes in plant composition towards dominance by high seral herbaceous species and improve soil physical, chemical, and microbial properties and biodiversity relative to season-long continuous grazing. These positive outcomes were generally not compromised with the BURN and HAY treatments, as both were managed with AMP grazing. The exception was HAY, which had increased soil penetration resistance compared to AMP but was still less than with HCG or MCG. AMP grazing also compared favorably with no grazing (EXCL) on the majority of parameters measured. The presence of low densities of trees had predominantly positive effects relative to treeless AMP and MCG for soil temperature, soil organic matter, and cation exchange capacity.

These findings provide evidence that AMP grazing is a powerful management strategy to achieve plant composition changes towards dominance by high seral herbaceous species. Doing so results in improved soil physical, chemical, and microbial properties and biodiversity relative to season-long continuous grazing as the foundation to enhance the provision of ecosystem services and economic benefits in Southern Tallgrass prairie.

CRediT authorship contribution statement

Richard Teague: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Writing – review & editing. **Steve Dowhower:** Methodology, Data curation, Formal analysis, Writing – review & editing.

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.

Acknowledgements

We thank the Dixon Water Foundation, Decatur, TX, USA and Texas A&M AgriLife Research under project H 8179 for funding this research. We also thank the owners of the Pittman, Danglemayr, and Mitchell ranches in Cooke County, Texas for permission to conduct the study on their properties. Special thanks go to Robbie Tuggle, Dixon ranch manager, for planning and managing the implementation of the AMP grazing management treatments on the Pittman ranch above his already busy management duties. We also thank Rhonda Daniel, Alan Waggoner, Diane Conover, Shannon Baker and the late Brady Surber for their invaluable help during the project.

Appendix. 1 Number of sites sampled for types of variables for grazing and treatments over years

Sample Type	Grazing and Pasture Treatments							
Years	HCG	MCG	AMP	AmpH	BURN	HAY	EXCL	TREE
Vegetation								
2009–2010		3	8	6	6	6		
2011–2016	3	3	9	6	6	6	3	3*
Microbe								
2016	3	3	3		3	3		
2017	3	3	3				3	3
Soil Physical								
2017	3	3	7	6	6	6	3	3
Soil Nutrient								
2017	3	3	4		3	3	3	3
Soil Temperature								
2010–2016	3	3	9	6	6	6	3	2
Multivariate								
vegetation-years	3	3	9	6	6	6	3	
All-mean	3	3	4		3	3	3	3*

* Tree vegetation was estimated and thus not compared to other treatment's vegetation.

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