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Tallgrass Prairie Responses to Management Practices and Disturbances: A Review

Pradeep Wagle * and **Prasanna H. Gowda**

USDA, Agricultural Research Service, Grazinglands Research Laboratory, El Reno, OK 73036, USA;
prasanna.gowda@ars.usda.gov
* Correspondence: pradeep.wagle@ars.usda.gov; Tel.: +1-405-262-5291; Fax: +1-405-262-0133

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Abstract: Adoption of better management practices is crucial to lessen the impact of anthropogenic disturbances on tallgrass prairie systems that contribute heavily for livestock production in several states of the United States. This article reviews the impacts of different common management practices and disturbances (e.g., fertilization, grazing, burning) and tallgrass prairie restoration on plant growth and development, plant species composition, water and nutrient cycles, and microbial activities in tallgrass prairie. Although nitrogen (N) fertilization increases aboveground productivity of prairie systems, several factors greatly influence the range of stimulation across sites. For example, response to N fertilization was more evident on frequently or annually burnt sites (N limiting) than infrequently burnt and unburnt sites (light limiting). Frequent burning increased density of C_4 grasses and decreased plant species richness and diversity, while plant diversity was maximized under infrequent burning and grazing. Grazing increased diversity and richness of native plant species by reducing aboveground biomass of dominant grasses and increasing light availability for other species. Restored prairies showed lower levels of species richness and soil quality compared to native remnants. Infrequent burning, regular grazing, and additional inputs can promote species richness and soil quality in restored prairies. However, this literature review indicated that all prairie systems might not show similar responses to treatments as the response might be influenced by another treatment, timing of treatments, and duration of treatments (i.e., short-term vs. long-term). Thus, it is necessary to examine the long-term responses of tallgrass prairie systems to main and interacting effects of combination of management practices under diverse plant community and climatic conditions for a holistic assessment.

Keywords: biomass; fertilization; grazing; burning; restoration

1. Introduction

Tallgrass prairie, North America's most endangered ecosystem, had occupied more than 68×10^6 ha of the North American Great Plains before European settlement and the acreage of native prairie has declined as high as 99.9% by now [1]. Tallgrass prairie grasslands still contribute heavily for livestock production in several states of the United States. These grasslands can range from unmanaged low productive systems to highly managed high productive systems. Overall, grasslands are usually managed less effectively than croplands. In addition, tallgrass prairie grasslands frequently experience several disturbances such as grazing, fire, and drought. Thus, understanding the consequences of different management practices and disturbances on the plant community composition and production, nutrient cycling, and microbial activities in tallgrass prairie is of great importance for both economic and conservation purposes. However, the response of tallgrass prairie systems to management practices and disturbances is complicated as the prairie system consists of both C_3 and C_4 grasses and C_3 forbs, and these species behave differently due to significant differences in phenology, root

morphology, and mycorrhizal dependence. Variability in the fraction of C_3 and C_4 species are correlated with several environmental and management factors [2,3]. Changes in plant growth and plant community composition due to different management practices and disturbances can have profound impacts on both quantity and quality of biomass (hay or forage) production, quantity and quality of organic substrates [4], and ultimately on soil microbes and their activities as soil microbes play a key role in cycling and storage of soil carbon (C) and nitrogen (N) via decomposition of root and litter inputs.

Although previous studies have explored the impacts of management practices and disturbances on responses of tallgrass prairie systems, the findings are inconsistent for different intensities, frequencies, climatic conditions, and timing of disturbances (e.g., grazing and burning) and management practices [5–7]. For examples, burning reduced microbial C during dry years but increased in normal or wet years [8]; application of fertilizers was more effective in wet years than dry years [9]; N fertilization was more effective to increase production on frequently or annually burnt sites compared to infrequently burnt and unburnt sites [10]. In addition, the focus of most past studies has been on a single treatment (e.g., burning or grazing) as the response of vegetation to a treatment might be affected by another treatment. For example, fire favors C_4 growth dominance, while fire and grazing together maximize diversity in tallgrass prairie [11]. In addition, as most studies are short-term (2–3 years), long-term impacts of treatments might change which remain poorly understood. For example, large shifts in plant compositional changes (shift towards C_4 grass dominance) occurred within three years of prairie establishment and became much smaller after three years, most likely due to competition of soil resources [12]. Likewise, the abundance of C_3 grasses decreased as the study progressed in N fertilized prairies [13]. Thus, it is necessary to assess long-term potential consequences of fertilization, grazing or removal of biomass by harvesting, and burning on forage production, microbial biomass and activity, and nutrient cycling in tallgrass prairie.

There have been increasing efforts including the Conservation Reserve Program (CRP) from government and private organizations to restore diverse prairie in agricultural sites with the goal of reestablishment of native plant species [14,15]. Some previous studies have reported that restored prairies little resembled the species richness of native remnants even after several decades of restoration [16]. However, changes in plant species composition and ecosystem properties in restored tallgrass prairies are not well understood [12]. The major goal of this article is to review the independent and interactive impacts of different common management practices and disturbances and tallgrass prairie restoration on plant species composition, plant growth and development, water and nutrient cycles, and microbial activities in tallgrass prairie systems. However, the response of tallgrass prairies to management practices and disturbances may show inconsistent results across space and time due to different functional traits (e.g., different mixture/proportion of C_3 and C_4 species, and root structures) and different geographical distributions (e.g., lowland prairie with deeper and moister soil and upland prairie with shallow and drier soil). By reviewing a wide range of research from different parts of the tallgrass prairie region, this article summarizes key and consistent responses, highlight inconsistent responses of tallgrass prairie to major management practices, and point out knowledge gaps. Having a thorough understanding of the impacts of major management practices and disturbances in different settings of climate, functional traits, and time periods can offer better insights into developing and adopting sustainable management practices and better predicting forage quality and quantity for tallgrass prairie systems.

2. Impacts of Management Practices and Disturbances

2.1. Fertilization

2.1.1. Biomass Production

It is well known that aboveground biomass is increased by fertilization, particularly N [17,18]. For example, aboveground biomass was increased by 24–44% with moderate (84 kg N ha^{-1} yr^{-1}) N

fertilization in a prairie site in Iowa [13]. However, previous studies have shown that the response of tallgrass prairie vegetation to N fertilization is influenced by other management practices or disturbance history. For example, N fertilization (100 kg N ha^{-1} yr^{-1}) increased aboveground biomass production by approximately 40% in more than three years older prairies and by >50% in 1–3 year old reconstructed prairies in southern Minnesota [12]. Fertilization (100 kg N ha^{-1} yr^{-1}) of a native tallgrass prairie in the Flint Hills regions of Kansas increased aboveground biomass by 57% in annually burnt sites but only by 15% in unburnt sites [19]. Similarly, N fertilization increased foliage biomass by an average of 9% on unburnt sites for over 15 years, by 68% on annually burnt sites, and by 45% on infrequently burnt sites in Konza Prairie, Kansas [10]. In addition, the response of biomass to N fertilization depends on availability of soil moisture. For example, N and phosphorus (P) fertilizers in a mixed prairie range site in Eastern Montana increased biomass yields by 32% in a dry year, but by up to 218% in a wet year [9]. Root biomass is generally higher in unfertilized prairie [20].

Some greenhouse-based studies showed that cool-season C_3 grasses (highly fibrous root systems) did not respond to mycorrhizae or P fertilization, but warm-season prairie C_4 grasses (coarser root systems) benefited significantly from mycorrhizae or P fertilization [21,22]. However, P responses are rarely observed in tallgrass prairie under natural system because of limitation of N and water [23]. The greenhouse experiments cannot be equated with natural situations. Another study in mixed prairie in eastern Montana also showed that responses to P occurred only when N was not limiting [9].

2.1.2. Plant Diversity

In general, N fertilization reduces plant diversity [18] by favoring plants species that are better competitors for light resource than for soil resources [24]. Species richness of N fertilized tallgrass prairie decreased significantly in Kansas [25]. Forb species showed stronger production response to N enrichment than did grasses [10]. Another study also found that forb species had the strongest response to N fertilization followed by C_3 grasses and C_4 grasses, but growth rates of legumes were not consistently stimulated when grown in monocultures in nutrient-limited soil [17]. As a result, fertilized prairies were characterized by forbs and C_3 grasses, whereas unfertilized prairies were characterized by C_4 grasses and legumes [13], but the abundance of C_3 grasses decreased as the study progressed.

Although the majority of studies have reported that N fertilization reduces prairie species diversity, early spring N application when used with a post-senescence annual harvest increased prairie diversity in August, while unfertilized prairie had higher diversity in June in Iowa [13]. This inconsistency on the influence of N fertilizer on species and functional group diversity was caused by the timing of the N fertilizer application as it was applied as a single dose of N in early spring while most studies apply N either in single or multiple doses during the growing season. Spring N application can stimulate growth of C_3 species and reduce the growth of C_4 grasses, which favors the abundance of forbs later in the growing season due to availability of more light resources [13]. These results highlight the impact of the timing of fertilization on plant diversity.

2.1.3. Soil Chemistry and Microbial Activities

Additions of N can promote aboveground plant biomass, resulting in greater C inputs [26]. Increased C inputs to the soil stimulates the abundance and activity of microbes. Thus, management practices that minimize the addition of C inputs in soils can reduce microbial activities. Consequently, enzyme activity, microbial biomass, and total soil C and N were greater in fertilized prairies than unfertilized prairies [27]. However, in a long-term (1986–1994) burnt tallgrass prairie in Kansas, N fertilization reduced microbial C and N due to increase in acid phosphatase activity (responsible for releasing P) and decrease in urease activity (negative relationship with inorganic N) [28]. Another study reported that short-term N fertilization to a previously unfertilized soil had little or no effect on microbial C and N, but long-term N fertilization increased microbial C and N by >60% in previously unfertilized soil than in previously fertilized soil in a grassland system [29]. Relatively larger

fluctuations in microbial biomass N, but not in microbial C was reported in fertilized prairies [27,30], indicating that microbes use added N without simultaneous increase in C.

Seasonality of microbial biomass associated with prairie phenology should also be considered. Microbial biomass showed seasonality in N fertilized tallgrass prairie (higher in early spring and late-summer/early fall, and lower between March and July with the initiation of plant growth) [8]. Decrease in Microbial N coincided with plant N uptake with the initiation of plant growth in tallgrass prairie. As a result, inorganic soil N concentration was lowest in August due to greater plant uptake even though a high amount of N (100 kg N ha^{-1}) was applied after June [28]. However, the concentration of soil N increased from August to October because of mineralized N from plant tissues returned to soil during vegetation senescence. Microbial activity in N fertilized prairie was dominated by bacteria (lower C:N ratio) than fungi [8]. In addition, N enrichment significantly altered bacterial community diversity in Konza prairie, Kansas [31].

2.2. Burning/Fire

Burning of tallgrass prairie is a commonly recognized disturbance regime and it has become a necessary and an important management tool for prairie systems to maintain dominant C$_4$ grass species, to stimulate plant production, and to improve quality of prairie grasslands. Burning of tallgrass prairie has a profound influence on plant physiological status and growth [32].

2.2.1. Plant Growth and Production

In general, burning of tallgrass prairie increases above- and belowground plant productivity [33]. Enhanced plant growth after burning can be attributed to earlier vegetation green-up due to greater soil heating, greater N availability due to increased N mineralization from soil organic matter (SOM) as a consequence of elevated soil temperature, increased solar radiation at the soil surface due to removal of the litter layer, changes in site biophysical properties, and plant physiological responses [34–36]. Soil warms more rapidly and remains warmer throughout or most of the growing season in burnt areas. Removal of dead vegetation by burning resulted in earlier greening-up and more rapid growth of warm-season C$_4$ grasses in the early growing season than at unburnt native prairie sites [37]. Burning also increased stem tiller density in tallgrass prairie [38]. Reduction in light levels by litter reduced plant growth in unburnt prairie [39]. Higher forage yields of burnt prairies than ungrazed, unmowed, and unburnt prairies [40], and similar forage yields of mowed or dead vegetation removed plots as compared to burnt plots [41,42] indicate that removal of old or dead vegetation is an important factor for higher yields in tallgrass prairie. Root growth was increased by 25% at the annual burnt site compared to the unburnt (for four years) site at Konza Prairie, Kansas as plants compensate for N limitation in annually burnt sites by increasing allocation of roots [43]. Infrequent fire at certain times of the year tends to increase plant growth and palatability of forages [44].

2.2.2. Species Composition and Nutrient Cycling

Absence of burning in tallgrass prairie systems for a long period may increase invasion of woody species and alter plant species composition [45,46]. Accumulation of detritus in absence of fire reduces available light energy, changes microclimate and plant physiological processes [34], and results in decline in species richness [47]. Warm-season C$_4$ grasses were favored in burnt tallgrass prairie plots at the expense of woody species and forbs [25].

Nutrients bound in litter are released as ash on the soil surface by burning. Because of the conducive conditions for free-living N fixers under burning and the ability of the dominant perennial C$_4$ grasses to translocate much of the N from aboveground vegetation to root systems prior to senescence [48], little N is lost by dormant-season fires. However, C and nutrient balance of grasslands are decreased by removing dead aboveground biomass in fires [34], resulting in low C and N inputs into the soil. Thus, frequent spring fires reduced mineralization rates and availability of N in burnt than unburnt prairie [49]. Moreover, plant N demand increases because of greater N uptake by greater

plant biomass in burnt sites [28]. This N deficient condition allows a competitive advantage to shift towards C_4 species with high nitrogen use efficiency (NUE), while build-up of a thick surface litter layer in the absence of fire slows down the decomposition of SOM and increases organic C and N, and consequently, favoring C_3 species [38]. Other studies also reported that high light and low N environments caused by burning favored the growth of dominant C_4 grasses in native tallgrass prairie [50,51].

Time of burning also alters species composition. Winter and spring burning increased species richness in ungrazed prairie in Kansas [52], while late spring burning decreased forbs [38]. All burn regimes increased big bluestem, spring burning increased Indian grass, and autumn and spring burning increased forbs. However, total biomass production did not show significant differences among autumn, winter, or spring burns [53]. The dominance of C_4 grasses was increased and the abundance of cool-season species was reduced in Konza prairie, Kansans by frequent spring burning [40], thereby reducing species richness [11]. However, species richness may increase under occasional spring burning [54], likely by opening spaces for seedling establishment. Summer burning increased the abundance of cool-season C_3 species and reduced C_4 grasses, and fall and spring burning increased forb density in a northern mixed prairie site, USA [55].

Frequency of fire is also important for regulating species composition, soil moisture, and nutrient cycling. Infrequent fire increased woody vegetation [56], while frequent fire increased C_4 grasses and decreased C_3 grasses and forbs and overall plant species richness and diversity. Another study also showed that the species richness of forbs was reduced by increased burn frequency in a tallgrass prairie at Konza, Kansas [57]. The frequency of burning affects nutrient (C and N) cycling differently due to differences in input of litter or pyrogenic organic matter (py-OM) [58]. Decomposition of aboveground litter is a major process of SOM accumulation. Decomposition of litter releases C and N in mineralized forms, while the py-OM remained unused and intact by soil decomposers for a long time [58]. Although substitution of litter inputs with more recalcitrant plant inputs such as py-OM by burning might contribute to C and N sequestration in the soil, input of py-OM which is resistant to microbial degradation and lack of fresh litter for microbial decomposition infers N limitation [58]. Consequently, regular burning of tallgrass prairie inhibits C and N cycling in soil. Over the short-term, fire in the tallgrass prairie at the Flint Hills near Manhattan, Kansas enhanced above- and belowground plant biomass, microbial activity, and NUE, but repeated annual burning over a long-term significantly reduced soil organic N, N availability, and microbial biomass, and increased C:N ratios in SOM [59]. Inorganic N increased by 14% after the first-year burning and decreased by 8% after repeated burning in tallgrass prairie [60] due to higher N uptake associated with more plant growth. Unburnt prairie sites had greatest, annually burnt sites had lowest, and infrequent burnt sites had intermediate levels of inorganic soil N and cumulative net N mineralization at Konza Prairie, Kansas [49].

Soil respiration was higher in frequently burnt tallgrass prairie due to greater root respiration and lower N mineralization rates relative to unburnt or infrequently burnt sites at Konza Prairie, Kansas [43]. Similarly, magnitudes and annual estimates of soil C emissions were higher in more productive burnt sites than in unburnt sites at Konza Prairie, Kansas [61]. The NO_3^- concentration in soil solution was higher in unburnt prairie [62]. Consequently, unburnt tallgrass prairie sites had higher denitrification and N_2O fluxes than in burnt sites [63].

2.2.3. Soil Water Availability

Soil water availability is low in burnt sites due to increase in bare soil evaporation and plant transpiration caused by earlier greening up and enhanced vegetation growth [6,41]. As a result, soil water content was significantly reduced by burning at all depths (up to 1.5 m) in bluestem prairie in the Flint Hills, Kansas [64]. In contrast, higher amounts of litter/mulch in unburnt sites intercept much precipitation and increase infiltration of water into soil as well as reduce soil evaporation [39]. Due to differences in soil water availability, the impact of drought on biomass production is higher at burnt sites than unburnt sites [65].

Time of burning also influences soil water availability. Comparison of the effects of time of burning on soil moisture of bluestem prairie in the Flint Hills, Kansas showed that the earliest burning reduced soil moisture the most due to greater runoff and less infiltration, and the reduction was greater in deeper soil layers [6,64]. However, multiple factors associated with burning can alter water use patterns of grasslands [66]. For example, dominance of C_4 grasses due to burning can reduce soil water content in top soil profile as C_4 grasses rely on water from the shallowest soil, but C_3 forbs and shrubs can utilize water from multiple soil layers based on availability of water [67–69].

2.2.4. Microbial Activities

Previous studies have shown that fires can significantly alter enzyme activity, microbial biomass, activity, and community as well. Burning affects soil enzymes, which are essential for SOM decomposition, nutrient cycling, and microbial biomass, which are labile portions of the organic content in soils and serve as source and sink of plant nutrients of tallgrass prairie soils [28]. However, different enzymes respond differently to burning. Long-term burning and N fertilization (1986–1994) of tallgrass prairie in Kansas reduced microbial C and N, but burning alone had little effect on microbial C and N [28]. Long-term burning increased urease and acid phosphatase activities, but decreased deaminase activity (responsible for releasing N from N compounds, contrary to urease enzyme) [28]. Such changes in microbial biomass and the production of enzymes in long-term burning were attributed to the change in rate of organic matter turnover. Long-term annual burning improved active pool of organic N (N availability) due to faster N turnover [70], thereby affecting microbial biomass and the production of enzymes.

Based on a meta-analysis of 42 published papers on microbial responses to fire, a study [71] reported that fire reduced microbial abundance as a whole and fungal abundance by an average of 33.2% and 47.6%, respectively, across sites. Reduction in microbial biomass can be attributed to microbial mortality due to burning of the organic layer and heat-transfer to soil [72], C substrate-limitation [73], and changes in soil moisture and nutrients [74,75]. However, response of microbes to fire varied among biome and fire types. Microbial biomass reduced greatly by wildfires than prescribed fires, and microbial biomass did not decline in grasslands but declined in boreal and temperate forests after fire [71]. This different microbial response among biomes might be related to differences in fire severity. Higher fuel loads can cause more severe fires in forests than in grasslands. In particular, previous studies have reported that high severity fires reduce microbial biomass greatly than low severity fires [76,77]. In addition, no reduction in microbial biomass in grasslands might be related to its adaptation to less severe fire. Despite significant changes in soil environment, plant species composition, and production by burning, there was little response to burning by the soil microbial community [31], indicating that changes in plant communities and soil microbial communities might correlate to each other.

2.3. Grazing or Removal of Biomass by Harvesting

Natural tallgrass prairies are grazed by wild/domestic herbivores. Grazing affects prairie systems in numerous ways as shown below:

2.3.1. Plant Community Composition and Diversity

Grazing by large herbivores can promote plant species diversity and structural heterogeneity in native tallgrass prairies [78,79] due to their preference on dominant C_4 grasses over subdominant C_3 grasses and forbs [50]. The impacts of cattle stocking densities and grazing systems on plant community composition and diversity were assessed for a period of 1992–1997 in tallgrass prairie in the Flint Hills region of Kansas [7]. The study showed that grazing increased diversity and richness of native plant species. However, grazing systems (season-long vs. late-season rest rotation) did not have significant effect on plant diversity. Animal density was a key management to influence plant species diversity and composition as diversity increased along with stocking density. The study reported that

the abundance of the dominant perennial tallgrasses decreased and the abundance of the C_4 perennial mid-grasses and short grasses increased with increasing cattle stocking densities, whereas C_3 perennial grasses and perennial forbs changed a little, but annual forbs were more abundant in grazed prairie than in ungrazed prairie. Another study in tallgrass prairie in Oklahoma also reported significantly higher number and cover of annuals on grazed treatments than on ungrazed treatments [11]. The study also reported increase in species richness with increasing disturbance intensity. Some other recent studies have also reported the increased abundance and growth of flowering plant communities [57,80] and forb species [81] in tallgrass prairies due to bison grazing.

Like grazing, removal of biomass from harvesting/mowing also alters aboveground community composition [79]. Clipping of biomass stimulated growth of C_3 species and suppressed growth of C_4 species in tallgrass prairie in Oklahoma [82]. The results indicate that shorter and shaded C_3 grasses can get more light due to more open plant canopy under grazing or clipping. Thus, the overall increase in richness and diversity by grazing, harvesting/mowing, and disturbances can be attributed to increase in light availability for other species due to reduction in aboveground biomass of dominant grasses [11].

2.3.2. Impacts on Soil Properties, Nutrient Cycling, and Microbial Activities

Soil compaction, greater bulk density, and deterioration of soil structure are direct impacts of grazing on soil [83]. Change in shoot-root ratio and resource partitioning [84], and reduction in C and N inputs to soil and substrate limitation to microbes [85] are indirect impacts of grazing/removal of biomass on soils. Heavy grazing of prairies at the Marvin Klemme Range Research Station, Oklahoma reduced the rate of SOM and soil nutrient accumulation due to reduced tallgrasses and litter accumulation [86]. Grazing reduced root growth and induced faster N cycling and increased N availability at Konza Prairie, Kansas [43]. Urination, defecation, and transforming and redistribution of N from recalcitrant plant tissue to more labile forms by grazer animals can also significantly increase soil N availability and cycling in grazed than in ungrazed prairie [43,79]. Enhanced biological activity and decomposition causes higher microbial biomass N in grazed relative to ungrazed prairie [80]. However, grazing increases C limitation as shoots regrow and plants allocate less C to root systems [69], thereby reducing belowground C inputs and microbial growth [87]. A lower soil C:N ratio also induces more rapid N cycling in grazed than in ungrazed prairie [43]. The higher floristic quality and species richness of grazed prairies was correlated to soil fertility traits (total soil N, organic C, and microbial biomass C pool) [80].

Grazing can alter soil moisture and water use dynamics of grasses in several ways. Allocation of more C to regrowth of aboveground biomass after grazing reduces root biomass, thereby limiting shallow water uptake by grasses [43]. Grazing can reduce transpiration due to removal of biomass, resulting in increased soil moisture [88]. In contrast, soil compassion by cattle during grazing can limit infiltration and decrease soil moisture [84].

3. Impacts of Tallgrass Prairie Restorations

3.1. Plant Diversity

Plant functional diversity changed over years in restored tallgrass prairies [12]. Annual and biennials dominated in the first year, perennial native composites dominated in the second year, and there was a significant shift to warm-season C_4 grasses after three years. These findings are consistent with the findings of other studies [16,89] that community composition in restored prairies shifts towards C_4 grass dominance within few years. The cover of C_4 grasses was comparable in a 5-year old restored prairie (81%) relative to an adjacent prairie remnant (79%) [16]. Similarly, the cover of C_4 grasses was 71–92% in a 35-year old restored prairie, while it was 59% in an adjacent remnant prairie [16]. Because of C_4 grass dominance, species richness of restored prairies in Illinois declined by 50% within 15 year of restoration [89], which is consistent with the findings of other studies [25,90] that

aboveground plant diversity decreases as restoration continues. Plant-mycorrhizal interactions can also promote C_4 dominance in restored prairies as biomass of C_4 grasses was enhanced by mycorrhizae but not of C_3 grasses or annuals [91]. Another study also showed that arbuscular mycorrhizal inoculum promoted establishment of prairie species in restored tallgrass prairies even though it had no effect on total percent of cover of plants [92].

3.2. Soil Quality

Prairie restorations can improve soil quality over time. Application of 100 kg N ha^{-1} yr^{-1} increased above ground biomass by more than 50% in 1–3 year old restored prairies and approximately by 40% after three years [12]. Belowground productivity, litter mass, and C mineralization rates were increased and N mineralization rate was decreased with the rise of C_4 grasses in restored prairies [12]. Another study also showed that virgin prairie remnant and long-term (21 and 24 years) prairie restorations had significantly greater soil moisture, water holding capacity, organic matter, total C, N, C:N, and microbial biomass, and significantly smaller soil bulk density and smaller levels of poly-β-hydroxybutyrate and phospholipid fatty acid analysis indicators of nutritional stress compared with the agricultural field and recently (7 years) restored prairie [93]. However, some studies have shown that C and N mass did not show significant change over a decade in CRP and restored grasslands [94,95]. Soil C and N on previously cultivated restored prairies was 30–40% lower than that in native prairies even after 30–50 years [86]. The results indicate that restoration prairie sites had intermediate soil quality indicators and microbial community structures compared with the virgin prairie and the agricultural sites even after multiple decades.

3.3. Microbial Community

Cessation of tillage-based agriculture increased the abundance of fungi relative to bacteria most likely due to reduced soil disturbance, and the ratio of fungi to bacteria declined through subsequent succession when tilling ceases [96]. Note that increasing the proportion of fungi relative to bacteria favors C accumulation as fungi are more C efficient and are composed of more recalcitrant C compounds. However, the ratio of fungi to bacteria decreased with soil organic carbon (SOC) in prairie soils [96], which is opposite of what has been reported in agricultural soils.

Comparison of soil microbial communities under recently established (2 years) intensive (located in research stations) and older (at least 10 years) extensive (located in working farms or reserves) corn, switchgrass, and prairie sites shows that soil type was more important than plant community at recently established intensive sites and plant community was more important than soil type at older extensive sites in determining microbial communities [97]. Higher bacterial and fungal biomass under perennial grasses than corn indicated a greater microbial processing potential for retention of carbon, water, and nutrients in perennial grasslands [97].

4. Discussion

4.1. Fertilization

Limitations of N and water are common for tallgrass prairies. Due to these limitations, P responses are rarely observed in tallgrass prairie [23]. Although N fertilization generally increases aboveground biomass and decreases root biomass in tallgrass prairies, the range of stimulation due to fertilization varies greatly across prairie sites, depending on several factors such as nutritional status of the sites, composition of dominant plant species, soil moisture availability, frequency of burning, and other management practices. For example, N fertilization was more effective in wet years than dry years [9]. Similarly, N fertilization was more effective to increase production on frequently or annually burnt sites (N limiting) compared to infrequently burnt and unburnt sites (light limiting) [10]. Overall, results illustrated that N limited sites such as annually burnt sites or newly constructed sites benefitted

more by addition of N. Results also suggest that unfertilized prairies should not be burnt frequently (N limiting) to maintain higher forage production.

Although N fertilization increases forage production, it can affect forage quality by altering plant species composition. Application of N fertilizers can bolster the competitive advantage to C_3 grasses and forbs. Consequently, forbs and C_3 grasses dominated fertilized prairies, and C_4 grasses and legumes dominated unfertilized prairies [13]. However, dominance of C_3 grass species declined over time, indicating the necessity of monitoring compositional changes for long-term in N fertilized prairies. In addition, the impact of the timing of fertilization on plant species composition should be considered. Differential production responses of plant species to N fertilization [10] further suggest that long-term production response of each species to N fertilization should be determined rather than examining the response of overall forage production. Because of temporal differences in plant species diversity [13], plant diversity should be monitored throughout the growing season. In addition, interaction effects of other disturbances or management practices and climatic variability on species diversity should be considered.

Inconsistent effects (increase or decrease) of N fertilization on microbial N were observed in tallgrass prairie [8,28], most likely due to differences in composition of microbial population and nutritional status of the sites. Microbial activity shows seasonal fluctuations, and seasonal dynamics varied in fertilized and unfertilized prairies [27]. These results indicate the necessity of investigating seasonality of biotic (i.e., plant growth, plant community composition) and abiotic (i.e., temperature, precipitation) factors that drive seasonal fluctuations in microbial activity to more fully understand the responses of microbial community to N fertilization.

4.2. Burning/Fire

In general, burning increases above- and belowground biomass production, decreases invasion of woody species, increases dominance of C_4 grasses, and reduces soil moisture, soil C, and nutrient balance in tallgrass prairie. However, the effect of burning in tallgrass prairie can vary across sites due to differences in soil types, burning time, duration, frequency, weather conditions (i.e., dry and normal rainfall years), dominant plant species, and several other factors. For example, drought impact was higher at burnt prairie sites than unburnt prairie sites [65] due to reduction in soil water availability at burnt sites. Burning reduced microbial C during dry years, but increased in normal and wet years in tallgrass prairie in Kansas [8]. These results highlight the interacting effects of disturbances/management practices and climatic variability on the responses of tallgrass prairie to burning.

Most of the previous studies have generally investigated a single cause of the effect of burning and compared results from burnt and unburnt sites. A study of the interaction of disturbances in tallgrass prairie in Oklahoma showed that burning reduced species diversity on ungrazed treatments and increased on grazed treatments [11], indicating the important interaction effects of burning and grazing on plant community structure in tallgrass prairie. Similarly, infrequent burning and grazing maximized plant species diversity, while frequently burnt ungrazed sites had lowest diversity [51]. As a result, grass cover was highest in infrequently burnt ungrazed sites and lowest in frequently burnt grazed sites, and abundance of C_3 forbs was maximum in infrequently burnt grazed sites [51]. Annual burning without grazing lowered N mineralization and induced severe N limitation, but combination of annul burning and grazing enhanced faster N cycling through deposition of labile N in urine and dung [98]. Mowing reduced root biomass and root C storage and resulted in shallower root distribution in annually burnt plots but root biomass in unburnt plots was not affected at Konza Prairie, Kansas [99]. In that study, soil N and C concentrations were not significantly influenced by burning alone, but burning and mowing reduced soil C and N concentrations by 20% and 17%, respectively. Similarly, the interaction effect of burning and N fertilization on microbial C and N was highly significant [28]. These results suggest that the interacting effects of other management practices or disturbances (e.g., interacting effect of burning and grazing) should be examined to

better understand the response of tallgrass prairie systems to burning as well as to recommend any particular timing and frequency of burning. In addition, the response of burning should be evaluated for long-terms since some responses might not evident in short periods. For example, long-term (>40 years) annual burning reduced microbial C and N, but they were not affected by 1–2 years of burning in tallgrass prairie [100].

4.3. Grazing or Removal of Biomass by Harvesting

In general, grazing or removal of biomass by harvesting decreases the abundance of dominant tallgrasses and increases species richness and diversity due to more light availability for shorter and annual species as shorter and shaded species can get more light under more open plant canopy. Consequently, species diversity increased along with stocking density [7] or disturbance intensity [11]. Removal of C inputs to soil by grazing or removal of biomass greatly influences soil characteristics, nutrient cycling, and microbial activities in prairie systems. Due to changes in light energy and nutrient availability, microclimate, and plant physiological status and growth, frequent burning and absence of burning reduce species richness and diversity of prairie, while infrequent burning and grazing maximize species richness. Grazing can modulate the effect of frequent fire on plant diversity by reducing C_4 grass dominance and increasing species diversity and richness [51]. Different fire and grazing regimes can cause heterogeneous landscape to maximize plant diversity [57]. Thus, occurrence of fire and grazing together can create highly productive, diverse, and heterogeneous ecosystems [50,51]. However, timing of burning and grazing should be considered since they influence species diversity and richness.

4.4. Tallgrass Prairie Restorations

Due to a significant community composition shifts towards C_4 grass dominance within 3–5 years of prairie restorations [12], studies have shown lower levels of species richness in restored prairies compared to native remnants [16,90]. A potential mechanism for the shift towards C_4 grass dominance can be competition of soil resources as restored prairie sites are limited by N and have been degraded by agricultural practices over a century [12]. The C_4 grass species can tolerate lower levels of N compared to early successional species [101]. In addition, reduction in light availability for shorter C_3 species with the dominance of taller C_4 grasses can be another possible reason for lower levels of species richness in restored prairies. However, it is not fully understood why C_4 grass dominance is higher in restored prairies than in remnant parries. In our opinion, still poor soil quality indicators and microbial community structures in restored prairies relative to virgin prairie should have been favored the dominance of C_4 grasses.

Studies have shown that restorations of prairie improve soil quality. As a result, biomass production had greater response to N in newly reconstructed prairies (<3 years old) compared to more than three years old prairies [12]. Although prairie restorations increase active pools of C and N rapidly [12], lack of a significant change in total C and N over several decades indicates that restored prairies may require additional inputs to restore SOM, C, and N at the level of the virgin prairie.

5. Summary and Future Directions

Although N fertilization increases aboveground biomass production in tallgrass prairie, the range of stimulation due to N fertilization varies greatly across tallgrass prairie sites due to differences in nutritional status of the sites, composition of dominant plant species, soil moisture availability, frequency of burning, and other management practices. Since N fertilization reduces C_4 grass dominance by bolstering the competitive advantage to other species, judicious use of N fertilization is important to minimize undesirable and invasive species and to maintain healthy native prairie stands.

Higher forage yields at burnt prairies than unburnt prairies, and similar forage yields of mowed or dead vegetation removed sites as compared to burnt sites indicate that removal of old and dead vegetation by burning or mowing is important for higher yields in tallgrass prairie. However,

prairie sites should be burnt infrequently to avoid N limitation to maintain higher forage production. Meanwhile, attention should be paid on the invasion of woody species since infrequent fire can increase woody encroachments. Fire-induced changes in nutrient cycling (i.e., N deficient condition under frequent burning) can influence plant species composition by shifting competitive advantage towards C_4 species with high NUE.

Fire and grazing together can create highly productive, diverse, and heterogeneous tallgrass prairie systems due to modulating the effect of frequent fire by grazing on plant diversity by reducing C_4 grass dominance and increasing species diversity and richness. As infrequent fire and grazing often maximize species richness in prairies and many restorations do not include infrequent burning and regular grazing, infrequent burning and regular grazing can be practiced to maximize species richness and diversity in restored prairies for biodiversity conservation, aesthetics, and support of wildlife.

Although prairie restoration improves soil quality over decades, additional inputs are required to restore soil quality indicators and microbial community structures at the level of virgin prairie. The succession process in restored prairies can be enhanced by increasing the amount of mycorrhizae because of the competitive advantage that mycorrhizae bestow on prairie species.

Since microbial biomass and soil enzymes respond immediately to management practices and tend to stabilize later, their temporal changes should be evaluated while evaluating the effect of management practices. In addition, temporal changes can vary between fertilized (more dynamic) and unfertilized prairies.

The responses of C_3/C_4 mixed tallgrass prairie systems to managements are complicated as the responses may vary as the growing season progresses due to shifts in plant species composition. Thus, the effect of management practices on biomass, plant community composition, soil properties, nutrient cycling, and microbial activities should be evaluated over various times (i.e., winter, spring, summer, fall) of the year.

Since interacting effects of multiple management practices and interannual climatic variability can modify the response of tallgrass prairie systems, a thorough understanding of the main and interactive effects of multiple management practices under diverse plant community (different proportion of C_3 and C_4 species), climatic conditions (different geographical distributions), and time periods (short- vs. long-term) is needed for a holistic assessment.

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