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Josiah D. Dallmann
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Plant Community Response to Disturbances in Nebraska Sandhills Upland Prairie

By

Josiah D. Dallmann

A THESIS

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PLANT COMMUNITY RESPONSE TO DISTURBANCES IN NEBRASKA

SANDHILLS UPLAND PRAIRIE

Josiah D. Dallmann, M.S.

University of Nebraska, 2018

Advisor: John A. Guretzky

Historically, disturbances shaped prairie ecosystems both directly through events like fire and soil moving by animals, as well as indirectly through dynamic rainfall patterns and periodic flux in seed availabilities. We hypothesized that the implementation of several distinct disturbance events in Nebraska Sandhills upland prairie would have measurable effects on plant community composition. We implemented mid-spring fire, soil disturbance in the form of disking, seed addition of native forbs on disked plots, as well as early summer supplemental watering (to mimic minor rainfall events during abnormally dry periods) during 2016 and 2017. Plant community response during the first and second growing season post-disturbance was quantified through measurements of June forb density as well as August percentage cover and herbage mass. In the first season, fire increased the cover of warm-season rhizomatous grasses as well as perennial forbs, such as western ragweed (*Ambrosia psilostachya* DC.), and reduced the cover of annual forbs and species richness. Fire had positive interactive effects on the cover of warm-season grasses in both seasons and on forb density in the second season. Perennial forb seedling establishment from spring seed addition was poor, possibly due to species-specific dormancy and abnormally dry June conditions. Seed availability did play a minor

role on cover of seeded leguminous species, although temporary and year-dependent. Water addition (two 0.64-cm events) and burning, however, improved seeded forb establishment. Disking had generally negative effects on plant cover. Minor water additions had both positive and negative interactive effects on various species, with the underlying drivers of this often unknown. We documented ecological interactions between disturbance events, as fire mediated the negative effect of disking on warm-season grasses and water mediated its negative effect on grasses as a whole. Overall, distinct disturbance events significantly altered plant composition of Sandhills prairie over two growing seasons.

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CHAPTER 1

LITERATURE REVIEW

Great Plains Prairie Ecosystems

The North American Great Plains region is a collection of diverse ecosystems spanning a vast territory from central Canada southward through the United States and into Mexico (Lauenroth et al. 1999). Many of these ecosystems have smooth transitions from one vegetative community to the next due to gradual shifts in precipitation and temperature regimes (Lauenroth et al. 1999). Within the Great Plains region, broad vegetation types of short- to mixed-grass to tallgrass prairies exist. Along the eastward increasing precipitation gradient, there is also a general increase vegetative biomass production (Dalgleish and Hartnett 2006). Broad partitioning of vegetative types also exists north to south through a transition from northern mixed-grass prairie, with a greater proportion of cool-season species (commonly employing the C_3 photosynthetic pathway) to southern mixed-grass prairie, with a greater proportion of warm-season species (commonly employing the C_4 photosynthetic pathway) (Lauenroth et al. 1999). Across the temperature and precipitation gradients, localized soil texture and topography play crucial roles in further determining species composition due to their effect on soil moisture dynamics (Barnes and Harrison 1982; Singh et al. 1998). As a result of these factors, unique ecological regions exist such as the Nebraska Sandhills prairie, which is a vast mixed-grass system including varying abundances of both tallgrass and short-grass prairie plant species (Keeler et al. 1980).

It is widely concluded, that prior to the subsequent rise of modern prairie communities, grassland communities occurred in central North America for at least the last 10,000 years (Axelrod 1985; Lauenroth et al. 1999). Prairie taxa evolved under varied historical regimes commonly involving fire (Howe 1994). According to Theodore Roosevelt (1889), the term 'prairie' originally was derived from the French word for meadow and came into use after European settlement of central North America. During the period of rapid European settlement, the keystone species American Bison (*Bison bison*), was nearly extirpated and cropland replaced large tracts of prairie, resulting in a reduction of tallgrass prairie ecosystems to $< 1\%$ of their original range in many states (Knapp et. al. 1999; Samson and Knopf 1994). In areas of remaining and re-established Great Plains prairie, a key challenge to biologists is a deeper understanding of the role and species-specific effects of disturbances under which prairie ecosystems were historically formed (Palmer et al. 1997).

Population Dynamics

Prairie plants propagate year after year by both vegetative growth and recruitment from the seed bank. The relative importance of vegetative (clonal) and seed reproduction to prairie plant populations has been debated; however, perennial species dominate most Great Plains prairie plant communities (Benson and Hartnett 2006; Hartnett and Keeler 1995; Schacht et al. 2000). Throughout their life history, they reproduce asexually by vegetative growth in the form of new tillers (e.g. ramets in forbs), rhizomes, stolons, and other modified stem structures (Hartnett and Keeler 1995). Upon reaching maturity these perennial grasses, forbs, and shrubs reproduce sexually by flowering and success of

sexual reproduction in these ecosystems is variable from species to species. In contrast to perennials and biennials, annual plants rely solely on sexual reproduction in order to propagate.

Although perennial species may be long lived, various factors such as disease, herbivory, competition, desiccation, and burning and their interactions can eventually cause mortality (Hartnett and Keeler 1995). Competition for water, nutrients, and light are often very important factors affecting plant community dynamics and relative contribution of both clonal and seed reproduction in prairies (Briske and Butler 1989; Hartnett and Bazzaz 1985). These stresses are especially great for prairie plants during recruitment from seed, and mortality rates of seedlings are often high (Hartnett and Keeler 1995). Additionally, competitive dynamics with neighboring plants are often different when comparing established bunchgrass tillers in a tighter clump to laterally spreading rhizomatous grasses or forb species (Hartnett and Keeler 1995). Consequently, response to disturbance can vary based on plant growth habit (Hartnett and Keeler 1995). Prairie communities are often home to nitrogen-fixing legume species such as purple prairieclover (*Dalea purpurea* Vent.) and roundhead lespedeza (*Lespedeza capitata* Michx.) (Ledgard 2001; Tlusty et al. 2004). These plants utilize effective strains of symbiotic rhizobia to provide a source of nitrogen, which invariably affects resource availability among species (Ledgard 2001; Tlusty et al. 2004). In addition, varying mycorrhizal associations on roots of different prairie species strongly influences competition (Hartnett et al. 1993; Hetrick et al. 1989; Marler et al. 1999). There is still much to learn, however, concerning the dynamics of mycorrhizal fungi in prairie ecosystems (Hartnett and Keeler 1995). It is likely that direct effects of certain

disturbances can be attributed, in part, to the indirect manipulation of mycorrhizal populations belowground (Hartnett and Keeler 1995).

Prairie plant population dynamics are strongly affected by disturbance or the lack thereof. While disturbances often directly affect the vegetative growth of dominant perennial species, they also influence dynamics of reproduction by seed. Certain disturbances have been documented to directly affect seed production as seed output of dominant warm-season grasses was shown to increase by annual burning when compared to no burning (Knapp and Hulbert 1986). Gibson (1989) found that plant community characteristics and type of disturbance are key to predicting plant response. Small-scale disturbances, such as localized soil disturbance by animals, and large-scale disturbances such as prescribed burns, intensive grazing, abnormal seed rain, drought, or excess precipitation can have significant impacts on plant growth pattern and reproduction, as well as on invasion of species into prairies (Hartnett and Keeler 1995; Hobbs and Huenneke 1992).

Disturbances and their Interactions

Disturbances shape Great Plains plant populations in many ways. Fire, soil disturbance, seed addition, and supplemental water can all interact in various ways.They also have unique individual roles in shaping plant community response at various spatial and temporal scales in prairie. Ecosystems as we know them today were formed under interacting disturbance regimes occurring across long periods and are in many ways a direct product of these distinct regimes (Denslow 1980). Some debate exists concerning the definition of 'natural' disturbances; however, in prairie ecosystems reinstating

completely natural disturbance regimes is often not possible (Baker 1992). Since these ecosystems developed under disturbances of varied scale, frequency, and intensity it is important imitate the range of historical disturbances as closely as possible when conducting landscape restoration (Baker 1992).

Definitions of a disturbance vary from narrow to quite broad. Narrow definitions often limit disturbance to the concept of immediate and physical biomass manipulation (Grime 1979). A more general definition of disturbance, however, includes "any relatively discrete event in time that disrupts eco-system, community or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985). Hobbs and Huenneke (1992) define disturbance to "include both direct disturbances (those affecting the survivorship of individuals directly) and indirect disturbance (those affecting resource levels or other conditions that then influence individuals in the patch)." Given this context, fire and soil disturbance would directly affect "survivorship" and thereby be direct disturbances (Hobbs and Huenneke 1992). Abnormal seed rain and supplemental watering or lack thereof, would be indirect disturbances as they involve a changing of "resource levels or other conditions" (Hobbs and Huenneke 1992). It should be noted, however, that many prairie studies seldom refer to water and seed regime alteration using the term disturbance.

According to Connell (1978) and Grime (1973), disturbances result in greatest species diversity when exhibited at intermediate frequencies and intensities; however, equilibrium in species composition is rarely attained. The hypothesis is that with reduced intensity and frequency of a disturbance, competitive exclusion and other factors can lead to a loss of diversity (Connell 1978; Grime 1973). Under high levels of disturbance a

lesser number of quickly maturing, colonizing species predominate at the expense of overall diversity, specifically that of species with different life histories (Connell 1978; Grime 1973). Field studies in the mixed-grass prairie of Oklahoma support this general hypothesis (Collins and Barber 1986).

Type and level of disturbance also have specific effects on colonization of grasslands by introduced or invasive species. Low level or absence of disturbance can increase invasibility. A 15-year study in Kansas tallgrass prairie, showed that annual burning reduced exotic cool-season species compared to the absence of burning (Smith and Knapp 1999). The application of supplemental water in the presence of spring fire reduced smooth bromegrass (*Bromus inermis* Leyss.) invasion in South Dakota tallgrass prairie, partly due to enhanced growth of competitive warm-season grasses (Blankespoor and Larson 1994). Some studies, however, have documented an increase in the invasion of native ecosystems due to increasing levels of disturbance (Hobbs and Huenneke 1992). Wet Wisconsin prairie has been shown susceptible to greater levels reed canarygrass (*Phalaris arundinacea* L.) invasion under greater intensities of flooding and sediment deposition and these disturbance effects were additive (Kercher and Zedler 2004). Vegetative composition is also important as a study in mixed-grass prairie demonstrated the effect of plant community type on degree of susceptibility to invasion; as riparian and more mesic communities experienced greater invasion by species such as leafy spurge (*Euphorbia esula* L.) and Kentucky bluegrass (*Poa pratensis* L.) (Larson et al. 2001). Additionally, anthropogenic soil disturbances, such as wheel tracks and firebreaks, have accelerated leafy spurge invasion in mixed-grass prairie and decreased native plant richness (Belcher and Wilson 1989).

Evaluation of disturbances in prairie ecosystems should consider the effects of scale. The degree of scale used commonly affects community heterogeneity, which is defined as "dissimilarity in species composition between samples" (Glenn et al. 1992). In the Konza tallgrass prairie of northeastern Kansas, grazing resulted in greater heterogeneity when viewed at a larger spatial scale, while burning caused greater heterogeneity when viewed at a smaller scale (Glenn et al. 1992). An additional study at Konza found that at a small-scale (10 square m) and in the presence of grazing, annual burning as opposed to longer fire return intervals resulted in increased spatial heterogeneity (Collins and Smith 2006). According to Fuhlendorf et al. (2010) this concept of fire and grazing interaction at small spatial scales, or patches, across the landscape has been termed 'pyric-herbivory' and cited as an evolutionary model that resulted in a "shifting mosaic of vegetation patterns across the landscape." Heterogeneity over time, or temporal heterogeneity, is also important to consider. Increasing fire frequency resulted in a decreased temporal heterogeneity (Collins and Smith 2006). Spring fire and soil disturbance from simulated plains pocket gopher (*Geomys bursarius*) activity generated complex interactive effects that were more evident at larger temporal and spatial scales (Rogers and Hartnett 2001b). In addition to the scale of measurement, the scale of the disturbance applied over space and time is also of importance. In short-grass prairie, blue grama (*Bouteloua gracilis* (Kunth) Lag. ex Griffiths) recovery from disturbance was highest under small patch disturbances compared to larger spatial disturbances (Coffin and Lauenroth 1988). Over a 4-year period, a reduced frequency of rainfall events while keeping total rainfall constant resulted in increased diversity but

reduced above ground net primary productivity (ANPP) in tallgrass prairie (Knapp et al. 2002).

Interactions of disturbances commonly have additive effects (the subsequent response is equal to the sum of the individual disturbance effects combined) and synergistic effects (the subsequent response is greater than the sum of the individual disturbances effects combined) (Hobbs and Huenneke 1992). Grazing and fire have been shown to have partially additive effects on tallgrass prairie species diversity, with the greatest plant diversity being found on burned and grazed areas (Collins 1987). A study in mixed-grass prairie of Oklahoma revealed highest species diversity under the synergistic effects of multiple natural disturbances occurring at an intermediate frequency and intensity (Collins and Barber 1986). They examined various combinations of grazing, fire, and soil disturbance from buffalo wallowing and prairie dogs (*Cynomys* spp.). The highest species diversity was found under grazing and wallowing as well as grazing, wallowing, and fire (Collins and Barber 1986).

Disturbances often interact to affect prairie ecosystems and the nature of these interactions can be quite complex. Some evidence shows the historical connection of fire and soil disturbance, and it has been found that prairie dog colony expansion was greater in adjacent burned instead of unburned prairie (Augustine et al. 2007). There was likely an additional interaction of rainfall on this effect, and in wetter years expansion may have been reduced (Augustine et al. 2007). One study examined the effects of spring fire on individual buffalo wallows and found that species richness increased within wallows due to burning (Collins and Uno 1983). An additional study found significant interactions on graminoid and forb biomass production between various intensities of pocket gopher

burrowing with and without fire (Rogers and Hartnett 2001b). Fire also has variable

effects on plant community composition depending on type of soil disturbance present

and on surrounding vegetation type (Gibson 1989). In tallgrass prairie, fire can alter

canopy water dynamics and this may affect species production (Knapp 1984). Leaf

surface temperature and water potential were less in unburned prairie early in the

growing season, a likely effect of standing dead vegetation slowing wind speeds through

the plant canopy (Knapp 1984). Interaction of disturbances invariably affects species

competition. In eastern Kansas, a study documented the interaction of spring fire

followed by mid-summer water stress and emphasized the slight dominance of big

bluestem (*Andropogon gerardii* Vitman) over switchgrass (*Panicum virgatum* L.) due to

its increased maintenance of photosynthetic activity over varying temperature and low

osmotic potential following these conditions (Knapp 1985).

Effects on plant community composition from interactions between seed addition

and soil disturbance under varying water availability or burning are also evident in the

literature. Fall sod interseeding followed by raking (to increase seed-soil contact) at an

Illinois Prairie Restoration, resulted in increased establishment of two out of four seeded

species over a 10-year period under occasional fall or spring burning (Packard and

Masters 2008). Purple prairieclover and prairie dropseed (*Sporobolus heterolepis* (A.

Gray) A. Gray) densities were three-fold greater under raking compared to without

(Packard and Masters 2008). An additional study documented the increased

establishment of interseeded legumes due to supplemental water application (Groya and

Sheaffer 1981). Soil disturbance can improve establishment of seeded grasses through a

reduction in competition and increase in water availability in Sandhills lowlands (Potvin

1984). A study in Oregon upland prairie incorporated fall fire followed by a broadcast seed addition and documented increased seedling establishment of native species, likely due to removal of plant litter (Maret and Wilson 2005). Additionally, an Iowa study in predominately cool-season grass roadsides documented an increase in certain broadcast native prairie species on burned versus unburned areas (Christiansen 1994). Greater grazing pressure combined with effects of increased water availability in topsoil (due to higher organic matter contents) have contributed to the dominance of introduced Kentucky bluegrass in Sandhills interdunal positions when compared to the adjacent uplands (Schacht et al. 2000). Ultimately, the combination of disturbance type, intensity, spatial extent, and frequency affects plant communities in unique ways. In Oklahoma for example, small-scale, high intensity, annual, bison wallowing increased landscape vegetative heterogeneity while other combinations of disturbance components resulted in different results (Collins and Barber 1986).

Interactions of several direct and indirect disturbance regimes over time including those of fire, soil movement, seed flux, and variable water regimes, often in the presence of grazing, helped to shape prairie ecosystems. With the recent disruption of many of these regimes across North American, the introduction of invasive species, and fragmentation of prairie habitats the re-implementation of disturbances can have large restorative effects in prairie ecosystems (Hobbs and Huenneke 1992). Disturbance type, frequency, intensity, and scale are all important factors in a discussion concerning the main and interactive effects of disturbances in a prairie environment.

Direct Disturbance

According to a broader definition of ecosystem disturbance, direct disturbances are "those affecting the survivorship of individuals directly" (Hobbs and Huenneke 1992). Direct disturbances commonly damage or remove existing vegetation immediately and include events such as burning, logging, flooding, mowing, tilling, and trampling (Blair et al. 2010; Hobbs and Huenneke 1992; Mayor et al. 2015; Petraitis et al. 1989; Smith et al. 2016; Van Klink et al. 2015; Weladji and Forbes 2002). Direct disturbances, however, inevitably result in both direct and indirect effects on plant communities as they directly and physically affect vegetation while indirectly affecting resource levels and competition (McIntyre et al. 1999).

Throughout the literature, there are multiple references to fire and soil disturbance as direct disturbances in perennial systems. Although both fire and appreciable soil disturbance do impact competition in communities, they directly damage or remove existing vegetation and thus can be classified accordingly. Fire is referenced as a direct disturbance with immediate effects on plant communities (Hobbs and Huenneke 1992; Lamb 2008; Weladji and Forbes 2002). In addition, soil-disturbing processes are ultimately referenced as direct disturbances through immediate vegetative effects (Mayor et al. 2015; Smith et al. 2016; Van Klink et al. 2015). Overall, fire and soil disturbance have unique roles in prairie plant communities (Gibson 1989).

Fire

Numerous peer-reviewed studies have addressed the effects of fire in prairie ecosystems. Although results of these studies are variable, depending on a host of factors,

there are several immediate and consistent effects of fire. Fire frequency, intensity, and seasonality are important factors in predicting vegetative response, which then depends on plant functional group (such as warm-season grasses, cool-season grasses, and forbs) or individual plant species (unique life history or growth habit). In addition, studies examining spring, summer, and fall fires in the Nebraska Sandhills have revealed interesting results on overall plant community response.

Historic fire regimes played a key role in driving community composition of prairie. Before European settlement of North America, fire return intervals of 1 to 6 years were common across much of the Great Plains (Frost 1998). Although substantial variability existed, an historic fire return interval of 4 to 8 years was likely in the Nebraska Sandhills (Guyette et al. 2012). Historically, the two major sources of fire ignition were lightning strikes and Native American activities (Frost 1998). Lightning strikes were most common in July and August across much of the northern Great Plains (Higgins 1984). Native Americans started fires throughout the year, but ignitions peaked in April and October (Higgins 1986). These fires, in a large part, were used to manipulate prairie vegetation to assist in hunting of bison herds (Higgins 1986). The presence of regular prairie fire, undoubtedly aided the suppression of woody plant invaders such as eastern redcedar (*Juniperus virginiana* L.) (Blewett 1986; Brigg et al. 2002; Petranka and McPherson 1979).

Certain immediate effects of fire do exist and trends in biomass production have been documented, often depending on prairie type. Directly following burning, prairie ecosystems typically exhibit a greater exposure of bare ground and reduction in litter (Curtis and Partch 1948; Hulbert 1969; Knapp and Seastedt 1986; Wilson and Shay

1990). The majority of studies on the effects of North American prairie fire were conducted in tallgrass prairie ecosystems, and many of these at the Konza Prairie in Kansas. In these ecosystems, dormant season burning increased early season growth rates of warm-season grasses (Ehrenreich and Aikman 1963; Hulbert 1969). An increased soil temperature and light incidence, hence an altered spring microclimate, have been attributed to causation for this earlier growth (Hulbert 1988, 1969; Knapp 1984; Peet et al. 1975; Rice and Parenti 1978). An immediate increase in available nitrogen following fire also may contribute to increased, rapid growth (Hulbert 1988; Ojima et al. 1994); long term effects of frequent fires, however, actually lead to a lower available nitrogen regime (Ojima et al. 1994; Risser and Parton 1982; Seastedt et al. 1991). In tallgrass prairie, fire can often stimulate greater biomass production (Adams and Anderson 1978; Hadley and Kieckhefer 1963; Kucera and Ehrenreich 1962; Rice and Parenti 1978; Schacht et al. 1998). This increase has been attributed, in part, to removal of thick standing vegetation and litter as well as stimulation of grass tiller production (Hubert 1969), but many factors are likely contributing. In review work by Oesterheld et al. (1999), 23 out of 25 studies in tallgrass prairie documented an increase in aboveground biomass due to burning. In cases where production is not increased, seasonality (Towne and Owensby 1984) and frequency of burning (Hulbert and Wilson 1983) are potential causes. In the semiarid short- and mixed-grass prairie, the majority of studies show a decrease in production due to fire (Dix 1960; Oesterheld et al. 1999). This may be due to increased water stress following burning from litter removal, increased runoff, and soil water evaporation (Anderson 1976). Production response, however, in these semiarid regions is highly variable and may increase at times or remain unchanged (Oesterheld et

al. 1999; Schacht and Stubbendieck 1985; Steuter 1987), depending on a host of factors (Schacht and Stubbendieck 1985; Scheintaub et al. 2009).

Fire frequency in prairie is an important factor helping to predict subsequent plant community response. In tallgrass prairie, annual burning when compared to longer fire return intervals promotes the growth of perennial warm-season grasses and suppresses perennial forb growth (Benson et al. 2004; Dalgleish and Hartnett 2009; Kucera and Koelling 1964; Seastedt et al. 1991). This trend is primarily attributed to a shift in belowground bud banks from a forb to grass component (Benson et al. 2004; Dalgleish and Hartnett 2009). Additionally, a lower available nitrogen regime due to long term annual burning favors more competitive warm-season grass species over forbs (Seastedt et al. 1991). Annually burned prairie also reduces growth and reproductive effort of forbs such as perennial prairie coneflower (*Ratibida columnifera* (Nutt.) Woot. & Standl.) compared to infrequently burned prairie (Hartnett 1991). Specific warm-season grasses, such as Indiangrass (*Sorghastrum nutans* (L.) Nash), seem more dependent on frequent burning intervals than other species, such as big bluestem (Hulbert and Wilson 1983). Annual burning regimes select for decreased spatial heterogeneity in plant species composition when compared to longer fire return intervals (Collins 1992), but plant species diversity may increase under annual burning in the presence of bison grazing (Hartnett et al. 1996).

In comparison to fire frequency, seemingly fewer studies have examined the effects of fire intensity on plant communities. According to Heward et al. (2013), "direct measurements of radiative energy released by the fire" define fire intensity while fire severity is more associated with the subsequent ecosystem response. At larger spatial

scales, fire intensity is a reasonable predictor of fire severity (Heward et al. 2013). One study from north-central Oklahoma, revealed that spring burned plots with higher intensity headfires resulted in greater production of tallgrasses and lesser production of forbs when compared to lower intensity backfires (Bidwell et al. 1990). On the Edwards Plateau of Texas, the quantity of fine fuel load available directly increased the degree of woody species suppression, and in dry conditions, a smaller quantity of fine fuel was needed to achieve the same level of tree scorch (Twidwell et al. 2009). High intensity fires can also be studied under dryer than normal conditions, and one study in Texas coastal prairie documented an increase in native forb richness compared to unburned areas after June fire in extreme drought conditions (Twidwell et al. 2012). Ultimately, further research will provide a more robust understanding of the effects of varying fire intensity on plant community response in prairie.

Seasonality of fire is also an important factor affecting prairie community dynamics. Typically, late-spring burns coinciding with rapid cool-season grass growth and the beginning of warm-season grass growth favor warm-season grass production over that of cool-season grasses; and the interplay of cool-season apical meristem elevation, carbohydrate reserve level, and soil moisture retention contribute to this trend (Anderson et al. 1970; Hover and Bragg 1981; Mitchell et al. 1996; Owensby and Anderson 1967; Schacht and Stubbendieck 1985; Steuter 1987; Towne and Owensby 1984; Willson and Stubbendieck 1995). Across a 54-year study period, annual late-spring burning (around 1 May) in Konza tallgrass prairie resulted in greater biomass production when compared to annual winter, early, and mid-spring burning (Towne and Owensby 1984). Dominant warm-season grasses such as big bluestem and Indiangrass also experienced greatest

recovery and subsequent production from late-spring burns (Anderson et al. 1970; Owensby and Anderson 1967; Towne and Owensby 1984). The cool-season, Kentucky bluegrass, was suppressed on all dates by fire, while sedges (*Carex* spp.) were suppressed by late-spring fires but increased under earlier burning dates (Towne and Owensby 1984). Perennial forb and prairie junegrass (*Koeleria macrantha* (Ledeb.) Schult.) production was favored by winter and early-spring burning, but perennial forbs declined with late-spring burning and overall were most abundant in unburned areas (Towne and Owensby 1984). Early to mid-spring burning favored little bluestem (*Schizachyrium scoparium* (Michx.) Nash), while late-spring or winter burning had adverse effects (Towne and Owensby 1984). Overall, early-spring burning maximized species richness while total biomass was relatively less at all burning dates before late-spring (Towne and Owensby 1984), likely due to early season soil moisture reductions (Anderson 1965; Willson and Stubbendieck 1995). Another study documented increases in Indiangrass, little bluestem, and pitcher sage (*Salvia azurea* Michx. ex Lam.), decreases in prairie dropseed, Kentucky bluegrass, cudweed sagewort (*Artemisia ludoviciana* Nutt.), western ragweed (*Ambrosia psilostachya* DC.), heath aster, and no effect on switchgrass, big bluestem, or leadplant (*Amorpha canescens* Pursh) due to annual mid-spring fire in Kansas tallgrass prairie uplands (Abrams and Hulbert 1987) Additionally, mid and late-spring burning has been shown to maximize forage production under grazed conditions (Owensby and Anderson 1967). From an economic standpoint, a Flint Hills study by Launchbaugh and Owensby (1978) demonstrated that late-spring burned prairie improved steer grazing distribution and daily gains when compared to unburned areas given season-long continuous stocking. In contrast, however, a review paper by Engle and Bidwell

(2001) showed that a majority of studies taking place in Oklahoma experienced highest herbage production following early dormant season fire instead of late-spring fire, likely due to an increased growing season length from soil and thermal related differences. Additional studies examining the effects of prairie fire timing have documented a marked suppression in cool-season grass growth by late-spring burning (Anderson et al. 1970; Hover and Bragg 1981; Mitchell et al. 1996). Cover of certain dominant warm-season grasses is commonly increased by spring burning (Anderson et al. 1970; Hover and Bragg 1981; Howe 2011; Mitchell et al. 1996). Little bluestem, although, is affected variously by spring burning (Anderson et al. 1970; Pfeiffer and Steuter 1990; Towne and Owensby 1984). Studies involving mid and late growing season fires often show decreases in total warm-season bunchgrass cover, especially that of little bluestem cover due to its susceptibility to high intensity burns (Engle et al. 1993; Ewing and Engle 1988; Pfeiffer and Steuter 1990; Volesky and Connot 2000). Reductions in cool-season bunchgrasses, however, such as needleandthread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) have also been documented (Vermeire et al. 2011). Late growing season fires often lead to increases in annual forb populations (Pfieffer and Steuter 1990; Towne and Kemp 2008; Volesky and Connot 2000). When seed is available, cool-season annual grasses may increase production due to late-summer fires (Ewing and Engle 1988).

Biondini et al. (1989) examined seasonality of fire and its direct effects on forb abundance and diversity in northern mixed-grass prairie. Annual burning over a 3-year period showed that summer burned and unburned treatments had the highest forb species diversity (Biondini et al. 1989). In contrast, overall forb abundance was greatest on spring and fall burns with nine dominant species, eight of which were perennials, responsible for

82% of forb density (Biondini et al. 1989). Cudweed sagewort and western ragweed showed the greatest positive response to fall fire, while stiff sunflower (*Helianthus pauciflorus* Nutt.) showed the largest increase from spring fire (Biondini et al. 1989). Generally, however, summer fires have beneficial effects on forb populations (Engle et al. 1993; Pfeiffer and Steuter 1990). Effects of fire on forb populations, however, are variable among studies and undoubtedly prone to the interactive roles of "fire frequency, fire-return interval, grazing history, herbicide use, successional stage, weather pattern, edaphic features, and topography" (Engle and Bidwell 2001).

A select few studies have aimed at quantifying the effects of wild and prescribed fire on plant communities in Nebraska Sandhills upland ecological sites. In these studies, vegetative response is often recorded from spring, late growing season, and fall fires. Although substantial variability in results does exist, certain key trends can be inferred from the literature.

Spring fires in the Nebraska Sandhills have immediate effects on current growing season vegetation. A reduction in ground cover and light interception as well as a rise in soil potassium levels are some immediate, documented effects of spring burning (Bragg 1998; Wolfe 1973). Additionally, a shift in growing season vegetative growth has been consistently documented (Bragg 1998, 1978; Pfeiffer and Steuter, 1994; Wolfe 1973). The occurrence of grazing after spring burning may affect same-year production, as one study examining early May prescribed burns highlighted an increase in standing crop of grass in the absence of grazing and a decrease in grass under grazing (Pfeiffer and Steuter 1994). Individual species response to May burning is varied (Bragg 1998; Pfeiffer and Steuter 1994; Wolfe 1973). An overall reduction in the number of forb species present

was also documented across topographic positions (Wolfe 1973). These spring fires can cause direct mortality of forb species, such as early growing species, that do not recover during the same growing season (Pfeiffer and Steuter 1994). In a study by Pfeiffer and Steuter (1994), same-year total forb cover remained constant in response to spring fire but there was a shift in forb species composition. Initial growing season response of western ragweed was unchanged by spring fire in a study by Wolfe (1973), but it was generally viewed as a fire-negative species in a study by Bragg (1998). At certain slope positions, silky prairieclover (*Dalea villosa* (Nutt.) Spreng.) increases during the year of spring burning (Bragg 1978; Wolfe 1973). Stiff sunflower seems to either increase or remain unchanged following spring fire in the Sandhills (Bragg 1998; Wolfe 1973).

The effect of spring burns in the Sandhills in subsequent years is varied. Overall, effects of spring burning seem less pronounced in years following the burn (Bragg 1998, 1978; Pfeiffer and Steuter 1994). In the second growing season post-fire, total herbage and forb production remained unchanged from spring burning in the absence of grazing (Pfeiffer and Steuter 1994). Significant shifts in rhizomatous grasses such as sand bluestem (*Andropogon hallii* Hack.), prairie sandreed (*Calamovilfa longifolia* (Hook.) Hack. ex Scribn. & Southw.), and switchgrass as well as bunchgrasses, such as little bluestem and needleandthread, in early years following fire have been documented; however results are not well defined (Bragg 1998; Pfeiffer and Steuter 1994). Some evidence exists, however, showing reductions in little bluestem and increases in sand bluestem and prairie sandreed (Bragg 1998; Pfeiffer and Steuter 1994) at certain slope positions in sands range sites. Spring burning tended to suppress the cool-season prairie Junegrass, but seemed to have little effect on the abundance of sedges (Bragg 1998).

Relative reductions in western ragweed and increases in stiff sunflower on most slope positions have also been documented in subsequent years following spring fire (Bragg 1998).

The effect of summer and late growing season fires on Sandhills rangeland has been shown to immediately reduce the total plant, grass, forb, and shrub cover during the current growing season (Bragg 1998). In addition, soil temperatures remain greater in the subsequent year (Volesky and Connot 2000). One study found a reduction in grass production but an increase in total forb production in the year after fire (Pfeiffer and Steuter 1995). An increase in forb production was also documented by Volesky and Connot (2000) in response to a late growing season wildfire. A reduction in certain bunchgrasses, such as little bluestem (Volesky and Connot 2000), and a marked reduction in certain "dominant rhizomatous" species, such as western ragweed, has been documented as well (Bragg 1998; Pfeiffer and Steuter 1994). Increases in certain rhizomatous grasses, such as prairie sandreed, as well as certain "annual and perennial taprooted" forbs, such as prairie spurge (*Euphorbia missurica* Raf.), have also been seen (Bragg 1998; Pfeiffer and Steuter 1995; Volesky and Connot 2000).

Fall burning in the Nebraska Sandhills has received minimal study. An early study by Morrison et al. (1986) found an initial increase in grass biomass during the June following an October wildfire. Fall fire, however, typically reduces total end of season plant and grass production (Bragg 1998; Morrison et al. 1986). Effects on forb production are contradicting (Bragg 1998; Morrison et al. 1986). Fall burning, when compared to other seasons of burning, seemed to have the longest lasting effects on plant diversity but these changes were not significant (Bragg 1998).

Ultimately, fire effects on prairie vegetation are diverse regionally. Studies specific to the Nebraska Sandhills show certain trends, but additional research will provide a broader understanding of fire in this context. Seasonality of fire has a large effect on plant response, as functional groups respond differently depending on life history traits (Biondini et al. 1989; Engle et al. 1993; Engle and Bidwell 2001; Owensby and Anderson 1967; Pfeiffer and Steuter 1990; Towne and Owensby 1984). Intensity (Bidwell et al. 1990; Heward et al. 2013; Twidwell et al. 2012, 2009) and frequency (Benson et al. 2004; Collins 1992; Dalgleish and Hartnett 2009; Hulbert and Wilson 1983; Kucera and Koelling 1964; Seastedt et al. 1991) of prairie fire have also been shown to predict production and suppression of plant species and functional groups. Fire has distinct in-season impacts on soil temperature, bare ground, and litter (Curtis and Partch 1948; Hulbert 1988, 1969; Knapp 1984; Knapp and Seastedt 1986; Peet et al. 1975; Rice and Parenti 1978; Wilson and Shay 1990). Total growing season biomass production after fire has been roughly correlated with prairie moisture regime (Oesterheld et al. 1999). Fire regimes have a long history of shaping North American prairie ecosystems and have gained recognition as a key direct disturbance "affecting the survivorship of individuals directly" (Hobbs and Huenneke 1992).

Soil Disturbance

Prairie plant communities are variably impacted by soil disturbance. Soil movement often displaces actively growing plants and can create spaces for new growth to occur through vegetative expansion of existing species or colonization from seed. Literature may incorporate the term 'patch dynamics' in reference to species colonization

into newly made space for growth (Hobbs 1989). Grassland soil disturbances provide microsites for establishment of both native and invasive plant species (Hobbs and Huenneke 1992). Primary hypotheses for this increase in establishment are an ephemeral nutrient and resource flux as well as a decrease in competitive constraints; and these two hypotheses typically interact to varying degrees in different prairie ecosystems (Hobbs and Huenneke 1992). Both historical disturbance regimes and human caused soil disturbances have unique effects on plant species richness and abundances across prairie ecosystems, including the Nebraska Sandhills.

Soil disturbance is not a new phenomenon in prairie ecosystems. According to Benedict et al. (1996), the most influential drivers of soil disturbance were prairie dogs, pocket gophers, and bison. As keystone species, bison (Knapp et al. 1999) and prairie dogs (Kotliar 1999) have especially critical roles to play in plant community diversity (Benedict et al. 1996). Historically the plains pocket gopher and black-tailed prairie dog (*Cynomys ludovicianus*) were responsible for much of the soil disturbance across the Great Plains region, but other animals such as badgers (*Taxidea taxus*) also created unique microhabitats through their burrowing activity (Benedict et al. 1996). Macro-invertebrates also have unique soil mixing roles, and historic frequent fire regimes have been linked to support the prevalence of native earthworm species over those introduced from Europe (*Aporrectodea* spp. and *Octolasion* spp.) (Callaham et al. 2003). Additionally, the distribution of bison and pocket gopher soil moving activities was likely influential in maintaining a diverse Sandhills prairie landscape (Steuter et al. 1995).

Prairie dog activities typically result in a vegetative shift from perennial mid-height grasses to annual forbs and short-grasses (Archer et al. 1987; Coppock et al. 1983;

Winter et al. 2002). Prairie dog selective grazing and mound building resulted in reduced grass cover relative to forb cover inside of prairie dog towns when compared to outside (Bonham and Lerwick 1976). Some species of annual forbs thrive under prairie dog mound building activities and are not directly consumed (Bonham and Lerwick 1976; Koford 1958). This increase in certain annual forb species has been attributed to the effects of soil disturbance, as these species grow directly on mounds (Bonham and Lerwick 1976; Koford 1958). Historically, prairie dog colonies were restricted from much of Sandhills prairie due to the high sand content soils (Sidle et al. 2001).

Bison cause significant and long-lasting soil disturbances through their wallowing activity. Historically, these wallows could be substantial in size (15 m in diameter) and formed depression like bowls on the landscape (Benedict et al. 1996). Wallows were often created by bull bison during the springtime mating season (Collins and Uno 1983), however wallowing activity has been documented to have both spring and fall peaks (McMillan et al. 2000). Active bison wallows have reduced cover of dominant perennial species and increased cover of annual species and exotics, resulting in a more heterogeneous prairie at larger spatial scales (Trager et al. 2004). Landscape level species diversity is also increased by wallowing (Collins and Barber 1986; Collins and Uno 1983). In relic bison wallows over 100 years old, annual species are still more abundant than in nearby undisturbed prairie (Gibson 1989). In a Kansas tallgrass prairie, relic bison wallows exhibited a significantly reduced presence of Indiangrass, Scribner's rosette grass (*Dichanthelium oligosanthes* (Schult.) Gould), white heath aster (*Symphyotrichum ericoides* (L.) G.L. Nesom), and cudweed sagewort; and had a significantly greater presence of common ragweed (*Ambrosia artemisiifolia* L.), heavy sedge (*Carex gravida*

L.H. Bailey), barnyardgrass (*Echinochloa crus-galli* (L.) P. Beauv.), inland rush (*Juncus interior* Wiegand), and green foxtail *(Setaria viridis* (L.) P. Beauv.) (Gibson 1989).

Plains pocket gophers significantly alter grassland ecosystems, especially by their mound building activities. Pocket gophers also consume plant matter, especially roots, and differentiating between soil moving and herbivory as the drivers of plant community shifts can be difficult (Foster and Stubbendieck 1980). Studies examining the effects of pocket gopher soil disturbances in tallgrass prairie generally document a decrease in species richness and a prevalence of perennial grass species on gopher mounds (Gibson 1989; Rogers et al. 2001). This perennial grass prevalence on gopher mounds is likely due to vegetative regrowth of buried plants (Gibson 1989; Rogers and Hartnett 2001a). Mound activity also reduces plant biomass on mounds with mound size affecting the rate of recolonization by prairie plants (Rogers and Hartnett 2001a). Smaller mounds are recolonized more quickly than larger ones (Rogers and Hartnett 2001a). Two years after disturbance, however, inactive mounds are noted to be visually identical to surrounding tallgrass prairie (Rogers and Hartnett 2001a). Additionally, western yarrow (*Achillea millefolium* L.), Great Plains flatsedge (*Cyperus lupulinus* (Spreng.) Marcks), and Scribner's rosette grass are negatively associated with pocket gopher mounds in tallgrass prairie (Gibson 1989). At larger spatial scales increased mound density leads to greater production of forbs and reduced production of graminoids, and over time species richness may decline (Rogers and Hartnett 2001b). According to the intermediate disturbance concept, intermediate levels of disturbance should result in greatest species richness. This idea is supported by Whicker and Detling's (1988) work with prairie dog disturbance. In Arizona short-grass prairie, this concept was mostly supported as highest species richness

was found at pocket gopher disturbances of intermediate age (Martinsen et al. 1990). This study found that higher levels of disturbance resulted in reduced grass cover and greater forb cover (Martinsen et al. 1990). Intermediate pocket gopher disturbance levels have been defined by both high percentages of bare areas from disturbance (Martinsen et al. 1990) and 1 to 2 years of mound building activity (Foster and Stubbendieck 1980).

The plains pocket gopher has a long history of burrowing activity in the Nebraska Sandhills and semiarid prairie regions (Schmeisser 2009). A study from the Sandhills showed that although mounds were present throughout the study area, annual taprooted forb patches seemed to have relatively higher amounts of mound activity (Steuter et al. 1995). An additional study in semiarid Nebraska prairie adjacent to the Sandhills, documented a decrease in plant biomass and increase in bare ground and litter due to gopher soil disturbance at larger spatial scales (Foster and Stubbendieck 1980). The study also found that perennial grass species were significantly reduced and perennial forbs, annual forbs, and annual grasses were generally increased compared to undisturbed prairie (Foster and Stubbendieck 1980). As mounds increased in age to 4 years, however, the proportion of perennial grasses to forbs and annual grasses increased (Foster and Stubbendieck 1980).

Soil disturbance from cattle hoof action, badger and prairie vole (*Microtus ochrogaster*) digging, and ant (*Formicidae*) colony activity also have quantifiable effects on prairie communities. Certain plant populations, such as that of bractless blazingstar (*Mentzelia nuda* (Pursh) Torr. & A. Gray), are greatly reduced in the absence of soil disturbance from cattle grazing (Keeler 1987). Colonization of disturbed areas from badger activity was also shown to vary depending on life history strategies of various

forb species (Platt 1975). Work in the Konza tallgrass prairie revealed that annual species were very common on badger mounds (Gibson 1989). Additionally, this study found that western ragweed populations were negatively affected by ant hill disturbance (Gibson 1989). Badger and prairie vole disturbances increased species richness when compared to undisturbed prairie (Gibson 1989).

Human caused soil disturbance has been implemented in various research studies to examine effects on prairie plant composition. A study in western Oklahoma sandy mixed-grass prairie, showed that disking did not alter forb, grass, and woody production compared to no disking, which demonstrates the resilience of the system to disturbance (Peoples et al. 1994). An additional study from Oklahoma tallgrass prairie, documented a large increase in total plant biomass two growing seasons following a winter plowing compared to unplowed prairie (Rice and Penfound 1954). The authors noted tremendous regrowth from buried plant structures and posited the increase was due to increased plant available nitrogen from incorporation and decomposition of plant material (Rice and Penfound 1954). Disking of Mississippi relic tallgrass prairie buffers positively affected forb prevalence and richness (Dollar 2011). In Iowa riparian grasslands, disking increased forbs, bare ground, and species richness and decreased grasses, litter and standing dead material (Benson et al. 2007). Human-induced soil disturbance can also be important in the establishment of prairie species from seed. A mixed-grass prairie study by Wilson and Gerry (1995), found that higher intensity tilling enhanced seedling establishment of drill-seeded native species. A select few studies have examined effects of human-induced soil disturbance in Nebraska prairie. Rototilling directly increased soil moisture availability in Sandhills lowland sites by suppressing perennial grass growth

and enhancing grass seed establishment (Potvin 1984). A study in south-central Nebraska mixed-grass prairie examined the effects of an 8 to 10 cm deep spring disking (Hart et al. 1985). Researchers documented a first-year decrease in vegetation cover and litter and an increase in bare ground and certain forbs, such as annual sunflower (*Helianthus annuus* L.) and western ragweed, when compared to the control (Hart et al. 1985). In the second year, there was no difference in total vegetation production due to disking (Hart et al. 1985).

Human-induced soil disturbance in prairie has had varied results but causes an immediate reduction in litter and increase in bare ground, and may facilitate seedling establishment (Benson et al. 2007; Hart et al. 1985; Potvin 1984; Wilson and Gerry 1995). Effects on total biomass vary; however, forb richness and abundance are often increased as dominant perennial grasses are suppressed (Benson et al. 2007; Dollar 2011; Hart et al. 1985). Prairie soil disturbances from mammal species such as badgers and voles have been shown to increase plant species richness and abundance of annuals (Gibson 1989; Keeler 1987; Platt 1975). In semiarid Nebraska prairie and tallgrass prairie elsewhere, pocket gopher disturbances typically increase forbs at the expense of dominant perennial grasses, but these contrasts diminish with age of mound (Foster and Stubbendieck 1980; Rogers and Hartnett 2001a, 2001b; Steuter et al. 1995). Plant species richness and biomass are typically reduced, but perennial grass species rapidly recolonize vegetatively (Gibson 1989; Rogers et al. 2001; Rogers and Hartnett 2001a, 2001b). Bison wallows increase species diversity (Collins and Barber 1986; Collins and Uno 1983), while prairie dog mounds and colonies are typically conducive to forb and annual grass prevalence (Archer et al. 1987; Bonham and Lerwick 1976; Coppock et al. 1983; Winter

et al. 2002). Ultimately, historic soil disturbance regimes across various prairie ecosystems are influential in governing patch-dynamic processes, and human-induced disturbances can play similar roles.

Indirect Disturbance

Indirect disturbances are "those affecting resource levels or other conditions that then influence individuals in the patch" and ultimately affect "resource levels and demographic processes" (Hobbs and Huenneke 1992). Examples of indirect disturbances documented in the literature include, but are not limited to, events such as nutrient inputs, certain erosion processes, alteration of sunlight or moisture levels, and occasionally propagule addition (Hobbs et al. 2006; Hobbs and Huenneke 1992; Mayor et al. 2015; Weladji and Forbes 2002). According to Petraitis et al. (1989), disturbances are classified as indirect when they "affect competitors, natural enemies and resource levels in ways that alter survival and fecundity" and do not result in direct death of individuals in a patch.

In comparison to direct disturbances, indirect disturbances are referred to less frequently as formal disturbance events, and often simply deemed induced fluxes in resource or propagule availability (Foster 2001; Knapp et al. 1993). According to Mayor et al. (2015), however, direct or indirect human alteration of ecosystem moisture conditions can be classified as a disturbance. Since such alteration results in changes to resource levels and often alters demographic processes and community structure in prairie, supplemental water can indeed be considered an indirect disturbance (Hobbs and

Huenneke 1992; White and Pickett 1985). Demographic processes and community

structure can also be manipulated through seed addition, as conditions influencing

individuals in a patch are affected by discrete addition events. Although prairie studies do

not commonly classify seed addition as a formal disturbance, definitions from White and

Pickett (1985) as well as Hobbs and Huenneke (1992), allow for such classification.

Hobbs and Huenneke (1992) note that "some forms of disturbance may affect the

availability of invasive propagules" and cite the example of grazers bringing "seed into

an area either on their coats or in feces" as a form of disturbance. Thus, seed addition and

supplemental water can often be viewed as indirect disturbance events and have

influential roles in predicting prairie plant response (Fay et al. 2008; Newman and

Redente 2001).

Seed Addition

Seed addition in prairie ecosystems can be considered an indirect disturbance

(Hobbs and Huenneke 1992). Seed rain in prairie ecosystems is dynamic and important

ecologically. Various studies deal with the role of seed in prairie plant populations and

investigate influential factors such as seed bank dynamics, seed dormancy, seedling

establishment, and interseeding across prairie ecosystems, including the Nebraska

Sandhills.

The role of seed in prairie plant communities, when compared to that of

vegetative propagation, is quite variable. Vegetative reproduction commonly dominates

in prairie ecosystems (Benson and Hartnett 2006; Hartnett and Keeler 1995; Schacht et

al. 2000). Benson and Hartnett (2006) observed that at the end of the growing season

more than 99% of tallgrass prairie plant shoots present derived from vegetative means rather than from seed. Population genetic considerations also come into play, however, as reproduction from seed can improve genetic diversity in a population while clonal growth has mixed effects (Hartnett and Keeler 1995; Schaal and Leverich 1996). Additionally, studies on this topic reveal that successful establishment of perennial species by seed is less common than that of annual or biennial species (Coffin and Lauenroth 1989; Glenn-Lewin et al. 1990). Vegetative reproduction is often more successful in perennial species due to the direct and continued supply of water and nutrients to the new modified shoot from the host plant, in contrast to the limited supply from the a seedling's endosperm (Hartnett and Keeler 1995). The relative contribution of seed to annual regeneration of plant populations is hypothesized to vary across the gradient of drier to wetter prairie ecosystems. Annual seed production may be reduced in dry years and is typically less in mesic prairie ecosystems when compared to wetter tallgrass ecosystems (Hartnett and Keeler 1995, Knapp and Hulbert 1986; Potvin 1988, 1984; Rabinowitz and Rapp 1980). Due to this reduced seed output in short-grass, mixed-grass, and Sandhill prairies, it has been speculated that seed availability could limit the prevalence of certain species (Potvin 1984).

The seed bank in prairie ecosystems is a dynamic entity, and its species composition is often much different from that of the aboveground plant community (Hartnett and Keeler 1995; Pérez et al. 1998). Prairie plant species vary in the viability of their seeds over time and in their proportional presence in the seed bank (Rice 1989). In addition, fluxes in seed bank composition are relatively common and are caused by various disturbances from either the environment or management practices (Coffin and

Lauenroth 1989; Lippert and Hopkins 1950). Seed banks are typically dominated by annual species as opposed to perennials, and as a functional group, forbs are often slightly more abundant than grasses (Pérez et al. 1998; Rice 1989). A seed bank study occurring in Sandhills prairie discovered the annual forb lambsquarters (Ch*enopodium album L.*) and the annual or biennial forb annual eriogonum (*Eriogonum annuum* Nutt.) were the most dominant species; however they had low germination rates of < 6% (Pérez et al. 1998). Forb species with greater levels of germination were woolly plantain (*Plantago patagonica* Jacq.) and Canadian horseweed (*Conyza canadensis* (L.) Cronquist) (Pérez et al. 1998). The most abundant perennial grasses were sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray) and sand lovegrass (*Eragrostis trichodes* (Nutt.) Alph. Wood), and together they had the highest germination rates of all species (Pérez et al. 1998). High amounts of rainfall likely contributed to increased total germination and seed rain in this study (Pérez et al. 1998). Seed number, species diversity, and germination rate were highest in the top 5 cm of soil and decreased with depth (Pérez et al. 1998). An additional study in tallgrass prairie, found the number of seeds germinating from the top 2 cm of soil to be twice of that collected from 2 to 10 cm of depth (Johnson and Anderson 1986).

An important factor directly affecting the recruitment of individuals from seed is species-specific seed dormancy. Many studies have examined effects of various stratification techniques on the germination of native prairie species. Most of these stratification techniques mimic natural processes that occur in prairie ecosystems. Not all species, however, seem to rely on stratification in the same way. According to Karssen (1980a), "temperature, absence of light or oxygen, presence of volatile or allelopathic

inhibitors and moisture conditions are among the factors which may contribute to inhibition of germination and thus to development of dormancy." An additional study by Karssen (1980b) highlighted the importance of nitrate level and its effect on the germination of certain forb species. Cold-moist stratification also improves germination of many prairie species (Bratcher et al. 1993; Johnson and Anderson 1986). And a pre-chilling treatment is important to the germination of many Sandhills prairie grass, grasslike, and forb species (Pérez et al. 1998). Germination response to cold treatment often varies by species due to specific temperature requirements, as was found in a study by Baskin et al. (1992). Stratification period and seed age also have varying effects when compared across different species of prairie penstemon (*Penstemon* spp.) (Lindgren and Schaaf 2004).

A study by Sorensen and Holden (1974), examined 23 species of tallgrass prairie forbs to see what factors could inhibit germination. Almost all species had very viable seed and nearly 70% germinated without any need to break dormancy (Sorensen and Holden 1974). Moist-cold stratification, however, was required for the germination of 22% of the species tested, and resulted in both positive and negative germination effects (Sorensen and Holden 1974). A similar study by Voigt (1977) tested 20 species of prairie forbs and found that only three out of the 20 species tested were able to germinate without moist-cold treatment. This study documented no negative effects of cold moist stratification (Voigt 1977). Voigt (1977) also found that seeds typically germinated 6 to 30 days, but on average about 2 weeks, after dormancy was broken by treatment. Sorensen and Holden (1974) as well as Voigt (1977) showed that physical scarification of the seed coat (waxy outer layer), was also important in breaking dormancy of certain

prairie forbs, especially for species in the legume family (*Fabaceae*). Certain species were found to benefit from a cold-moist treatment followed by scarification. A few species, such as blacksamson echinacea (*Echinacea angustifolia* DC.), experienced greater germination rates when the rough seed covering was eliminated altogether (Sorensen and Holden 1974). Additionally, both of these studies found that certain chemical treatments such as rootone, gibberellate spray, and triphenyl tetrazolium chloride could induce greater germination in certain species.

Seedling establishment is limited and improved by a multiple factors in prairie ecosystems. It is generally accepted that the vast majority of seeds produced never result in an established seedling. Factors responsible for this limited recruitment include seed viability, dormancy, winter kill, disease, competition, predation, and lack of proper microsite conditions for establishment (Glenn-Lewin et al. 1990; Gurevitch 1986; Potvin 1984). Microsite conditions providing adequate water, nutrients, and light are often limiting in prairie ecosystems and can directly affect plant populations (Briske and Butler 1989; Hartnett and Bazzaz 1985). The above-mentioned stresses can cause high mortality in seedlings, affecting annual recruitment from the seed bank (Hartnett and Keeler 1995). In addition, the role of mycorrhizal fungi in facilitating seedling establishment is of great importance and these fungi can positively affect seedling nutrient uptake as well as disease resistance (Hartnett and Keeler 1995; Koide and Schreiner 1992). Vegetative cover of tallgrass prairie seedlings has been shown to be greater with the inoculation of arbuscular mycorrhizal fungi at seeding when compared to non-inoculated plantings (Smith et al. 1998). These positive effects occur with a high degree of variability between the same and different species that grow in close proximity (Chiariello et al. 1982;

Newman et al. 1992). Populations of certain prairie species, such as Platte thistle

(*Cirsium canescens* Nutt.), are severely limited by flower and seed predation as well as

seedling competition with dominant grass species (Louda et al. 1990). In more water

stressed prairie ecosystems, adequate soil moisture is a key factor limiting seedling

establishment (Groya and Sheaffer 1981; Potvin 1984). Certain species of prairie plants

have more prolific seed production than others and may germinate seed throughout the

growing season (Hartnett and Keeler 1995). Although much of this germinated seed will

not survive, a greater percentage of individuals are established due to appropriate timing

with rainfall and microsite conditions (Hartnett and Keeler 1995).

Various studies have implemented seed addition in established prairie through

interseeding. These studies often incorporate some sort of sod suppression technique

prior to interseeding to enhance germination and establishment of the desired species.

Common methods of sod suppression include disking, burning, and applying herbicide

and often result in enhanced establishment of seeded species (Christiansen 1994; Dovel et

al. 1990; Link et al. 2017; Maret and Wilson 2005; Mortensen et al. 2005). Additional

methods can include grazing, mowing, or raking (Packard and Masters 2008; Rowe

2010). Common methods of interseeding include seed addition by drill or broadcast

application, and often incorporate diverse seed mixtures with local ecotype seed origin

(Rowe 2010). Studies in Canadian prairie documented that broadcast seeding of native

grasses resulted in similar initial, but greater long-term establishment when compared to

drill seeding (Bakker et al. 2003; Wilson et al. 2004). Results, however, were highly

variable due to weather conditions and establishment was reduced by drier summers

(Bakker et al. 2003; Wilson et al. 2004). A 20-year study in northwestern Colorado,

documented no difference in plant community composition between broadcast and drill

interseeding (Newman and Redente 2001). Interestingly enough, however, the study

documented differences in plant community composition by functional group between

seeded areas and undisturbed reference areas (Newman and Redente 2001). There are

advantages to both methods given specific timing, as broadcasting during the dormant

season can mimic natural seed rain and benefit some small seeded forb species that take

advantage of freeze-thaw action (Rowe 2010). Spring drilling, however, has an advantage

of direct seed-soil contact that benefits other species (Rowe 2010). Seedings that take

place in late summer must allow for adequate development of seedlings prior to winter in

order to avoid injury and winter kill (Suttie 2008). Seeding rate is also important to

interseeding success, and species diversity can be reduced by including too high of rates

of grass seed relative to forb seed (Dickson and Busby 2009; Rowe 2010). Seed quality,

size, and germination rate are additional considerations in interseeding (Diboll 1997;

Schramm 1990). Studies demonstrating successful interseeding into an established sod

commonly use easily established forage legumes such as alfalfa, Illinois bundleflower

(*Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald), clovers (*Trifolium*

spp.), and others (Dovel et al. 1990; Mortensen et al. 2005; Taylor et al. 1972). Native

prairie grasses and forbs, however, can also be successfully established (Christiansen

1994; Diboll 1997; Dickson and Busby 2009; Rowe 2010). Overall forb establishment

can be enhanced by many methods, including seeding multiple species of forbs compared

to a single species; which has been found increase establishment and long-term

persistence of a stand (Sheley and Half 2006).

Studies involving interseeding often utilize a form of sod suppression prior to seeding and a variety of other methods to improve establishment (Christiansen 1994; Dickson and Busby 2009; Dovel et al. 1990; Maret and Wilson 2005; Mortensen et al. 2005; Packard and Masters 2008; Rowe 2010; Sheley and Half 2006). Successful establishment of seed is variable and depends heavily on appropriate microsite conditions (Briske and Butler 1989; Glenn-Lewin et al. 1990; Gurevitch 1986; Hartnett and Bazzaz 1985; Hartnett and Keeler 1995; Potvin 1984). Various disturbances and environmental gradients can cause flux in prairie seed bank composition (Coffin and Lauenroth 1989; Lippert and Hopkins 1950; Rice 1989), and seed dormancy can inhibit germination of some species (Bratcher et al. 1993; Johnson and Anderson 1986; Karssen 1980a, 1980b; Pérez et al. 1998; Sorensen and Holden 1974; Voigt 1977). Seed availability may limit the presence of certain species, especially in semiarid prairie (Hartnett and Keeler 1995, Knapp and Hulbert 1986; Potvin 1988, 1984; Rabinowitz and Rapp 1980). Annual regeneration of prairie communities, however, is dominated by vegetative growth (Benson and Hartnett 2006; Hartnett and Keeler 1995; Schacht et al. 2000). Overall, multiple factors influence the role of seed addition as an indirect disturbance in prairie.

Supplemental Water

Plant communities in arid and semiarid regions of the world often experience water stress (Chabot and Mooney 1985). The shifting precipitation gradient eastward across the Great Plains from short-grass to mixed-grass to tallgrass prairie, results in an increasing underground bud bank density (Dalgleish and Hartnett 2006) which contributes to biomass production and canopy height in plant communities (Lane et al.

2000). Within regions of semiarid prairie, soil texture and topographic position greatly affect soil water availability and vegetative production (Barnes and Harrison 1982; Singh et al. 1998). A water addition study by Fay et al. (2008) highlighted the importance and interactions of three factors of growing season rainfall: "total quantity (Q), the interval between rainfall events (I), and individual event size (SE)." These factors are important to understanding the natural effects of precipitation in prairie, but most studies do not consider their interactive effects. Various studies, however, have investigated the effects of water stress and supplemental water on the diversity and productivity of prairie communities and one study directly examined effects of yearly precipitation variation on Sandhills vegetation.

In a prairie ecosystem decreasing plant water potentials over a growing season has been shown to reduce plant biomass produced (Hake et al. 1984). In tallgrass prairie, belowground biomass was reduced, especially in the top 10 cm of soil, in a drought year when compared to a wet year (Hayes and Seastedt 1987). Although seasonal shortages in rainfall can reduce belowground production (Fiala et al. 2009), biomass partitioning strategies in certain climates remain constant; and the proportion of belowground to aboveground biomass in drier climates is generally greater (Hui and Jackson 2006). Additionally, prairie grass root to shoot ratios often increase as soil water content decreases in response to growing season water stress (Fay et al. 2003; Hunt et al. 1998). Under these conditions, some perennial grasses, such as prairie cordgrass (*Spartina pectinata* Link) and big bluestem, relocate nitrogen from shoots to underground structures (rhizomes and roots), while more drought tolerant species, such as little bluestem, do not (Heckathorn and DeLucia 1996, 1994). Increased rainfall variability and

reduced rainfall quantity in tallgrass prairie has been shown to reduce ANPP (Piper 1995), and especially the production of subdominant warm-season grasses (Fay et al. 2003). A 4-year study in tallgrass prairie examined long-term rainfall variability, and documented an increase in species diversity but decrease in ANPP in response to reduced frequency of rain events with total rainfall constant (Knapp et al. 2002). Plant species have varying abilities to adjust osmotically in response to drought (Knapp 1984). Grass and forb competition for limited water can be important to the abundance of certain forb species, and when grasses are suppressed through grazing, western ragweed and western ironweed (*Vernonia baldwinii* Torr.) have been shown to increase production (Fahnestock and Knapp 1993). In general, perennial C_3 forbs when compared to perennial C_4 grasses have a greater stomatal conductance and positive change in leaf water potential in response to rain events after drought (Martin et al. 1991). Both groups, however, are adapted to deal with incidence of occasional severe drought (Martin et al. 1991). Competition for soil moisture on interdune soils in the Nebraska Sandhills has led to a high density of shallow rooted cool-season grasses that quickly utilize soil moisture from rainfall events and typically outcompete deep rooted warm-season-grasses, the latter which tend to dominate greater sand content dune soils (Barnes and Harrison 1982). Additionally, grass seedling growth is reduced under drought conditions, with mixed-grass prairie and upland species usually showing greater resilience than tallgrass and lowland species (Mueller and Weaver 1942). Difficulties in drilled perennial grass and forb establishment in Idaho were found in response to drought when compared to wetter years (Ratzlaff and Anderson 1995). A study in the Nebraska Sandhills by Potvin (1984), demonstrated the importance of growing season soil moisture availability to seedling

establishment. Although water-holding capacity was greater on lowland sites, the available mid-summer soil moisture (to aid in seedling establishment) was greater on upland areas due to reduced transpiration rates from less total vegetative cover (Potvin 1984). Overall, water stress typically restricts the growth of individual species with distinct impacts on plant community dynamics.

Water addition studies have been shown to markedly affect plant communities. One 5-year addition study in Colorado short-grass prairie found an increase in overall biomass and a community shift towards increasing warm-season grasses and forbs (especially legumes), as well as half-shrubs, and temporary increases in cool-season grasses and forbs, while succulents declined (Lauenroth et al. 1978). Despite an initial flush of cool-season annual species, perennial warm-season species dominated over time in this semiarid ecosystem (Lauenroth et al. 1978). Another study in semiarid Canada grassland found an increase in grass biomass after 1 year of increased water availability from watering; however, there was no effect on light penetration due to this increased cover (Köchy and Wilson 2004). An 8-year water addition study on the western edge of the tallgrass prairie found increases in vegetative production due to reduced water stress, and demonstrated that water availability limits production in most years (Knapp et. al. 2001). In addition, this study documented a dominance of C_4 warm-season grasses under water-limited conditions and a two-fold increase in C_3 forb biomass from water additions over the course of the study (Knapp et al. 2001). One study documented an increase in root production due to supplemental water in a highland, grassland environment, but not in lowlands (Fiala et al. 2009). The effect of minor rainfall events on plant response in semiarid climates is also of interest, as it affects plant community dynamics in water-

limited environments. One study recorded significant increases in blue grama leaf water potential and leaf water vapor conductance in response to a simulated 5 mm rainfall event in northeastern Colorado rangeland. (Sala and Lauenroth 1982). Supplemental water generally increases plant growth and biomass accumulation, but has differing effects depending on plant functional group.

Long-term precipitation patterns and effects on Sandhills prairie vegetation were documented in a study by Guretzky et al. (2016). This 26-year study found that basal cover was most affected by late summer rainfall, despite the fact that peak rainfall typically occurred in early summer (Guretzky et al. 2016). A few species, including hairy grama (*Bouteloua hirsuta* Lag.), prairie sandreed, sand lovegrass, western ragweed, and needleandthread were negatively correlated with increasing precipitation (Guretzky et al. 2016). Increasing precipitation was negatively correlated with forb and cool-season grass basal cover and positively correlated with warm-season grass cover, while sedge cover was unaffected (Guretzky et al. 2016). The study concluded that "*S. scoparium* and warm-season grass cover as a whole did not explain basal cover responses of most other species and functional groups, providing weak support for competition as a factor that regulates plant community composition in Sandhills prairie" (Guretzky et al. 2016).

Overall, both water stress and abundance in prairies causes flux in plant species composition and productivity (Hartnett and Keeler 1995). Plant functional groups in the Sandhills are variably and strongly affected by precipitation regime (Guretzky et al. 2016). Increased water availability has generally been shown to have positive impacts on forb production relative to certain grasses; however studies in Nebraska that include grazing have found evidence supporting an opposite trend (Fahnestock and Knapp 1993;

Guretzky et al. 2016; Knapp et al. 2001; Lauenroth et al. 1978). Minor rainfall events often have significant effects on plant response in dry prairie environments, and biomass production can be severely reduced by water stress (Hake et al. 1984; Sala and Lauenroth 1982). In addition, partitioning of resources and biomass belowground at the expense of aboveground growth is a common prairie plant response to drought (Fay et al. 2003; Heckathorn and DeLucia 1996, 1994; Hui and Jackson 2006; Hunt et al. 1998). Growing season rainfall patterns and variation across the Great Plains are important factors predicting plant community composition (Barnes and Harrison 1982; Dalgleish and Hartnett 2006; Lane et al. 2000; Singh et al. 1997). Ultimately, supplemental water application, or the lack thereof, can act as an indirect disturbance "affecting resource levels or other conditions that then influence individuals in the patch" (Hobbs and Huenneke 1992).

Literature Cited

Abrams, M.D., Hulbert, L.C., 1987. Effect of Topographic Position and Fire on Species Composition in Tallgrass Prairie in Northeast Kansas. The American Midland Naturalist 117, 442–445. doi:10.2307/2425988.

Adams, D.E., Anderson, R.C., 1978. The Response of a Central Oklahoma Grassland to Burning. The Southwestern Naturalist 23, 623–631. doi:10.2307/3671184.

Anderson, H.W., 1976. Fire effects on water supply, floods, and sedimentation [forest fire]., in: Proceedings Tall Timbers Fire Ecology Conference, 15: 249–260.

Anderson, K.L., 1965. Time of Burning as It Affects Soil Moisture in an Ordinary Upland Bluestem Prairie in the Flint Hills. Journal of Range Management 18, 311–316. doi:10.2307/3895421.

Anderson, K.L., Smith, E.F., Owensby, C.E., 1970. Burning Bluestem Range. Journal of Range Management 23, 81–92. doi:10.2307/3896105.

Archer, S., Garrett, M.G., Detling, J.K., 1987. Rates of Vegetation Change Associated with Prairie Dog (Cynomys ludovicianus) Grazing in North American Mixed-Grass Prairie. Vegetatio 72, 159–166.

Augustine, D.J., Cully, J.F., Johnson, T.L., 2007. Influence of Fire on Black-Tailed Prairie Dog Colony Expansion in Shortgrass Steppe. Rangeland Ecology & Management 60, 538–542.

Axelrod, D.I., 1985. Rise of the Grassland Biome, Central North America. Botanical Review 51, 163–201.

Baker, W.L., 1992. The landscape ecology of large disturbances in the design and management of nature reserves. Landscape Ecol 7, 181–194. doi:10.1007/BF00133309.

Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G., Waddington, J., 2003. Contingency of Grassland Restoration on Year, Site, Competition from Introduced Grasses. Ecological Applications 13, 137–153.

Barnes, P.W., Harrison, A.T., 1982. Species Distribution and Community Organization in a Nebraska Sandhills Mixed Prairie as Influenced by Plant/Soil-Water Relationships. Oecologia 52, 192–201.

Baskin, C.C., Baskin, J.M., Hoffman, G.R., 1992. Seed Dormancy in the Prairie Forb Echinacea angustifolia Var. Angustifolia (Asteraceae): Afterripening Pattern During Cold Stratification. International Journal of Plant Sciences 153, 239–243.

Belcher, J.W., Wilson, S.D., 1989. Leafy Spurge and the Species Composition of a Mixed-Grass Prairie. Journal of Range Management 42, 172–175. doi:10.2307/3899318.

Benedict, R.A., Freeman, P.W., Genoways, H.H., 1996. Prairie legacies-mammals, in: Prairie Conservation: Preserving North America's Most Endangered Ecosystem. Island Press, Washington, DC. pp. 149–166.

Benson, E.J., Hartnett, D.C., 2006. The Role of Seed and Vegetative Reproduction in Plant Recruitment and Demography in Tallgrass Prairie. Plant Ecol 187, 163–178. doi:10.1007/s11258-005-0975-y.

Benson, E.J., Hartnett, D.C., Mann, K.H., 2004. Belowground bud banks and meristem limitation in tallgrass prairieplant populations. Am. J. Bot. 91, 416–421. doi:10.3732/ajb.91.3.416.

Benson, T.J., Dinsmore, J.J., Hohman, W.L., 2007. Responses of Plants and Arthropods to Burning and Disking of Riparian Habitats. The Journal of Wildlife Management 71, 1949–1957.

Bidwell, T.G., Engle, D.M., Claypool, P.L., 1990. Effects of Spring Headfires and Backfires on Tallgrass Prairie. Journal of Range Management 43, 209–212. doi:10.2307/3898674.

Biondini, M.E., Steuter, A.A., Grygiel, C.E., 1989. Seasonal Fire Effects on the Diversity Patterns, Spatial Distribution and Community Structure of Forbs in the Northern Mixed Prairie, USA. Vegetatio 85, 21–31.

Blair, B.C., Letourneau, D.K., Bothwell, S.G., Hayes, G.F., 2010. Disturbance, Resources, and Exotic Plant Invasion: Gap Size Effects in a Redwood Forest. Madroño 57, 11–19. doi:10.3120/0024-9637-57.1.11.

Blankespoor, G.W., Larson, E.A., 1994. Response of Smooth Brome (Bromus inermis Leyss.) to Burning under Varying Soil Moisture Conditions. The American Midland Naturalist 131, 266–272. doi:10.2307/2426252.

Blewett, T.J., 1986. Eastern redcedar's (Juniperus virginiana L.) expanded role in the prairieforest border region. Canandian Journal of Forest Research 4, 222–228.

Bonham, C.D., Lerwick, A., 1976. Vegetation Changes Induced by Prairie Dogs on Shortgrass Range. Journal of Range Management 29, 221–225. doi:10.2307/3897280.

Bragg, T.B., 1998. Fire in the Nebraska Sandhills prairie, in: Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription. Tall Timbers Fire Ecol. Conf. Proc.(TL Pruden and LA Brennan, Eds.). pp. 179–194.

Bragg, T.B., 1978. Effects of burning, cattle grazing, and topography on vegetation of the choppy sands range site in the Nebraska Sandhills prairie. Proc. First Int'l rangelands Cong 248–253.

Bratcher, C.B., Dole, J.M., Cole, J.C., 1993. Stratification Improves Seed Germination of Five Native Wildflower Species. HortScience 28, 899–901.

Briggs, J.M., Knapp, A.K., Brock, B.L., 2002. Expansion of Woody Plants in Tallgrass Prairie: A Fifteen-year Study of Fire and Fire-grazing Interactions. The American Midland Naturalist 147, 287–294. doi:10.1674/0003-0031(2002)147[0287:EOWPIT]2.0.CO;2.

Briske, D.D., Butler, J.L., 1989. Density-Dependent Regulation of Ramet Populations Within the Bunchgrass Schizachyrium Scoparium: Interclonal Versus Intraclonal Interference. Journal of Ecology 77, 963–974. doi:10.2307/2260816.

Callaham Jr., M.A., Blair, J.M., Todd, T.C., Kitchen, D.J., Whiles, M.R., 2003. Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass. Soil Biology and Biochemistry 35, 1079–1093. doi:10.1016/S0038-0717(03)00153-6.

Chiariello, N., Hickman, J.C., Mooney, H.A., 1982. Endomycorrhizal Role for Interspecific Transfer of Phosphorus in a Community of Annual Plants. Science 217, 941–943. doi:10.1126/science.217.4563.941.

Christiansen, P.A., 1994. Establishment of prairie species by overseeding into burned roadside vegetation, in: Proceedings of the 14th North American Prairie Conference. Kansas State University, Manhattan. pp. 167–169.

Coffin, D.P., Lauenroth, W.K., 1989. Spatial and Temporal Variation in the Seed Bank of a Semiarid Grassland. American Journal of Botany 76, 53–58. doi:10.2307/2444773.

Coffin, D.P., Lauenroth, W.K., 1988. The Effects of Disturbance Size and Frequency on a Shortgrass Plant Community. Ecology 69, 1609–1617. doi:10.2307/1941658.

Collins, S.L., 2000. Disturbance Frequency and Community Stability in Native Tallgrass Prairie. The American Naturalist 155, 311–325. doi:10.1086/303326.

Collins, S.L., 1992. Fire Frequency and Community Heterogeneity in Tallgrass Prairie Vegetation. Ecology 73, 2001–2006. doi:10.2307/1941450.

Collins, S.L., 1987. Interaction of Disturbances in Tallgrass Prairie: A Field Experiment. Ecology 68, 1243–1250. doi:10.2307/1939208.

Collins, S.L., Barber, S.C., 1986. Effects of Disturbance on Diversity in Mixed-Grass Prairie. Vegetatio 64, 87–94.

Collins, S.L., Smith, M.D., 2006. Scale-Dependent Interaction of Fire and Grazing on Community Heterogeneity in Tallgrass Prairie. Ecology 87, 2058–2067.

Collins, S.L., Uno, G.E., 1983. The Effect of Early Spring Burning on Vegetation in Buffalo Wallows. Bulletin of the Torrey Botanical Club 110, 474–481. doi:10.2307/2996281.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Coppock, D.L., Detling, J.K., Ellis, J.E., Dyer, M.I., 1983. Plant-Herbivore Interactions in a North American Mixed-Grass Prairie. I. Effects of Black-Tailed Prairie Dogs on Intraseasonal Aboveground Plant Biomass and Nutrient Dynamics and Plants Species Diversity. Oecologia 56, 1–9.

Curtis, J.T., Partch, M.L., 1948. Effect of Fire on the Competition Between Blue Grass and Certain Prairie Plants. The American Midland Naturalist 39, 437–443. doi:10.2307/2421594.

Dalgleish, H.J., Hartnett, D.C., 2009. The effects of fire frequency and grazing on tallgrass prairie productivity and plant composition are mediated through bud bank demography. Plant Ecol 201, 411–420. doi:10.1007/s11258-008-9562-3.

Dalgleish, H.J., Hartnett, D.C., 2006. Below-ground bud banks increase along a precipitation gradient of the North American Great Plains: a test of the meristem limitation hypothesis. New Phytologist 171, 81–89. doi:10.1111/j.1469-8137.2006.01739.x.

Denslow, J.S., 1980. Patterns of Plant Species Diversity during Succession under Different Disturbance Regimes. Oecologia 46, 18–21.

Diboll, N., 1997. Designing seed mixes. The Tallgrass Restoration Handbook: For Prairies, Savannas and Woodlands 135–150.

Dickson, T.L., Busby, W.H., 2009. Forb Species Establishment Increases with Decreased Grass Seeding Density and with Increased Forb Seeding Density in a Northeast Kansas, U.S.A., Experimental Prairie Restoration. Restoration Ecology 17, 597–605. doi:10.1111/j.1526-100X.2008.00427.x.

Dix, R.L., 1960. The Effects of Burning on the Mulch Structure and Species Composition of Grasslands in Western North Dakota. Ecology 41, 49–56. doi:10.2307/1931938.

Dollar, J.G., 2011. Responses of butterfly and forb communities to management of semi-natural grassland buffers. Ph.D. Dissertation. Mississippi State University.

Dovel, R.L., Hussey, M.A., Holt, E.C., 1990. Establishment and Survival of Illinois Bundleflower Interseeded into an Established Kleingrass Pasture. Journal of Range Management 43, 153–156. doi:10.2307/3899035.

Ehrenreich, J.H., Aikman, J.M., 1963. An Ecological Study of the Effect of Certain Management Practices on Native Prairie in Iowa. Ecological Monographs 33, 113–130. doi:10.2307/1948558.

Engle, D.M., Bidwell, T.G., 2001. Viewpoint: The Response of Central North American Prairies to Seasonal Fire. Journal of Range Management 54, 2–10. doi:10.2307/4003519.

Engle, D.M., Stritzke, J.F., Bidwell, T.G., Claypool, P.L., 1993. Late-Summer Fire and Follow-Up Herbicide Treatments in Tallgrass Prairie. Journal of Range Management 46, 542–547. doi:10.2307/4002869.

Ewing, A.L., Engle, D.M., 1988. Effects of Late Summer Fire on Tallgrass Prairie Microclimate and Community Composition. The American Midland Naturalist 120, 212–223. doi:10.2307/2425901.

Fahnestock, J.T., Knapp, A.K., 1993. Water Relations and Growth of Tallgrass Prairie Forbs in Response to Selective Grass Herbivory by Bison. International Journal of Plant Sciences 154, 432–440.

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2003. Productivity responses to altered rainfall patterns in a C4-dominated grassland. Oecologia 137, 245–251. doi:10.1007/s00442-003-1331-3.

Fay, P.A., Kaufman, D.M., Nippert, J.B., Carlisle, J.D., Harper, C.W., 2008. Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. Global Change Biology 14, 1600–1608. doi:10.1111/j.1365-2486.2008.01605.x.

Fiala, K., Tůma, I., Holub, P., 2009. Effect of Manipulated Rainfall on Root Production and Plant Belowground Dry Mass of Different Grassland Ecosystems. Ecosystems 12, 906–914.

Foster, B.L., 2001. Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. Ecology Letters 4, 530–535. doi:10.1046/j.1461-0248.2001.00266.x.

Foster, M.A., Stubbendieck, J., 1980. Effects of the Plains Pocket Gopher (Geomys bursarius) on Rangeland. Journal of Range Management 33, 74–78. doi:10.2307/3898233.

Frost, C.C., 1998. Presettlement fire frequency regimes of the United States: A first approximation, in: Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription, Ed. TL Pruden and LA Brennan. pp. 70–81.

Fuhlendorf, S.D., Townsend, D.E., Elmore, R.D., Engle, D.M., 2010. Pyric-Herbivory to Promote Rangeland Heterogeneity: Evidence From Small Mammal Communities. Rangeland Ecology & Management 63, 670–678.

Gibson, D.J., 1989. Effects of Animal Disturbance on Tallgrass Prairie Vegetation. The American Midland Naturalist 121, 144–154. doi:10.2307/2425665.

Glenn-Lewin, D.C., Johnson, L.A., Jurik, T.W., Akey, A., Leoschke, M., Rosburg, T., 1990. Fire in central North American grasslands: vegetative reproduction, seed germination, and seedling establishment. Fire in North American tallgrass prairies 28–45.

Glenn, S.M., Collins, S.L., Gibson, D.J., 1992. Disturbances in tallgrass prairie: local and regional effects on community heterogeneity. Landscape Ecol 7, 243–251. doi:10.1007/BF00131255.

Griebel, R.L., Winter, S.L., Steuter, A.A., 1998. Grassland birds and habitat structure in sandhills prairie managed using cattle or bison plus fire. Great Plains Research 8, 255–268.

Grime, J.P., 2006. Plant strategies, vegetation processes, and ecosystem properties. John Wiley & Sons.

Grime, J.P., 1973. Competitive Exclusion in Herbaceous Vegetation. Nature 242, 344–347. doi:10.1038/242344a0.

Groya, F.L., Sheaffer, C.C., 1981. Establishment of Sod-seeded Alfalfa at Various Levels of Soil Moisture and Grass Competition. Agronomy Journal 73, 560–565. doi:10.2134/agronj1981.00021962007300030036x.

Guretzky, J.A., Dunn, C., Hillhouse, H., 2016. Long-term Sandhills prairie responses to precipitation, temperature, and cattle stocking rate. Plant Ecol 217, 969–983. doi:10.1007/s11258-016-0622-9.

Gurevitch, J., 1986. Competition and the Local Distribution of the Grass Stipa Neomexicana. Ecology 67, 46–57. doi:10.2307/1938502.

Guyette, R.P., Stambaugh, M.C., Dey, D.C., Muzika, R.-M., 2012. Predicting fire frequency with chemistry and climate. Ecosystems 15, 322–335.

Hadley, E.B., Kieckhefer, B.J., 1963. Productivity of Two Prairie Grasses in Relation to Fire Frequency. Ecology 44, 389–395. doi:10.2307/1932186.

Hake, D.R., Powell, J., McPherson, J.K., Claypool, P.L., Dunn, G.L., 1984. Water Stress of Tallgrass Prairie Plants in Central Oklahoma. Journal of Range Management 37, 147–151. doi:10.2307/3898903.

Hart, M., Waller, S.S., Lowry, S.R., Gates, R.N., 1985. Discing and Seeding Effects on Sod Bound Mixed Prairie. Journal of Range Management 38, 121–125. doi:10.2307/3899253.

Hartnett, D.C., 1991. Effects of Fire in Tallgrass Prairie on Growth and Reproduction of Prairie Coneflower (Ratibida columnifera: Asteraceae). American Journal of Botany 78, 429–435. doi:10.2307/2444965.

Hartnett, D.C., Bazzaz, F.A., 1985. The Integration of Neighbourhood Effects by Clonal Genets in Solidago Canadensis. Journal of Ecology 73, 415–427. doi:10.2307/2260484.

Hartnett, D.C., Hetrick, B.A.D., Wilson, G.W.T., Gibson, D.J., 1993. Mycorrhizal Influence on Intra- and Interspecific Neighbour Interactions among Co-Occurring Prairie Grasses. Journal of Ecology 81, 787–795. doi:10.2307/2261676.

Hartnett, D.C., Hickman, K.R., Walter, L.E.F., 1996. Effects of Bison Grazing, Fire, and Topography on Floristic Diversity in Tallgrass Prairie. Journal of Range Management 49, 413–420. doi:10.2307/4002922.

Hartnett D.C., Keeler K.H., 1995. Population Processes, in: Joern A. Keeler K.H. (eds) The Changing Prairie: North American Grasslands. Oxford University Press, New York, pp. 82–99.

Hayes, D.C., Seastedt, T.R., 1987. Root dynamics of tallgrass prairie in wet and dry years. Can. J. Bot. 65, 787–791. doi:10.1139/b87-105.

Heckathorn, S.A., Delucia, E.H., 1996. Restranslocation of Shoot Nitrogen to Rhizomes and Roots in Prairie Grasses May Limit Loss of N to Grazing and Fire during Drought. Functional Ecology 10, 396–400. doi:10.2307/2390289.

Heckathorn, S.A., DeLucia, E.H., 1994. Drought-Induced Nitrogen Retranslocation in Perennial C4 Grasses of Tallgrass Prairie. Ecology 75, 1877–1886. doi:10.2307/1941592.

Hetrick, B.A.D., Wilson, G.W.T., Hartnett, D.C., 1989. Relationship between mycorrhizal dependence and competitive ability of two tallgrass prairie grasses. Can. J. Bot. 67, 2608–2615. doi:10.1139/b89-337.

Heward, H., Smith, A.M.S., Roy, D.P., Tinkham, W.T., Hoffman, C.M., Morgan, P., Lannom, K.O., 2013. Is burn severity related to fire intensity? Observations from landscape scale remote sensing. Int. J. Wildland Fire 22, 910–918. doi:10.1071/WF12087.

Higgins, K.F., 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains (Federal Government Series No. 161), Resource Publication. U.S. Fish and Wildlife Service, Washington, D.C.

Higgins, K.F., 1984. Lightning Fires in North Dakota Grasslands and in Pine-Savanna Lands of South Dakota and Montana. Journal of Range Management 37, 100–103. doi:10.2307/3898892.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R., Zobel, M., 2006. Novel Ecosystems: Theoretical and Management Aspects of the New Ecological World Order. Global Ecology and Biogeography 15, 1–7.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, Diversity, and Invasion: Implications for Conservation. Conservation Biology 6, 324–337.

Hobbs, R.J., others, 1989. The nature and effects of disturbance relative to invasions. Biological invasions: a global perspective 389–405.

Hover, E.I., Bragg, T.B., 1981. Effect of Season of Burning and Mowing on an Eastern Nebraska Stipa-Andropogon Prairie. The American Midland Naturalist 105, 13–18. doi:10.2307/2425005.

Howe, H.F., 2011. Fire Season and Prairie Forb Richness in a 21-y Experiment. Ecoscience 18, 317–328. doi:10.2980/18-4-3421.

Howe, H.F., 1994. Managing Species Diversity in Tallgrass Prairie: Assumptions and Implications. Conservation Biology 8, 691–704.

Hui, D., Jackson, R.B., 2006. Geographical and interannual variability in biomass partitioning in grassland ecosystems: a synthesis of field data. New Phytologist 169, 85–93. doi:10.1111/j.1469-8137.2005.01569.x.

Hulbert, L.C., 1988. Causes of Fire Effects in Tallgrass Prairie. Ecology 69, 46–58. doi:10.2307/1943159.

Hulbert, L.C., 1986. Fire effects on tallgrass prairie, in: Proceedings of the Ninth North American Prairie Conference. GK Clambey and RH Pemble [eds.], Fargo, North Dakota. pp. 138–l42.

Hulbert, L.C., 1969. Fire and Litter Effects in Undisturbed Bluestem Prairie in Kansas. Ecology 50, 874–877. doi:10.2307/1933702.

Hulbert, L.C., Wilson, J.K., 1983. Fire interval effects on flowering of grasses in Kansas bluestem prairie, in: Proceedings of the Seventh North American Prairie Conference. Southwest Missouri State University, Springfield, Missouri, USA. pp. 255–257.

Hunt, H.W., Morgan, J.A., Read, J.J., 1998. Simulating Growth and Root-shoot Partitioning in Prairie Grasses Under Elevated Atmospheric CO_2 and Water Stress. Ann Bot 81, 489–501. doi:10.1006/anbo.1998.0584.

Johnson, R.G., Anderson, R.C., 1986. The Seed Bank of a Tallgrass Prairie in Illinois. The American Midland Naturalist 115, 123–130. doi:10.2307/2425842.

Jordan, W.R., 1997. The Tallgrass Restoration Handbook: For Prairies, Savannas, and Woodlands. Island Press.

Karssen, C.M., 1980a. Environmental Conditions and Endogenous Mechanisms Involved in Secondary Dormancy of Seeds. Israel Journal of Botany 29, 45–64. doi:10.1080/0021213X.1980.10676875.

Karssen, C.M., 1980b. Patterns of Change in Dormancy During Burial of Seeds in Soil. Israel Journal of Botany 29, 65–73. doi:10.1080/0021213X.1980.10676876.

Keeler, K.H., 1987. Survivorship and Fecundity of the Polycarpic Perennial Mentzelia nuda (Loasaceae) in Nebraska Sandhills Prairie. American Journal of Botany 74, 785–791. doi:10.2307/2443859.

Keeler, K.H., Harrison, A.T., Vescio, L.S., 1980. The Flora and Sandhills Prairie Communities of Arapaho Prairie, Arthur County. Prairie Naturalist 12:65-78.

Kercher, S.M., Zedler, J.B., 2004. Multiple disturbances accelerate invasion of reed canary grass (Phalaris arundinacea L.) in a mesocosm study. Oecologia 138, 455–464. doi:10.1007/s00442-003-1453-7.

Knapp, A.K., 1985. Effect of Fire and Drought on the Ecophysiology of Andropogon gerardii and Panicum virgatum in a Tallgrass Prairie. Ecology 66, 1309–1320. doi:10.2307/1939184.

Knapp, A.K., 1984. Water Relations and Growth of Three Grasses during Wet and Drought Years in a Tallgrass Prairie. Oecologia 65, 35–43.

Knapp, A.K., 1984. Post-Burn Differences in Solar Radiation, Leaf Temperature and Water Stress Influencing Production in a Lowland Tallgrass Prairie. American Journal of Botany 71, 220–227. doi:10.2307/2443749.

Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., Towne, E.G., 1999. The Keystone Role of Bison in North American Tallgrass Prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. BioScience 49, 39–50. doi:10.1525/bisi.1999.49.1.39.

Knapp, A.K., Briggs, J.M., Koelliker, J.K., 2001. Frequency and Extent of Water Limitation to Primary Production in a Mesic Temperate Grassland. Ecosystems 4, 19–28. doi:10.1007/s100210000057.

Knapp, A.K., Fahnestock, J.T., Hamburg, S.P., Statland, L.B., Seastedt, T.R., Schimel, D.S., 1993. Landscape Patterns in Soil-Plant Water Relations and Primary Production in Tallgrass Prairie. Ecology 74, 549–560. doi:10.2307/1939315.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., McCarron, J.K., 2002. Rainfall Variability, Carbon Cycling, and Plant Species Diversity in a Mesic Grassland. Science 298, 2202–2205. doi:10.1126/science.1076347.

Knapp, A.K., Hulbert, L.C., 1986. Production, Density and Height of Flower Stalks of Three Grasses in Annually Burned and Unburned Eastern Kansas Tallgrass Prairie: A Four Year Record. The Southwestern Naturalist 31, 235–241. doi:10.2307/3670564.

Knapp, A.K., Seastedt, T.R., 1986. Detritus Accumulation Limits Productivity of Tallgrass Prairie. BioScience 36, 662–668. doi:10.2307/1310387.

Köchy, M., Wilson, S.D., 2004. Semiarid Grassland Responses to Short-Term Variation in Water Availability. Plant Ecology 174, 197–203.

Koford, C.B., 1958. Prairie Dogs, Whitefaces, and Blue Grama. Wildlife Monographs 3–78.

Koide, R.T., Schreiner, R.P., 1992. Regulation of the vesicular-arbuscular mycorrhizal symbiosis. Annual review of plant biology 43, 557–581.

Kotliar, N.B., Baker, B.W., Whicker, A.D., Plumb, G., 1999. A Critical Review of Assumptions About the Prairie Dog as a Keystone Species. Environmental Management 24, 177–192. doi:10.1007/s002679900225.

Kucera, C.L., Ehrenreich, J.H., 1962. Some Effects on Annual Burning on Central Missouri Prairie. Ecology 43, 334–336. doi:10.2307/1931993.

Kucera, C.L., Koelling, M., 1964. The Influence of Fire on Composition of Central Missouri Prairie. The American Midland Naturalist 72, 142–147. doi:10.2307/2423217.

Lamb, E.G., 2008. Direct and Indirect Control of Grassland Community Structure by Litter, Resources, and Biomass. Ecology 89, 216–225.

Lane, D.R., Coffin, D.P., Lauenroth, W.K., 2000. Changes in Grassland Canopy Structure across a Precipitation Gradient. Journal of Vegetation Science 11, 359–368. doi:10.2307/3236628.

Larson, D.L., Anderson, P.J., Newton, W., 2001. Alien Plant Invasion in Mixed-Grass Prairie: Effects of Vegetation Type and Anthropogenic Disturbance. Ecological Applications 11, 128–141. doi:10.2307/3061061.

Lauenroth, W.K., Burke, I.C., Gutmann, M.P., 1999. The structure and function of ecosystems in the central North American grassland region. Great Plains Research 9, 223–259.

Lauenroth, W.K., Dodd, J.L., Sims, P.L., 1978. The Effects of Water- and Nitrogen-Induced Stresses on Plant Community Structure in a Semiarid Grassland. Oecologia 36, 211–222.

Launchbaugh, J.L., Owensby, C.E., 1978. Kansas rangelands. Kansas Agricultural Experiment Station Bulletin 622, 56.

Ledgard, S.F., 2001. Nitrogen cycling in low input legume-based agriculture, with emphasis on legume/grass pastures. Plant and Soil 228, 43–59. doi:10.1023/A:1004810620983.

Lindgren, D.T., Schaaf, D.M., 2004. Influence of Seed Stratification and Seed Age on Emergence of Penstemon. HortScience 39, 1385–1386.

Link, A., Kobiela, B., DeKeyser, S., Huffington, M., 2017. Effectiveness of Burning, Herbicide, and Seeding Toward Restoring Rangelands in Southeastern North Dakota. Rangeland Ecology & Management 70, 599–603. doi:10.1016/j.rama.2017.03.001.

Lippert, R.D., Hopkins, H.H., 1950. Study of Viable Seeds in Various Habitats in Mixed Prairie. Transactions of the Kansas Academy of Science (1903-) 53, 355–364. doi:10.2307/3626149.

Louda, S.M., Potvin, M.A., Collinge, S.K., 1990. Predispersal Seed Predation, Postdispersal Seed Predation and Competition in the Recruitment of Seedlings of a Native Thistle in Sandhills Prairie. The American Midland Naturalist 124, 105–113. doi:10.2307/2426083.

Maret, M.P., Wilson, M.V., 2005. Fire and Litter Effects on Seedling Establishment in Western Oregon Upland Prairies. Restoration Ecology 13, 562–568. doi:10.1111/j.1526-100X.2005.00071.x.

Marler, M.J., Zabinski, C.A., Callaway, R.M., 1999. Mycorrhizae Indirectly Enhance Competitive Effects of an Invasive Forb on a Native Bunchgrass. Ecology 80, 1180–1186. doi:10.2307/177065.

Martin, C.E., Harris, F.S., Norman, F.J., 1991. Ecophysiological Responses of C3 Forbs and C4 Grasses to Drought and Rain on a Tallgrass Prairie in Northeastern Kansas. Botanical Gazette 152, 257–262.

Martinsen, G.D., Cushman, J.H., Whitham, T.G., 1990. Impact of Pocket Gopher Disturbance on Plant Species Diversity in a Shortgrass Prairie Community. Oecologia 83, 132–138.

Mayor, S.J., Jr, J.F.C., He, F., Boutin, S., 2015. Scaling Disturbance Instead of Richness to Better Understand Anthropogenic Impacts on Biodiversity. Plos One 10, e0125579. doi:10.1371/journal.pone.0125579.

McIntyre, S., Lavorel, S., Landsberg, J., Forbes, T.D.A., 1999. Disturbance Response in Vegetation: Towards a Global Perspective on Functional Traits. Journal of Vegetation Science 10, 621–630. doi:10.2307/3237077.

McMillan, B.R., Cottam, M.R., Kaufman, D.W., 2000. Wallowing behavior of American bison (Bos bison) in tallgrass prairie: an examination of alternate explanations. The American Midland Naturalist 144, 159–167.

Mitchell, R.B., Masters, R.A., Waller, S.S., Moore, K.J., Young, L.J., 1996. Tallgrass Prairie Vegetation Response to Spring Burning Dates, Fertilizer, and Atrazine. Journal of Range Management 49, 131–136. doi:10.2307/4002682.

Mooney, H.A., Chabot, B.F., 1985. Physiological Ecology of North American Plant Communities. Chapman and Hall.

Morrison, L.C., DuBois, J.D., Kapustka, L.A., 1986. The vegetational response of a Nebraska Sandhills grassland to a naturally occurring fall burn. Prairie Naturalist 18, 179–184.

Mortenson, M.C., Schuman, G.E., Ingram, L.J., Nayigihugu, V., Hess, B.W., 2005. Forage Production and Quality of a Mixed-Grass Rangeland Interseeded With Medicago sativa ssp. falcata. Rangeland Ecology & Management 58, 505–513. doi:10.2111/1551-5028(2005)58[505:FPAQOA]2.0.CO;2.

Mueller, I.M., Weaver, J.E., 1942. Relative Drought Resistance of Seedlings of Dominant Prairie Grasses. Ecology 23, 387–398. doi:10.2307/1930125.

Newman, E.I., Eason, W.R., Eissenstat, D.M., Ramos, M.I.R.F., 1992. Interactions between plants: the role of mycorrhizae. Mycorrhiza 1, 47–53. doi:10.1007/BF00206135.

Newman, G.J., Redente, E.F., 2001. Long-Term Plant Community Development as Influenced by Revegetation Techniques. Journal of Range Management 54, 717–724. doi:10.2307/4003677.

Oesterheld, M., Loreti, J., Semmartin, M., Paruelo, J.M., 1999. Grazing, fire, and climate effects on primary productivity of grasslands and savannas. Ecosystems of the world 287–306.

Ojima, D.S., Schimel, D.S., Parton, W.J., Owensby, C.E., 1994. Long- and Short-Term Effects of Fire on Nitrogen Cycling in Tallgrass Prairie. Biogeochemistry 24, 67–84.

Packard, S., Masters, L., 2008. Interseeding with and without Raking (Illinois). Ecological Rest. 26, 113–114. doi:10.3368/er.26.2.113.

Palmer, M.A., Ambrose, R.F., Poff, N.L., 1997. Ecological Theory and Community Restoration Ecology. Restoration Ecology 5, 291–300. doi:10.1046/j.1526-100X.1997.00543.x.

Pausas, J.G., Keeley, J.E., 2009. A Burning Story: The Role of Fire in the History of Life. BioScience 59, 593–601. doi:10.1525/bio.2009.59.7.10.

Peet, M., Anderson, R., Adams, M.S., 1975. Effect of Fire on Big Bluestem Production. The American Midland Naturalist 94, 15–26. doi:10.2307/2424534.

Peoples, A.D., Lochmiller, R.L., Leslie, D.M., Engle, D.M., 1994. Producing Northern Bobwhite Food on Sandy Soils in Semiarid Mixed Prairies. Wildlife Society Bulletin (1973-2006) 22, 204–211.

Pérez, C.J., Waller, S.S., Moser, L.E., Stubbendieck, J.L., Steuter, A.A., 1998. Seedbank Characteristics of a Nebraska Sandhills Prairie. Journal of Range Management 51, 55–62. doi:10.2307/4003564.

Petraitis, P.S., Latham, R.E., Niesenbaum, R.A., 1989. The Maintenance of Species Diversity by Disturbance. The Quarterly Review of Biology 64, 393–418.

Petranka, J.W., McPherson, J.K., 1979. The Role of Rhus Copallina in the Dynamics of the Forest-Prairie Ecotone in North-Central Oklahoma. Ecology 60, 956–965. doi:10.2307/1936864.

Pfeiffer, K.E., Steuter, A.A., 1994. Preliminary Response of Sandhills Prairie to Fire and Bison Grazing. Journal of Range Management 47, 395–397. doi:10.2307/4002337.

Piper, J.K., 1995. Composition of prairie plant communities on productive versus unproductive sites in wet and dry years. Can. J. Bot. 73, 1635–1644. doi:10.1139/b95-177.

Platt, W.J., 1975. The Colonization and Formation of Equilibrium Plant Species Associations on Badger Disturbances in a Tall-Grass Prairie. Ecological Monographs 45, 285–305. doi:10.2307/1942425.

Potvin, M.A., 1988. Seed rain on a Nebraska Sandhills prairie. Prairie Naturalist 20, 81–89.

Potvin, M.A., 1984. Factors affecting native grass seedling establishment along topographic gradients in the Nebraska Sandhills: an experimental approach. ETD collection for University of Nebraska - Lincoln 1–165.

Rabinowitz, D., Rapp, J.K., 1980. Seed Rain in a North American Tall Grass Prairie. Journal of Applied Ecology 17, 793–802. doi:10.2307/2402656.

Ratzlaff, T.D., Anderson, J.E., 1995. Vegetal Recovery following Wildfire in Seeded and Unseeded Sagebrush Steppe. Journal of Range Management 48, 386–391. doi:10.2307/4002239.

Rice, E.L., Parenti, R.L., 1978. Causes of Decreases in Productivity in Undisturbed Tall Grass Prairie. American Journal of Botany 65, 1091–1097. doi:10.2307/2442326.

Rice, E.L., Penfound, W.T., 1954. Plant Succession and Yield of Living Plant Material in a Plowed Prairie in Central Oklahoma. Ecology 35, 176–180. doi:10.2307/1931114.

Rice, K.J., 1989. Impacts of seed banks on grassland community structure and population dynamics. Ecology of soil seed banks 211, 230.

Risser, P.G., Parton, W.J., 1982. Ecosystem Analysis of the Tallgrass Prairie: Nitrogen Cycle. Ecology 63, 1342–1351. doi:10.2307/1938862.

Rogers, W.E., Hartnett, D.C., 2001a. Vegetation Responses to Different Spatial Patterns of Soil Disturbance in Burned and Unburned Tallgrass Prairie. Plant Ecology 155, 99–109.

Rogers, W.E., Hartnett, D.C., 2001b. Temporal vegetation dynamics and recolonization mechanisms on different-sized soil disturbances in tallgrass prairie. Am. J. Bot. 88, 1634–1642.

Rogers, W.E., Hartnett, D.C., Elder, B., 2001. Effects of Plains Pocket Gopher (Geomys bursarius) Disturbances on Tallgrass-prairie Plant Community Structure. The American Midland Naturalist 145, 344–357. doi:10.1674/0003-0031(2001)145[0344:EOPPGG]2.0.CO;2.

Roosevelt, T., 1894. The Winning of the West. U of Nebraska Press.

Rowe, H.I., 2010. Tricks of the Trade: Techniques and Opinions from 38 Experts in Tallgrass Prairie Restoration. Restoration Ecology 18, 253–262. doi:10.1111/j.1526-100X.2010.00663.x.

Sala, O.E., Lauenroth, W.K., 1982. Small Rainfall Events: An Ecological Role in Semiarid Regions. Oecologia 53, 301–304.

Samson, F., Knopf, F., 1994. Prairie Conservation in North America. BioScience 44, 418–421. doi:10.2307/1312365.

Schaal, B.A., Leverich, W.J., 1996. Molecular Variation in Isolated Plant Populations. Plant Species Biology 11, 33–40. doi:10.1111/j.1442-1984.1996.tb00106.x.

Schacht, W.H., Smart, A.J., Anderson, B.E., Moser, L.E., Rasby, R., 1998. Growth Responses of Warm-Season Tallgrasses to Dormant-Season Management. Journal of Range Management 51, 442–446. doi:10.2307/4003331.

Schacht, W.H., Volesky, J.D., Bauer, D., Smart, A., Mousel, E., 2000. Plant community patterns on upland prairie in the eastern Nebraska sandhills. Agronomy–Faculty Publications 339.

Schacht, W., Stubbendieck, J., 1985. Prescribed Burning in the Loess Hills Mixed Prairie of Southern Nebraska. Journal of Range Management 38, 47–51. doi:10.2307/3899332.

Scheintaub, M.R., Derner, J.D., Kelly, E.F., Knapp, A.K., 2009. Response of the shortgrass steppe plant community to fire. Journal of Arid Environments 73, 1136–1143. doi:10.1016/j.jaridenv.2009.05.011.

Schmeisser, R.L., Loope, D.B., Wedin, D.A., 2009. Clues to the medieval destabilization of the nebraska sand hills, usa, from ancient pocket gopher burrows. Palaios 24, 809–817. doi:10.2110/palo.2009.p09-037r.

Schramm, P., 1990. Prairie restoration: a twenty-five year perspective on establishment and management, in: Proceedings of the Twelfth North American Prairie Conference. pp. 169–177.

Seastedt, T.R., Briggs, J.M., Gibson, D.J., 1991. Controls of Nitrogen Limitation in Tallgrass Prairie. Oecologia 87, 72–79.

Sheley, R.L., Half, M.L., 2006. Enhancing Native Forb Establishment and Persistence Using a Rich Seed Mixture. Restoration Ecology 14, 627–635. doi:10.1111/j.1526-100X.2006.00174.x.

Sidle, J.G., Johnson, D.H., Euliss, B.R., 2001. Estimated areal extent of colonies of black-tailed prairie dogs in the northern great plains. Journal of Mammalogy 82, 928–936. doi:10.1644/1545-1542(2001)082<0928:EAEOCO>2.0.CO;2.

Singh, J.S., Milchunas, D.G., Lauenroth, W.K., 1998. Soil Water Dynamics and Vegetation Patterns in a Semiarid Grassland. Plant Ecology 134, 77–89.

Smith, C.R., Blair, P.L., Boyd, C., Cody, B., Hazel, A., Hedrick, A., Kathuria, H., Khurana, P., Kramer, B., Muterspaw, K., Peck, C., Sells, E., Skinner, J., Tegeler, C., Wolfe, Z., 2016. Microbial community responses to soil tillage and crop rotation in a corn/soybean agroecosystem. Ecol Evol 6, 8075–8084. doi:10.1002/ece3.2553.

Smith, M.D., Knapp, A.K., 1999. Exotic plant species in a C4-dominated grassland: invasibility, disturbance, and community structure. Oecologia 120, 605–612. doi:10.1007/s004420050896.

Smith, M.R., Charvat, I., Jacobson, R.L., 1998. Arbuscular mycorrhizae promote establishment of prairie species in a tallgrass prairie restoration. Can. J. Bot. 76, 1947–1954. doi:10.1139/b98-205.

Sorensen, J.T., Holden, D.J., 1974. Germination of Native Prairie Forb Seeds. Journal of Range Management 27, 123–126. doi:10.2307/3896747.

Steuter, A.A., 1987. C3/ C4 Production Shift on Seasonal Burns: Northern Mixed Prairie. Journal of Range Management 40, 27–31. doi:10.2307/3899356.

Steuter, A.A., Steinauer, E.M., Hill, G.L., Bowers, P.A., Tieszen, L.L., 1995. Distribution and Diet of Bison and Pocket Gophers in a Sandhills Prairie. Ecological Applications 5, 756–766. doi:10.2307/1941983.

Suttie, J.M., 2008. Forages, The Science of Grassland Agriculture; Volume II; Edited by BarnesR. F, NelsonC J., MooreK. J and CollinsM.. Ames, Iowa and Oxford: Blackwell Publishing (2007). pp. 790,\pounds 90.00. ISBN 978-081304217.

Taylor, T.H., Foote, J.S., Snyder, J.H., Smith, E.M., Templeton, W.C., 1972. Legume Seedlings Stands Resulting from Winter and Spring Sowings in Kentucky Bluegrass (Poa pratensis L.) Sod. Agronomy Journal 64, 535–538. doi:10.2134/agronj1972.00021962006400040037x.

Tlusty, B., Grossman, J.M., Graham, P.H., 2004. Selection of rhizobia for prairie legumes used in restoration and reconstruction programs in Minnesota. Can. J. Microbiol. 50, 977–983. doi:10.1139/w04-084.

Towne, E.G., Kemp, K.E., 2008. Long-Term Response Patterns of Tallgrass Prairie to Frequent Summer Burning. Rangeland Ecology & Management 61, 509–520. doi:10.2111/08-043.1.

Towne, G., Owensby, C., 1984. Long-Term Effects of Annual Burning at Different Dates in Ungrazed Kansas Tallgrass Prairie. Journal of Range Management 37, 392–397. doi:10.2307/3899622.

Trager, M.D., Wilson, G.W.T., Hartnett, D.C., 2004. Concurrent Effects of Fire Regime, Grazing and Bison Wallowing on Tallgrass Prairie Vegetation. The American Midland Naturalist 152, 237–247. doi:10.1674/0003-0031(2004)152[0237:CEOFRG]2.0.CO;2.

Twidwell, D., Fuhlendorf, S.D., Engle, D.M., Taylor, C.A., 2009. Surface Fuel Sampling Strategies: Linking Fuel Measurements and Fire Effects. Rangeland Ecology & Management 62, 223–229.

Twidwell, D., Rogers, W.E., McMahon, E.A., Thomas, B.R., Kreuter, U.P., Blankenship, T.L., 2012. Prescribed Extreme Fire Effects on Richness and Invasion in Coastal Prairie. Invasive Plant Science and Management 5, 330–340. doi:10.1614/IPSM-D-12-00017.1.

Van Klink, R., Van der Plas, F., Van Noordwijk, C.G.E. (Toos), WallisDeVries, M.F., Olff, H., 2015. Effects of large herbivores on grassland arthropod diversity. Biol Rev 90, 347–366. doi:10.1111/brv.12113.

Vermeire, L.T., Crowder, J.L., Wester, D.B., 2011. Plant Community and Soil Environment Response to Summer Fire in the Northern Great Plains. Rangeland Ecology & Management 64, 37–46.

Voigt, J.W., 1977. Seed Germination of True Prairie Forbs. Journal of Range Management 30, 439–441. doi:10.2307/3897806.

Volesky, J.D., Connot, S.B., 2000. Vegetation Response to Late Growing-Season Wildfire on Nebraska Sandhills Rangeland. Journal of Range Management 53, 421–426. doi:10.2307/4003754.

Walker, L.R., 1999. Ecosystems of Disturbed Ground. Elsevier.

Weladji, R.B., Forbes, B.C., 2002. Disturbance Effects of Human Activities on Rangifer Tarandus Habitat: Implications for Life History and Population Dynamics. Polar Geography 26, 171–186. doi:10.1080/789610191.

Whicker, A.D., Detling, J.K., 1988. Ecological consequences of prairie dog disturbances. BioScience 38, 778.

White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: an introduction. Unknown Journal 3–13.

Willson, G.D., Stubbendieck, J., 1995. Soil moisture and temperature differences between burned and unburned smooth brome-and big bluestem-dominated sites, in: Proceedings of the 14th Annual North American Prairie Conference. pp. 79–83.

Wilson, S.D., Bakker, J.D., Christian, J.M., Li, X., Ambrose, L.G., Waddington, J., 2004. Semiarid Old-Field Restoration: Is Neighbor Control Needed? Ecological Applications 14, 476–484.

Wilson, S.D., Gerry, A.K., 1995. Strategies for Mixed-Grass Prairie Restoration: Herbicide, Tilling, and Nitrogen Manipulation. Restoration Ecology 3, 290–298. doi:10.1111/j.1526-100X.1995.tb00096.x.

Wilson, S.D., Shay, J.M., 1990. Competition, Fire, and Nutients in a Mixed-Grass Prairie. Ecology 71, 1959–1967. doi:10.2307/1937604.

Winter, S.L., Cully, J.F., Pontius, J.S., 2002. Vegetation of Prairie Dog Colonies and Non-Colonized Shortgrass Prairie. Journal of Range Management 55, 502–508. doi:10.2307/4003230.

Wolfe, C.W., 1973. Effects of fire on a sand hills grassland environment. Tall Timbers Research Station, pp. 241-255.

CHAPTER 2

PLANT COMMUNITY RESPONSE TO DISTURBANCES IN

NEBRASKA SANDHILLS UPLAND PRAIRIE

Introduction:

North American prairie communities were formed under the influence of periodic disturbance events (Howe 1994; Palmer et al. 1997). These disturbances shaped plant populations by altering growth patterns, reproductive potentials, and competitive dynamics (Hartnett and Keeler 1995; Hobbs and Huenneke 1992). White and Pickett (1985) defined a disturbance as "any relatively discrete event in time that disrupts eco-system, community or population structure and changes resources, substrate availability, or the physical environment." Hobbs and Huenneke (1992), further classified disturbance events into direct disturbances ("those affecting the survivorship of individuals directly") and indirect disturbances ("those affecting resource levels or other conditions that then influence individuals in the patch"). In the Nebraska Sandhills, distinct disturbances have variable effects on upland plant composition (Bragg 1998, 1978; Foster and Stubbendieck 1980; Guretzky et al. 2016; Morrison et al. 1986; Pfeiffer and Steuter, Potvin 1993; 1984; Schmeisser 2009; Steuter et al. 1995; Volesky and Connot 2000; Wolfe 1973). Direct disturbances such as spring fire and soil disturbance as well as indirect disturbances such as seed addition and supplemental water have unique roles, influencing plant community response in Sandhills prairie.

Prior to European settlement, fires resulting from lightning strikes and Native American activities played a key role in maintaining prairie vegetation dynamics across the Great Plains and fire return intervals of 1 to 6 years were common (Blewett 1986; Briggs et al. 2002; Frost 1998; Higgins 1986, 1984; Petranka and McPherson 1979). Specific effects following fire vary geographically, but immediate reductions in litter cover and increases in bare ground have been documented (Curtis and Partch 1948; Hulbert 1969; Knapp and Seastedt 1986; Wilson and Shay 1990). This reduction in litter cover can have positive effects on seedling establishment (Christiansen 1994; Maret and Wilson 2005). Spring fire increases soil temperature, light incidence, and temporarily certain plant-available nutrients, which positively influences warm-season grasses (Bragg 1998; Hulbert 1988, 1969; Knapp 1984; Peet et al. 1975; Rice and Parenti 1978, Ojima et al. 1994; Wolfe 1973). Timing of spring fire, however, is important as burns coinciding with active growth of susceptible cool-season species can reduce production of these species (Anderson 1976; Towne and Owensby 1984). In the Nebraska Sandhills, spring burning positively affects warm-season grasses, and reduces the cover of certain forbs (Bragg 1998; Pfeiffer and Steuter 1994).

Historically, prairie soil disturbance occurred through the soil moving activity of various animals and resulted in unique microhabitat formation that affected plant community response (Benedict et al. 1996; Knapp et al. 1999; Kotliar 1999; Hobbs 1989; Hobbs and Huenneke 1992). In the Nebraska Sandhills, American bison (*Bison bison*) wallows and plains pocket gopher (*Geomys bursarius*) mounds were important drivers of landscape diversity (Steuter et al. 1995). Various studies have also examined the effects of human-induced soil disturbance on prairie response. Disturbance of soil, from pocket

gopher mound building or disking with agricultural implements, immediately reduces

production of various forb and grass species and exposes more bare ground (Benson et al.

2007; Dollar 2011; Foster and Stubbendieck 1980; Hart et al. 1985; Steuter et al. 1995;

Rogers and Hartnett 2001a, 2001b). Timing of soil disturbance also influences species

response (Hobbs and Mooney 1985). Growth habit is important as bunchgrass species,

for example, may be more susceptible to soil disturbance than rhizomatous or

stoloniferous grasses that more vigorously recolonize disturbed areas (Hart et al. 1985).

Recolonization of disturbed areas often occurs rapidly but is slower on larger disturbed

regions, and forb recovery may exceed that of graminoids (Foster and Stubbendieck

1980; Gibson 1989; Rogers et al. 2001; Rogers and Hartnett 2001a, 2001b; Steuter et al.

1995). Additionally, soil disturbance variably affects competition for resources (Wilson

and Shay 1990). Historically, there is also evidence for ecological interactions between

soil disturbance and fire in prairie plant communities (Augustine et al. 2007; Collins and

Uno 1983; Rogers and Hartnett 2001a).

Although vegetative reproduction dominates in prairie ecosystems (Benson and

Hartnett 2006; Hartnett and Keeler 1995; Schacht et al. 2000), availability of seed could

limit the abundance of certain species (Hartnett and Keeler 1995, Knapp and Hulbert

1986; Potvin 1988, 1984; Rabinowitz and Rapp 1980). Historically, fluxes in seed bank

composition occurred due to changing environmental conditions or seed introduction by

grazing animals (Coffin and Lauenroth 1989; Lippert and Hopkins 1950; Hobbs and

Huenneke 1992). Establishment of perennial forbs can be more difficult than annuals

(Coffin and Lauenroth 1989; Glenn-Lewin et al. 1990), and species-specific seed

dormancy often constrains germination (Heiser et al. 1969; Lindgren and Schaaf 2004;

Sorensen and Holden 1974; Voigt 1977). Additionally, low soil moisture can limit seedling establishment in semi-arid prairie systems such as the Nebraska Sandhills (Potvin 1993).

Growing season precipitation (Dalgleish and Hartnett 2006; Lane et al. 2000) and topographic position (Barnes and Harrison 1982; Singh et al. 1998) play key roles in regulating plant composition in North American prairies. Prairie species vary in their response to drought and water stress (Heckathorn and DeLucia 1996, 1994; Knapp 1984). They also differ in response to minor rainfall events (Sala and Lauenroth 1982) and the frequency of those events during dry conditions (Fay et al. 2003). Competition for soil water between species with major physiological and morphological differences often determines species prevalence (Blankespoor and Larson 1994), and this is true at various topographical locations in the Nebraska Sandhills (Barnes et al. 1984; Barnes and Harrison 1982; Keeler et al. 1980 Potvin 1993). Biomass and leaf water potential response to various timings and amounts of water addition differs based on photosynthetic pathway or rooting habit (Lauenroth et al. 1978; Martin et al. 1991; Nippert and Knapp 2007). Additionally, the application of supplemental water often enhances seedling establishment (Groya and Sheaffer 1981; Potvin 1993; 1984). The exact role and relative importance of water competition in predicting plant community structure in the Nebraska Sandhills, however, remains largely undetermined (Guretzky et al. 2016).

In light of these direct and indirect disturbance events and their general roles in shaping prairies, we designed a study to investigate the effects of several, one-time disturbance events on plant community composition in Nebraska Sandhills prairie. This is

a unique prairie system, in which the specific functions of these disturbances are not fully defined. Additionally, disturbance treatment interactions are often lacking in studies of prairie ecosystems. We hypothesized that the application and subsequent interactions of the disturbance events would alter prairie community composition. Mid-spring fire is a direct disturbance, mimicking historic Native American ignitions of prairie that peaked in spring and fall (Frost 1998; Higgins 1986), that we predicted would benefit perennial warm-season grasses and have mixed effects on forbs. Mid-spring disking is a direct disturbance, causing intense soil perturbation similar in some regards to pocket gopher spring mound building (Case and Jasch 1994; Hobbs and Huenneke 1992), that we predicted would have negative effects on perennial plant cover. Seed addition is a form of indirect disturbance, mimicking fluxes in seed bank composition (Coffin and Lauenroth 1989; Lippert and Hopkins 1950) or seed introduction by grazing ruminants (Hobbs and Huenneke 1992). We predicted that seed availability limits abundance of specific prairie forbs (Hartnett and Keeler 1995, Knapp and Hulbert 1986; Potvin 1988, 1984; Rabinowitz and Rapp 1980) and addition should increase their cover. Early summer supplemental water applications can be a form of indirect disturbance, by mimicking minor rainfall events during abnormally dry periods, with the intention of provoking a plant community or species-specific response (Hobbs and Huenneke 1992; Sala and Lauenroth 1982). We predicted that these minor water additions would enhance forb seedling establishment without large effects on other species.

Materials and Methods

Study Site

We conducted research during 2016 and 2017 at the University of Nebraska-Lincoln Barta Brothers Ranch near Rose, NE (42° 13' 32'' N, 99° 38' 09'' W). Our study site was located in upland prairie within the Major Land Resource Area 65 on Nebraska Sandhills, sands ecological sites in the high precipitation zone (USDA-NRCS 2018). We selected dune slope (5-15%) topographical positions (Schacht et al. 2000) with south to southwest aspects. Soils consisted of Valentine fine sands (mixed, mesic Typic Ustipsamments), which are characteristic of Sandhills upland prairie sites (Zink et al. 1985), with 1.1% organic matter content and 6.2 pH in the surface 15 cm. Climate is typical of semi-arid prairie with a characteristic rise and peak in precipitation nearly parallel to that of temperature during the growing season. Across the previous 16 years (2000-2015), the average annual precipitation was 542 mm with highest precipitation occurring during the month of June and lowest during January (HPRCC 2017; NOAA 2017). During the growing season months of April through September, the area received an average of 412 mm of precipitation (HPRCC 2017; NOAA 2017). Average maximum temperatures reached 31.1°C in July with average minimum temperatures dropping to -10.6°C in January (HPRCC 2017).

Vegetation of the study site is typical of Nebraska Sandhills uplands and dominated by graminoid species. Grasses such as Scribner's rosette grass (*Dichanthelium oligosanthes* (Schult.) Gould), little bluestem (*Schizachyrium scoparium (*Michx.) Nash), needlegrasses (*Hesperostipa spp.*), switchgrass (*Panicum virgatum* L.), and prairie

sandreed (*Calamovilfa longifolia (*Hook.) Hack. ex Scribn. & Southw.) are abundant
(Schacht et al. 2000). Common forb species include western ragweed (*Ambrosia*
psilostachya DC.), stiff sunflower (*Helianthus pauciflorus* Nutt.), and cudweed sagewort
(*Artemisia ludoviciana* Nutt.) (Schacht et al. 2000). Sedges (*Carex spp.*), cacti (*Opuntia*
spp.), and shrub species such as leadplant (*Amorpha canescens* Pursh) and prairie rose
(*Rosa arkansana* Porter) are also common (Schacht et al. 2000). South-facing slopes
typically experience greater light intensities and evapotranspiration rates, and generally
have lesser densities of cool-season species and greater densities of warm-season species
when compared to north-facing slopes (Schacht et al. 2000).

Experimental Design

The study was conducted as a randomized complete block design with a $2 \times 3 \times 2$
factorial arrangement of fire (no fire and fire), soil disturbance (no soil disturbance, soil
disturbance, and soil disturbance with seed addition), and water addition (no water and
water) treatments. The study design required establishment of five, new blocks of these
treatments in 2016 and in 2017. Our experimental units (plots) were 1.52×3.05 m
individual plots oriented north to south, parallel to the downslope flow of water, with
0.91×3.05 m buffers between (to the west and east of) each unit to mediate edge effects.
All treatments occurred within a single established 54-ha pasture. Cattle were excluded
from treatment areas at the onset of treatment initiation and this continued throughout the
entire study. According to the definition of grazing pressure index described by Smart et
al (2010), cumulative grazing pressure during the 2015 grazing season (18 June to 18
August) was 14.92 AUD/Mg in the areas where the treatments were applied in 2016. In

the 2017 treatment areas, cumulative grazing pressure was 22.38 AUD/Mg during the 2016 grazing season (17 May to 1 September).

Mid-spring fire treatments were applied on 3 May 2016 and 27 April 2017. In both years, fire occurred two days after a rainfall event and the average air temperature, relative humidity, and wind speed during the burns were 20.7°C, 36.0%, and 9.0 mph in 2016 and 15.6°C, 33.8%, and 7.4 mph in 2017, respectively. Fuel loads averaged 3572 kg/ha in 2016 and 2815 kg/ha in 2017 on a dry matter basis. We used a meter high, rectangular, metal burn box without a top, as a safety precaution to contain fire within individual plots (Kral et al. 2015). Use of this box helped homogenize fire intensity by reducing the variable effect of wind speed.

Soil disturbance treatments, including a paired seed addition, were applied two days after mid-spring fire in both years. Mid-spring soil disturbance consisted of a light disking with a 3-m wide, single gang disk with eight notched, 0.41-m diameter disk blades (Worksaver, Inc., Litchfield, IL) pulled up-slope behind an all-terrain vehicle (ATV). Seed addition occurred immediately after disking and was only implemented on plots that had been disked in order to facilitate seed-soil contact for spring germination (Rowe 2010). We used a walk-behind, small plot cone seeder (Carter Manufacturing Company, Inc., Brookston, IN) to seed downhill a four-species, native, perennial, forb seed mix consisting of purple prairieclover (*Dalea purpurea* Vent.), roundhead lespedeza (*Lespedeza capitata* Michx.), largeflowered penstemon (*Penstemon grandiflorus* Nutt.), and stiff sunflower. Each species was seeded at a rate of 162 pure live seeds (PLS) m^{-2}. Largeflowered penstemon and stiff sunflower seeds were of Nebraska Sandhills local ecotype origin. Purple prairieclover and roundhead lespedeza seeds were of plant

adaptation region origin (Vogel et al., 2005) suited for the appropriate USDA plant hardiness zone and ecoregion, and seeded with the correct species of inoculum.

Early summer supplemental water treatments depended on the frequency of precipitation event days, as they were applied according to a specific event interval criteria. From May through July of 2016 and 2017, 0.64 cm of water was applied if the number of days without precipitation exceeded the previous 16-year average number of days between precipitation events plus one standard deviation in the 16-year data for a given month. Precipitation amounts as small as 0.03 cm were included as valid precipitation events, and 0-day values between consecutive precipitation event days were excluded from the 16-year frequency data averages. According to the frequency of precipitation during the study, we applied supplemental water treatments on 8 June and 25 June 2016, and on 14 June and 6 July 2017. Precipitation data were collected from the High Plains Regional Climate Center (HPRCC 2017) weather station located approximately 3 km northwest of the treatment areas.

Vegetation Sampling

On 16 June 2016 and 15 June 2017, we used frequency grids (Vogel and Masters 2001) to estimate June forb density of total forbs, of other selected forb species [western ragweed, Canadian horseweed (*Conyza canadensis* (L.) Cronquist), and cudweed sagewort], and on seeded plots only, of the four seeded species. Notably common perennial forbs, western ragweed and cudweed sagewort (Schacht et al. 2000), and a notably abundant and easily identifiable annual forb, Canadian horseweed (Pérez et al. 1998), were selected to measure initial, mid-season forb response to disturbances. Each

frequency grid contained 25, 15 × 15 cm cells, and four frequency grids were sampled

per plot for 100 cells. In each cell, we recorded presence or absence of the respective forb

species. In the case of the four seeded species (on seeded plots only), however, we

sampled presence or absence of immature plants (< 100 mm in height) during the first

growing season post-disturbance and presence or absence of any size of plant during the

second growing season in an effort to better estimate seedling establishment. Frequency

of occurrence (number of squares with species present out of 100 total squares)

multiplied by a factor of 0.4 provided a conservative estimate of plant density (plants/m^2)

as described by Vogel and Masters (2001).

From 10 to 11 August 2016 and 9 to 10 August 2017, we estimated percentage

cover by species to determine first and second growing season post-disturbance effects on

plant community composition. Cover of individual plant species was estimated on a

nonoverlapping basis such that any cover present in the plot was counted regardless of

vertical obstruction by other plant species. Cover of bare ground and litter was estimated

on an overlapping basis such that only what cover was visible from a vertical view of the

canopy was counted. We conducted cover sampling according to general methods

outlined by Daubenmire (1959). Because of difficulty in field identification, various

sedge species were not differentiated. Six sampling frames (20 × 50 cm) were sampled

from the center of each plot for a total of 0.6 m^2 sampling area per plot. We classed cover

as: < 5%, 5-25%, 25-50%, 50-75%, 75-95%, or 95-100% for each species present and for

bare ground and litter, and total values were not required to sum to 100%. We then

computed species, bare ground, and litter averages using midpoint values of the above-

mentioned cover classes for each respective observation.

On 15 August 2017, the 2016 treatment plots (n=60) were hand-clipped to determine second growing season-post disturbance herbage mass by the following functional groups: warm-season grass, cool-season grass, forb, shrub, sedge, cactus, standing dead, and litter. We did not clip the first growing season post-disturbance plots in 2016 or 2017, so as not to introduce additional disturbance before the second growing season post-disturbance data collection. For all categories other than standing dead and litter, current year production was clipped (e.g., new leaf and stem material for shrubs). We clipped two, 0.25 m^2 quadrats at ground level in the south half of each plot. Herbage was sorted according to functional group and oven-dried at 60°C before weighing. We defined litter as non-living plant material that was no longer rooted in the soil, and standing dead as non-living plant material that was not produced that growing season yet remained rooted in soil.

Data Analysis

Analysis of variance of forb density, percentage cover, and herbage mass of plant species or groups was conducted with a general linear mixed models procedure in SAS 9.4 (SAS Institute Inc., Cary, NC). The effects of year and replication were considered random. We used an alpha level of 0.05 to determine the significance of treatment direct tests. To determine statistically significant differences between treatment combination means for two-, three-, and four-way interactions, the least significant difference (LSD) method was used. A subsequent examination of the simple effects was used for further investigation into the nature of interactions. Although significant main and interactive effects were included for all response variables, in the absence of a simple effects

analysis, a select few response variables had treatment combination means that did not differ significantly according to the conservative T-grouping LSD test.

In addition to cover by species, we summed cover values into following groups for analysis: graminoid, grass, warm-season grass, warm-season bunchgrass, warm-season rhizomatous grass, cool-season grass, cool-season bunchgrass, cool-season rhizomatous grass, forb, annual forb, biennial forb, perennial forb, shrub, cactus, and standing cover (sum of all species cover without litter and bare ground values). In addition to herbage of clipped functional groups, we summed herbage values into the following broader groups for analysis: total live herbage, live grass, live graminoid, and total standing herbage mass (sum of all clipped functional group herbage values without litter). Plant community response was shown in the results as well as the tables and figures section, and statistically significant main and interactive effects were included. All species as well as above-mentioned plant groups not discussed in the results or tables and figures section were unaffected by treatment.

Results

Precipitation and Temperature

Highest average temperatures were reached during July 2016 and 2017, matching the previous 16-year average (Fig. 2-1). Average July temperatures, however, were lower by 95% of the average in 2016 and higher by 106% of the average in 2017 (Fig. 2-1). In 2016, temperatures were notably above average during June and October, by 110% and

130%, respectively (Fig. 2-1). In 2017, temperatures were below average by 91% and 90% during May and August, respectively (Fig. 2-1).

Monthly precipitation deviated widely from the 16-year average over the 2-year study. The 16-year average annual peak in precipitation during June was not experienced in 2016 or 2017 (Fig. 2-2). In June 2016, total rainfall accumulation was 43% of the 16-year average, and in 2017, it was a mere 9%. During the 2017 growing season, this resulted in moderate drought throughout the region (U.S. Drought Monitor 2017). Additionally, 2016 precipitation amounts were above average during April, May, July, and September, and below average during August and October (Fig. 2-2). April and July 2016 precipitation were 250% and 224% of the 16-year average, respectively, while August was 6% of the average. In 2017, precipitation was above average during May, July, August, September, and October (Fig. 2-2). May 2017 precipitation was 193% of the average, while July and August were 240% and 193% of the average, respectively. The frequency of rain events was relatively low during June of both years and exceeded the event interval criteria (for supplemental water application) for June of 7 days, twice in 2016 and once in 2017. The frequency of rain events also was low in July 2017 and exceeded the event interval criteria for July of 9 days, once (HPRCC 2017).

First Growing Season Post-Disturbance

June Forb Density

June forb density sampling of total forbs, seedlings of seeded forb species on seeded plots, and selected forb species revealed several significant main and interactive effects. Fire and year had main effects on total forb plant density. Burned plots had a forb

density of 21.6 plants/m^2 compared to 26.9 plants/m^2 on unburned plots. Forb density

was 31.9 plants/m^2 in 2016 and 16.7 plants/m^2 in 2017.

There was a two-way interaction between fire and early summer supplemental

water on plant density of the perennial forb, western ragweed (Table 2-1). Burning

increased western ragweed density, but this only occurred on plots that received

supplemental water. Additionally, there was a three-way interaction between mid-spring

fire, supplemental water, and soil disturbance on June density of the annual forb,

Canadian horseweed (Table 2-2). Across all treatment combinations, fire reduced

Canadian horseweed densities. In the absence of burning and disking, supplemental

watering increased Canadian horseweed densities by 171% (Table 2-2). Disking and

disking plus seeding decreased Canadian horseweed density on the unburned and watered

treatment (Table 2-2).

Across disked plus seeded plots there were two significant two-way and a single

significant three-way interaction on seeded perennial forb seedlings. Year and fire as well

as year and water interacted on purple prairieclover seedling density (Table 2-3). Both

fire and water increased density in 2016, and these densities were greater than in 2017

(Table 2-3). Year, fire, and supplemental water all interacted to affect density of

roundhead lespedeza seedlings (Table 2-4). Roundhead lespedeza seedling density on the

burned treatment was greater in 2016 than 2017 (Table 2-4). In 2016, the application of

fire and supplemental water together increased density (Table 2-4). Across seeded plots,

few to no stiff sunflower or largeflowered penstemon seedlings were recorded during the

first growing season post-disturbance. Average height of seedlings varied but was < 65

mm at time of sampling.

<center>*August Cover*</center>

Main Effects of Disturbances

August cover data from the first growing season post-disturbance revealed that total standing cover averaged 41% and was unaffected by treatment combination or year. Mid-spring fire had several significant effects on plant community composition. Relative to unburned prairie, burning reduced species richness from 17 to 15 species/0.6 m^2. Burning increased warm-season rhizomatous grass and perennial forb cover and decreased sedge, forb, and annual forb cover (Fig. 2-3). Compared to unburned plots burning decreased the cover of the annual forbs: Canadian horseweed, woolly plantain (*Plantago patagonica* Jacq.), and pepperweed (*Lepidium densiflorum* Schrad.) from 3.0% to 0.4%, 1.0% to 0.1%, and 0.2% to < 0.1%, respectively. Fire increased the cover of western ragweed, and the warm-season bunchgrass, sand dropseed, (*Sporobolus cryptandrus* (Torr.) A. Gray) from 2.4% to 4.7%, and 1.2% to 2.0%, when comparing unburned plots to burned plots, respectively. The perennial forb, narrowleaf puccoon (*Lithospermum incisum* Lehm.), however, was reduced by fire and was 0.4% on unburned plots compared to 0.2% on burned plots.

First growing season post-disturbance data also showed significant main effects of early summer supplemental water and year on specific plant groupings and species. The addition of early summer supplemental water decreased cover of the warm-season bunchgrass, little bluestem, from 4.5% on unwatered plots to 2.7% on watered plots. Additionally, total forb and perennial forb cover was affected by year and was 10.7% and 7.0% on 2016 plots compared to 7.9% and 4.5% on 2017 plots, respectively. Western

ragweed had a greater cover of 4.9% in 2016 compared to 2.3% in 2017, while

narrowleaf puccoon had a reduced cover of 0.1% in 2016 compared to 0.4% in 2017.

Cover of the warm-season bunchgrass, hairy grama (*Bouteloua hirsuta* Lag.), was also

greater in 2016 than 2017 and decreased from 1.7% to 0.6%.

Interactions of Disturbances

During the first growing season post-disturbance there were three significant two-

way interactions involving mid-spring fire, mid-spring soil disturbance, early summer

supplemental water, and year. First, year interacted with fire on cover of litter (Table 2-

5). Within a given year, burned plots had less litter cover than unburned plots (Table 2-5).

Litter cover was greater in 2017 than 2016 within a given fire treatment (Table 2-5).

Second, water interacted with soil-disturbance on cover of warm-season bunchgrasses,

fall rosette grass (*Dichanthelium wilcoxianum* (Vasey) Freckmann) (a cool-season

bunchgrass), and clammy groundcherry (*Physalis heterophylla* Nees) (a perennial forb).

On undisked plots, minor water addition had a negative effect on the cover of warm-

season bunchgrasses and fall rosette grass and a positive effect on clammy groundcherry

(Table 2-6). On unwatered plots, disking reduced warm-season bunchgrasses, and on

watered plots, it reduced clammy groundcherry (Table 2-6). Third, year interacted with

soil disturbance on the warm-season rhizomatous grass, Indiangrass (*Sorghastrum nutans*

(L.) Nash), and purple prairieclover cover. In 2016, the disked and disked plus seeded

treatments seemingly reduced Indiangrass cover when compared to the undisked

treatment; but in 2017, to a lesser extent an opposite trend was observed. Indiangrass

treatment combination means ranged from 0.7% to 2.8% cover. Although a significant

two-way interaction was present, treatment means of Indiangrass did not differ significantly according to the conservative T-grouping LSD test. Purple prairieclover cover was statistically greatest in 2016 on the disked plus seeded plots at a cover of 0.2%, and the remaining treatment means did not differ statistically. The other soil disturbance treatments had cover values of < 0.05%, and in 2017, purple prairieclover was absent altogether.

Four, significant three-way interactions were documented involving mid-spring fire, mid-spring soil disturbance, early summer supplemental water, and year. First, fire interacted with water and soil disturbance to affect cover of bare ground, prairie sandreed, cactus, brittle cactus (*Opuntia fragilis* (Nutt.) Haw.) (Table 2-7), and skeletonplant (*Lygodesmia juncea* (Pursh) D. Don ex Hook.). Fire increased bare ground cover across all treatment combinations, except on the unwatered and disked plus seeded treatment (Table 2-7). Disking and disking plus seeding tended to increase bare ground cover in the presence of supplemental water on both burned and unburned plots, while supplemental water led to an increase only on the burned and disked plus seeded treatment (Table 2-7). Disking and disking plus seeding decreased cover of the rhizomatous grass, prairie sandreed, on the unburned and watered treatment, while burning increased cover of prairie sandreed on the watered and disked plus seeded and the unwatered and disked treatments (Table 2-7). Fire reduced total cactus and brittle cactus cover on both the unwatered and undisked treatment as well as the watered and disked plus seeded treatment (Table 2-7). Skeletonplant treatment combination means ranged from 0.0% to 0.2% cover. Early summer supplemental water seems to have increased cover of the perennial forb, skeletonplant, on the unburned and disked plus

seeded treatment. Although a significant three-way interaction was present, in the absence of a simple effects analysis means of skeletonplant cover did not differ significantly according to the conservative T-grouping LSD test. Second, year interacted with water and fire on the percentage of bare ground cover (Table 2-8). Burning increased bare ground regardless of year or addition of supplemental water, and supplemental water increased bare ground on burned plots in 2017 (Table 2-8). Third, year interacted with fire and soil disturbance on cover of warm-season grasses, the warm-season rhizomatous grass, sand bluestem (*Andropogon hallii* Hack.) (Table 2-9), and the annual forb, rough false pennyroyal (*Hedeoma hispida* Pursh). Burning increased cover of warm-season grasses in 2017 on undisked plots (Table 2-9). Disking and disking plus seeding decreased the cover of sand bluestem on burned plots in 2017, but disking plus seeding increased its cover on burned plots in 2016 (Table 2-9). Burning increased sand bluestem cover in 2017 on undisked plots, and overall, sand bluestem cover was greater in 2017 than 2016 on the burned and undisked treatment (Table 2-9). Rough false pennyroyal cover was statistically greatest in 2016 on the unburned and disked plus seeded treatment at a cover of 0.8%, and the other treatment means did not differ statistically. Cover was 0.0% on the unburned and undisked treatment in 2017 and ranged from 0.1% to 0.3% on the other unburned treatment combinations. Rough false pennyroyal was absent on burned plots. Fourth, year interacted with water and soil disturbance on cover of cactus and brittle cactus. Both cactus and brittle cactus treatment combination means ranged from 0.3% to 1.3% cover. Water addition seemed to decrease cactus and brittle cactus cover in 2017 on undisked plots, but treatment means did not differ significantly according to the conservative T-grouping LSD test.

A single four-way interaction was documented between year, mid-spring fire, early summer supplemental water, and mid-spring soil-disturbance on the cover of cool-season bunchgrasses, Scribner's rosette grass (a cool-season bunchgrass) (Table 2-10), and roundhead lespedeza. Fire increased cover of cool-season bunchgrasses and Scribner's rosette grass in 2017 on the watered and disked plus seeded treatment, and decreased cover of the cool-season bunchgrasses in 2016 on the unwatered and disked treatment (Table 2-10). Disking plus seeding decreased cover of cool-season bunchgrasses and Scribner's rosette grass in 2017 on the unburned and watered treatment, and disking decreased cool-season bunchgrasses in 2017 on the unburned and unwatered treatment (Table 2-10). Water increased cool-season bunchgrasses and Scribner's rosette grass in 2017 on the unburned and disked treatment (Table 2-10). Scribner's rosette grass cover was greater in 2017 than 2016 on the unburned, unwatered, and disked treatment. Roundhead lespedeza cover was statistically greatest in 2016 on the burned, watered and disked plus seeded treatment at 0.3%, and it was absent from all other treatment combinations.

Second Growing Season Post-Disturbance

June Forb Density

June forb density sampling revealed no main effects and a significant two-way interaction of fire and soil disturbance on density of forbs (Table 2-11). Burned plots had a greater total forb density than unburned plots across both undisked and disked treatments (Table 2-11). In addition, disking plus seeding increased forb density on unburned plots (Table 2-11). On disked plus seeded plots, all four seeded species were

present in varying abundances and immature plants were observed. Average densities (plants/m^2), however, of 0.1, 0.3, 0.3, and 1.0 for roundhead lespedeza, purple prairieclover, largeflowered penstemon, and stiff sunflower, respectively, indicated few seedlings emerged in the second growing season post-disturbance

<u>*August Cover and Herbage Mass*</u>

Main Effects of Disturbances

August cover and herbage data from the second growing season post-disturbance revealed that total standing cover averaged 41% and total standing herbage mass averaged 1900 kg/ha. Neither was affected by treatment. A cumulative of 68 species were identified across the first and second growing season post-disturbance plots. Species richness, however, was unaffected by treatments in the second season. Mid-spring fire had significant main effects on bare ground, litter, and sedge. Fire increased cover of bare ground from 13.9% on unburned plots to 26.7% on burned plots. Fire decreased cover of litter from 37.1% on unburned plots to 21.0% on burned plots. Herbage mass of litter and sedge was significantly greater on unburned compared to burned prairie. Fire decreased herbage mass of litter from 65.0 to 19.6 g/0.5m^2 and herbage mass of sedge from 5.6 to 2.1 g/0.5m^2 on unburned compared to burned plots, respectively.

Second growing season post-disturbance data also showed a significant increase in 2017 shrub herbage mass due to 2016 mid-spring soil disturbance (Fig. 2-4). Herbage mass of shrubs was substantially greater on disked plots when compared to both undisked and disked plus seeded plots (Fig. 2-4).

Interactions of Disturbances

Two significant, two-way interactions were found involving the effects of mid-spring fire, mid-spring soil disturbance, and early summer supplemental water on various components of the plant community during the second growing season post-disturbance. First, fire interacted with soil disturbance to affect cover of warm-season grasses and warm-season bunchgrasses (Table 2-12). Disking and disking plus seeding decreased cover of warm-season grasses and warm-season bunchgrasses in the absence of fire, while fire increased warm-season grasses on disked plus seeded plots (Table 2-12). Second, soil disturbance and supplemental water interacted to affect the cover of grasses, warm-season grasses, warm-season bunchgrasses, hairy grama, and sand bluestem (Table 2-13). Disking decreased grasses, warm-season grasses, warm-season bunchgrasses, and hairy grama in the absence of supplemental water (Table 2-13). Disking plus seeding also decreased hairy grama cover in the absence of water (Table 2-13). Supplemental water decreased cover of warm-season grasses, warm-season bunchgrasses, and hairy grama on undisked plots and increased hairy grama on disked plots (Table 2-13). Sand bluestem cover was increased by disking plus seeding on unwatered plots and decreased by supplemental water on disked plus seeded plots (Table 2-13).

There was a significant three-way interaction between mid-spring fire, early summer supplemental water, and mid-spring soil disturbance on herbage mass of cool-season grasses and cover of clammy groundcherry (Table 2-14). Early summer supplemental water decreased mass of cool-season grasses on unburned and undisked plots (Table 2-14). Additionally, supplemental water increased clammy groundcherry

cover on the unburned and disked plus seeded treatment (Table 2-14). Disking plus

seeding increased clammy groundcherry on the unburned and watered treatment, while

fire decreased its cover on the watered and disked plus seeded treatment.

Discussion

First Growing Season Post-Disturbance

June Forb Density

The negative effect of spring fire on June density of forbs was consistent with

long-term late spring burning data from Konza prairie in northeastern Kansas (Towne and

Owensby 1984). Much of the reduction was attributable to a marked suppression of the

dominant annual forb, Canadian horseweed, as fire reduced its density through direct

mortality of early season rosettes. The positive interactive effect of fire, however, on

western ragweed density when supplemented with water agreed with a documented

increase associated with spring burning (Hopkins et al. 1948) and could be due to the

late season growth habit, rhizomatous nature, and efficient use of soil moisture by this

species. The positive interactive effect of fire on density of purple prairieclover and

roundhead lespedeza seedlings in 2016, though small, was attributable to the removal of

the restrictive litter layer, allowing increased light incidence and improved microsite

conditions that enhanced germination (Maret and Wilson 2005).

Year of sampling had significant effects on various forb species densities, and

much of this could be related to weather patterns. Greater total forb density in 2016

compared to 2017 could have been caused by weather during the months of April, May,

and June; which was several degrees warmer on average and may have benefited early season forb species (Fig. 2-1). Additionally, greater precipitation during April and June 2016 would have aided this effect, though rainfall was less in May (Fig. 2-2). Increased June establishment of the two leguminous, seeded species in 2016 compared to 2017, may be due to slightly warmer spring temperatures and greater June rainfall in 2016. Slightly reduced seed viability, however, could have played a role as the same seed stock was used in both years. Scarification prior to seeding might have improved legume seedling densities (Sorensen and Holden 1974; Voigt 1977), but well-below average June rainfall in both years caused mortality of germinated seedlings and contributed to reduced August cover values.

In both 2016 and 2017, June was much drier than the 16-year average (Fig. 2-2) and forb species likely underwent appreciable water stress. Despite the fact that in both years only one of two watering events were applied prior to density sampling, responsiveness to minor rain events was observed as significant results were recorded. The positive interactive response of western ragweed and Canadian horseweed to the recent 0.64-cm water application is consistent with documented forb responsiveness to moisture after water stress conditions (Knapp et al. 2001; Martin et al. 1991). The benefit of supplemental water on the seeded leguminous species agrees with our prediction of an enhancement in seedling establishment. Potvin (1993) also observed benefits from supplemental water in combination with disking on establishment of grass seedlings in Sandhills uplands. The negative interactive effect of disking and disking plus seeding on Canadian horseweed density indicates that where it was not markedly suppressed by fire, soil disturbance played a similar but less severe role, causing direct mortality to rosettes.

August Cover

Fire

In the first growing season after disturbance, mid-spring fire played the largest role of all disturbance treatments in altering August plant community structure. The reduction in species richness after the first season post-disturbance was mainly attributable to a reduction in specific forb species. This observation is supported by literature in the northern mixed-grass prairie, as studies by Biondini et al (1989) and Wolfe (1973) documented reductions in forb species richness, and Bragg (1998), a slight reduction in total species richness from spring fire. The overall positive effect of fire on bare ground and negative effect on litter are expected and well documented in the literature (Curtis and Partch 1948; Hulbert 1969; Knapp and Seastedt 1986; Wilson and Shay 1990). The rise in bare ground mostly represents a shift from higher litter cover, as total standing cover of species was unchanged by burning.

The effects of mid-spring fire on cover of graminoid species were generally positive. The positive effect of spring fire on warm-season rhizomatous grass and sand dropseed cover, as well as positive interactive effects on the cover of warm-season grasses, prairie sandreed, and sand bluestem agrees with documented increases in warm-season grass species after burning that has been previously documented in the Nebraska Sandhills (Bragg 1998; Pfeiffer and Steuter 1994). These findings support our predicted beneficial effects of fire on warm-season grass cover. An early-season increase in soil temperature, light incidence, and temporary flux in nutrients such as available nitrogen and potassium all coincide with initiation of warm-season grass tiller growth and are

potential drivers (Bragg 1998; Hulbert 1988, 1969; Knapp 1984; Peet et al. 1975; Rice

and Parenti 1978, Ojima et al. 1994; Wolfe 1973). Reduced cover of sedges in response

to fire may be due to onset of sedge growth in late April and early May coinciding with

burn timing (Towne and Owensby 1984); results that contradict the fire positive

classification of sedges according to Bragg (1998). The positive interaction on cool-

season bunchgrasses and Scribner's rosette grass may be attributable to the interactive

role of supplemental water in addition to warmer soil temperatures during a month where

nightly lows were well below C_3 growth optimums, as well as to the aforementioned

increase in nutrients and light incidence. The negative interaction on cool-season

bunchgrasses in the absence of water, however, may have stemmed from increased water

stress associated with litter removal and soil water evaporation post-fire (Anderson

1976), a time when these C_3 species were actively growing.

Studies show variable support for our documented effects of mid-spring fire on

non-graminoid populations. Varied effects on forb populations agrees with our initial

prediction concerning the overall effect of fire. The reduction in total forb cover is

consistent with spring fire literature from the Konza prairie, as many cool-season forb

species have begun growth and are vulnerable to direct mortality from fire (Towne and

Owensby 1984). Annual species that had formed rosettes at this time were susceptible to

season-long suppression. The reduction in annual forb species (including Canadian

horseweed, woolly plantain, pepperweed, skeletonplant, and rough false pennyroyal)

from spring burning is partially supported by Pfeiffer and Steuter (1994) who found a

similar reduction in interstitial Sandhills forb species (which included annual forbs). Our

documented increase in perennial forbs was primarily driven by western ragweed, which

accounted for 62% of total perennial forb cover across all treatments. This result is not wholly supported in Sandhills fire literature as western ragweed was classified as a fire negative species by Bragg (1998) or was generally unchanged in response to spring fire (Pfeiffer and Steuter 1994; Wolfe 1973). The increase, however, may be due to the warm-season nature of western ragweed that matches well with improved light and nutrient conditions upon initiation of active growth in late May and early June. A positive western ragweed response to fall fire was documented in a mixed-grass prairie study by Biondini et al. (1989). Reductions in narrow-leaved puccoon were expected as it was actively growing at the time of fire, and this result was also observed by Bragg (1998). In 2016, the positive interactive effects of burning and watering followed by seeding on roundhead lespedeza (a seeded species) was likely due to a removal of the litter layer and an increase in light incidence enhancing germination and persistence. The benefit of burning prior to seeding on establishment of prairie species has also been documented in the literature (Christiansen 1994; Maret and Wilson 2005). Negative effects on cactus can be attributed to direct mortality from burning and subsequently slow regrowth.

Soil Disturbance

Mid-spring soil disturbance in the form of disking did not have any positive interactions on individual species or functional groups, and this supports our prediction of immediate effects of disking on perennial plant cover. Disking and disking plus seeding, however, had some positive interactive effects on bare ground cover due to the exposure of soil by disk blade action. Studies examining pocket gopher soil disturbances (Foster and Stubbendieck 1980) and disking support this finding (Benson et al. 2007; Dollar

2011; Hart et al. 1985). The negative interactive effect of disking on cover of warm-season bunchgrasses, cool-season bunchgrasses, prairie sandreed, and sand bluestem has been well documented in literature on overall perennial grass response to human-induced (Benson et al. 2007; Dollar 2011; Hart et al. 1985) and pocket gopher (Foster and Stubbendieck 1980; Rogers and Hartnett 2001a , 2001b; Steuter et al. 1995) soil disturbance. Bunchgrasses, specifically, are usually more susceptible to suppression than are vigorously tillering species that can rapidly recolonize exposed ground. This result was documented in a Nebraska mixed-grass prairie study where production of the bunchgrass, blue grama (*Bouteloua gracilis* (Kunth) Lag. ex Griffiths), was reduced from disking while production of the stoloniferous, buffalograss (*Bouteloua dactyloides* (Nutt.) Columbus), was not (Hart et al. 1985). Suppression of clammy groundcherry was partially attributable to direct mortality from disk blade action.

Disking plus seeding allowed for some additional soil disturbance as well as smoothing and packing of soil through the action of the seven large disc-blade openers followed by five press wheels, a drag chain, and foot traffic behind this walk-behind unit. The abundance of rough false pennyroyal and the seeded purple prairieclover and roundhead lespedeza on disked plus seeded plots is attributable to increased seedling establishment due to microsite creation (Briske and Butler 1989; Hartnett and Bazzaz 1985; Hartnett and Keeler 1995; Hobbs and Huenneke 1992). Seed-soil contact through soil disturbance is important to establishment of native legumes such as purple prairieclover (Packard and Masters 2008). This result supports our prediction of seed availability limiting abundance of two of the four seeded forb species, however, cover of these species was low ($< 0.5\%$) and only increased in 2016. In contrast to disking,

disking plus seeding did not negatively affect warm-season bunchgrasses; and we posit

that firming of soil post-disking allowed the dormant, displaced root and crown material

to be covered and essentially re-planted in soil. This also may have been responsible for

varied positive and negative effects on other warm-season rhizomatous grasses, such as

prairie sandreed and sand bluestem, when compared to disked plots alone. In contrast,

cool-season bunchgrasses, including Scribner's rosette grass, experienced damage to

actively growing leaf and crown material to such a degree that the covering and

replanting in soil could not mediate. A study in tallgrass prairie also documented

decreases in Scribner's rosette grass from soil disturbances, specifically, bison wallows

and pocket gopher mounds (Gibson 1989).

Supplemental Water

The negative effect of early summer supplemental water on little bluestem cover

was unexpected and contrary to our initial predictions. Little bluestem is a warm-season

species that can experience crown damage from high intensity burns (Engle et al. 1993;

Ewing and Engle 1988; Pfeiffer and Steuter 1990; Towne and Owensby 1984; Volesky

and Connot 2000). Species that experience appreciable fire injury followed by mid-

season water application may be suppressed through competition with more fire-positive

species; as in the case of smooth bromegrass (*Bromus inermis* Leyss.) suppression by

competition with warm-season dominants due to fire followed by water addition

(Blankespoor and Larson 1994). In contrast to other perennial grasses, however,

additional research has shown little bluestem does not reallocate nitrogen from above- to

below-ground structures under water stress, and this should lead to increased

responsiveness to water additions after drought (Heckathorn and DeLucia 1996, 1994).

The well-below average June rainfall in 2016 and moderate drought conditions in 2017

caused appreciable water stress in many species. Although fire did not suppress little

bluestem, any slight damage caused as well as damage documented from disking may

have allowed for increased competition in the presence of water application. Although we

did not see an interactive effect on little bluestem, competition is one potential driver for

the reduction documented, and the notable increase in Canadian horseweed density on

watered plots may be a specific example (Table 2-2). Negative interactive effects of

supplemental watering on warm-season bunchgrasses and fall rosette grass occurred only

on undisked plots and also may have been influenced by competition with nearby species

that began vigorous rhizomatous regrowth in June. Sedge, switchgrass, Indiangrass, blue

grama, porcupine grass (*Hesperostipa spartea* (Trin.) Barkworth), needleandthread

(*Hesperostipa comata* (Trin. & Rupr.) Barkworth), leadplant, prairie rose, pepperweed,

rough false pennyroyal, Canadian horseweed, annual eriogonum (*Eriogonum annuum*

Nutt.), woolly white hymenopapus (*Hymenopappus tenuifolius* Pursh), Missouri

goldenrod (*Solidago missouriensis* Nutt.), cudweed sagewort, cut-leaf ironplant

(*Xanthisma spinulosum* (Pursh) D.R. Morgan & R.L. Hartm.), upright prairie coneflower

(*Ratibida columnifera* (Nutt.) Woot. & Standl.), prairie spurge (*Euphorbia missurica*

Raf.), as well as other forb species increased across treatments in response to water

addition although these increases were not statistically significant.

The positive interactive effect of water on cool-season bunchgrasses and

Scribner's rosette grass is consistent with a temporary increase in cool-season grass cover

documented in Colorado short-grass prairie in response to season long water additions

(Lauenroth et al. 1978). Positive interactions on clammy groundcherry, skeletonplant, and roundhead lespedeza are supported by some literature documenting a greater responsiveness of C_3 forb species than C_4 grasses to rainfall events following water stress (Martin et al. 1991), and greater biomass production in response to water additions (Knapp et al. 2001). Appreciable responsiveness of a wide variety of forb species, however, has been documented due to water addition in prairie (Lauenroth et al. 1978). Other literature shows the importance of supplemental water to the establishment of interseeded legumes (Groya and Sheaffer 1981) and interseeded Sandhills grass seedlings (Potvin 1984). Our results partially support our predicted role of water to enhance seedling establishment, although as previously noted, overall cover was low. We documented, however, various significant effects on other species contrary to our initial prediction. Our recorded negative effects on cacti from supplemental water were also seen in Colorado short-grass prairie (Lauenroth et al. 1978) and could be due to increased insect predation caused by early June watering (Houston 1963). The increase of bare ground from supplemental water and its interactions with with burning and disking plus seeding was supported by our visual observations. On burned plots the drill drag chain notably removed ash and plant material, and this may have allowed water addition that coincided with low June rainfall to increase decomposition rates of the remaining ash, resulting in greater bare ground detected in August. Lastly, the role of competition in Nebraska Sandhills ecosystems remains largely unresolved as work by Guretzky et al. (2016) revealed competition may not play a strong role in plant community dynamics over the long-term, potentially due to differing moisture uptake habits between grass and forb species (Nippert and Knapp 2007). Nevertheless, other research suggests that

competition for soil water is influential in determining species composition at various

Sandhills topographic positions (Barnes et al. 1984; Barnes and Harrison 1982; Keeler et

al. 1980 Potvin 1993). Thus, the primary drivers behind cover decreases related to minor

water addition in this study remain uncertain.

Year

In the first growing season after disturbance, year of sampling affected species

and functional group prevalence. With the exception of narrowleaf puccoon, reduced

cover of forbs (total forbs, rough false pennyroyal, perennial forbs, western ragweed) in

2017 may have been caused by drought in June and slightly cooler temperatures in April,

May, and June (Fig. 2-1).The drivers behind generally greater litter cover in 2017 may be

a greater cumulative, cattle grazing pressure and increased forage trampling during the

previous growing season.

Potvin and Harrison (1984) showed that May precipitation was the strongest

predictor of Sandhills C_3 grass production but April and June were also important.

Although May precipitation was greater in 2017, greater 2016 precipitation in April and

(233% of that in 2017) and June (466% of that in 2017) likely contributed to greater

cover of the C_3 grass, Scribner's rosette grass, on a certain 2016 treatment combination.

In 2017, the study site received slightly greater July and substantially greater August

precipitation than 2016 and this may have contributed to greater cover the C_4 grass, sand

bluestem, which was actively growing at that time. In contrast to deeper rooting C_4

species, shallower-rooting *Bouteloua* species respond positively to April through August

precipitation in Sandhills ecosystems (Potvin and Harrison 1984). From April through

mid-August sampling, 2017 had only received 87% of the precipitation received in 2016, and this likely contributed to reductions in hairy grama cover.

Second Growing Season Post-Disturbance

June Forb Density

Positive interactive effects of fire on second season, June forb density seemed to be driven by non-significant increases in Canadian horseweed (2.6 plants/m^2 on unburned compared to 6.3 plants/m^2 on burned plots) and western ragweed (2.4 plants/m^2 on unburned compared to 5.7 plants/m^2 on burned plots). A study in South Dakota mixed-grass prairie also documented an increase in total forb density following spring fire, except the study was conducted on annually burned prairie without second-season post disturbance values (Biondini et al. 1989). Meanwhile, the increase in forb density from disking plus seeding on unburned plots agrees with an ephemeral flush in forb cover documented on > 1-year old pocket gopher mounds in the Sandhills, though this increase was less evident in subsequent years (Foster and Stubbendieck 1980).

The general lack of stiff sunflower and largeflowered penstemon germination in the first growing season compared to the presence of those species in the second growing season could be attributable to lack of cold-moist stratification and subsequent seed dormancy issues (Heiser et al. 1969; Lindgren and Schaaf 2004). Broadcast seeding during the dormant season instead of spring drilling may help overcome seed dormancy problems (Larson et al. 2011). Low establishment of seeded species on disked plus seeded plots, supports the concept that establishment of perennial species in the Sandhills by seeding following disking is difficult without average or above-average precipitation

(Potvin 1993), especially during the month of June. Furthermore, an observed reduction in mean plant density of roundhead lespedeza and purple prairieclover in the second compared to the first growing season, suggests that seedlings emerging during the first growing season had inadequate seedling development to persist overwinter (Barnes et al. 2007).

<p style="text-align:center"><u>August Cover and Herbage Mass</u></p>

Fire

By the end of the second growing season post-disturbance, treatments still played a large role influencing plant community composition; however, there were fewer main and interactive effects. Fire did not significantly alter total standing herbage mass and this is consistent with results found by Pfeiffer and Steuter (1994). Fire no longer influenced species richness as the spring suppression of certain annual forb species did not occur in the second season. As in the first year, though, fire positively affected bare ground and negatively affected litter cover. Bragg (1998) also documented this specific continued effect of fire into a second year.

Fire had continued positive effects on graminoid species into the second year. The decreased sedge herbage mass, however, is likely a lasting effect from early season suppression the previous year. Warm-season grasses and bunchgrasses were positively affected by fire as predicted, although through an interaction with soil disturbance. On disked plus seeded plots fire increased cover of warm-season grasses, and since litter and bare ground trends continued into the second growing season it is likely that increased light incidence and spring soil temperatures also persisted and contributed to this

increase. Fire interacted with soil disturbance to mediate the negative effects of disking and disking plus seeding on warm-season grasses and bunchgrasses. In a Konza prairie study, negative effects of simulated pocket gopher disturbances on graminoid biomass were also mediated by burning (Rogers and Hartnett 2001a), showing evidence for an ecological interaction. Although fire interacted with other treatments to affect herbage mass of cool-season grasses, it was not significant in a simple effects analysis.

Soil Disturbance

Biotic and abiotic drivers of the increase in shrub herbage mass on disked plots remain largely unresolved. One such driver, however, could be the ability of woody species to withstand disking and outcompete nearby, suppressed graminoid species for water, nutrients and light. A study in northern mixed-grass prairie documented the importance of competition with neighboring species as the elimination of nearby plants, within a 30-cm radius, mediated the negative effects of competition (Wilson and Shay 1990). Although this study examined grass species, the same principles might apply to shrub competition with suppressed nearby herbaceous plants. Soil texture could also affect response, as an additional study documented relatively increased regrowth of shrubs following soil perturbation on higher sand content soils (Wonkka et al. 2016). The increase in shrub cover, however, does not agree with our predicted cover reductions due to disking.

Negative interactive effects of disking on the cover of grasses, warm-season grasses, warm-season bunchgrasses, and hairy grama support our prediction of negative effects of soil disturbance on perennial plant cover. This reduction seems to be a

continuation, and to some degree intensification, of the negative effects inflicted in the first growing season post-disturbance. Reductions would likely not have been as severe had initial disturbance events been reduced in spatial scale (Rogers and Hartnett 2001b). The decrease in grasses, however, did not occur in the presence of watering and these events were important in mediating the reduction from disking. In the case of warm-season grasses and bunchgrasses, the reduction not seen on burned plots indicates that the beneficial effects of fire extending into the second year were sufficient to counteract the negative effects of soil disturbance. These trends provide evidence for ecological interactions between soil disturbance and minor rainfall events as well as with fire.

The drivers behind the negative interactive effects of disking and disking plus seeding on the cover of warm-season grasses, warm-season bunchgrasses, and hairy grama are likely direct damage and burying from disk blades. Declines in warm-season grasses and bunchgrasses on disked plus seeded plots, however, were not as severe and may be due to improved soil water uptake from partial replanting of crown material. The positive interactive response of the rhizomatous grass, sand bluestem, to disking plus seeding is consistent with the general concept of a graminoid recolonization via vegetative structures in the years following disturbance (Gibson 1989; Rogers et al. 2001; Rogers and Hartnett 2001a, 2001b). Due to the large spatial extent of disturbance, however, this process is slowed and the expected ephemeral increase in forb, cover such as that of clammy groundcherry, was observed during the second growing season. It is expected that these contrasts will diminish over time, however, as graminoid re-colonization continues (Foster and Stubbendieck 1980; Rogers and Hartnett 2001a, 2001b; Steuter et al. 1995). Although soil disturbance interacted with other treatments to

affect herbage mass of cool-season grasses, soil disturbance alone did not have a significant simple effect. Seed availability did not limit the cover of seeded forb species in the second season, providing weak support for our seed addition prediction during the second year.

Supplemental Water

The negative interactive effect of minor water additions on cover of warm-season grasses and bunchgrasses on undisked plots was likely driven by a continued reduction of little bluestem from the first growing season (41% reduction in the second season on watered plots, although not statistically significant). Competition with forbs, cool-season bunchgrasses, and warm-season rhizomatous grasses was also a potential factor in the second year as these functional groups had slightly increased cover on watered plots, although not statistically significant. In the case of total grass cover, reductions due to disking were not seen in the presence of minor water application. This provides evidence for the mediating effects of early summer supplemental water on grasses in general after undergoing stress from disking. Negative interactive effects on cool-season grass herbage mass could be due to greater litter cover on watered, undisked, and unburned plots. This litter may have suppressed early season growth through possible reductions in light interception and soil temperature. Varied interactive effects on hairy grama and a positive interactive effect on clammy groundcherry are supported by the concept of responsiveness of *Bouteloua* species in semi-arid prairie (Barnes and Harrison 1982; Brown and Trlica 1977; Detling 1979) and C_3 forb species (Martin et al. 1991) to minor rain events; potentially through more efficient use of surface soil moisture. Overall,

contrary to our prediction, minor rainfall events occurring the year prior (two 0.64-cm events) did not affect second season, seeded forb persistence and had continued significant effects on species cover.

Conclusions

We observed both positive and negative impacts of disturbance events on plant species and groups in Sandhills prairie. Although years varied in environmental conditions and affected abundance of some species, we can make certain key inferences. This study showed that mid-spring fire can be a beneficial tool in the first season post-disturbance establishment of perennial, spring-drilled legume species, however, establishment may be limited by June water stress. Minor precipitation events during dry periods in early summer were important to seedling establishment and the abundance of certain forb species. From a grazing perspective, the first season increase in good forage value, warm-season rhizomatous grasses, interactive increases in warm-season grasses during both seasons, and suppression of annual forbs without a reduction in total standing cover are benefits of fire. First season perennial forb (largely western ragweed) and second season forb density increases as well as decrease in sedges due to burning, however, may not be as desirable. From an ecological perspective, seed availability did play a role on cover of seeded leguminous species but effects were minimal, short-lived, year-dependent, and possibly dormancy-constrained. Additionally, the interaction between fire and soil disturbance on warm-season grasses in the second year shows the mediating effects of fire that may have occurred historically on Sandhills pocket gopher mounds. Furthermore, the negative role of disking on second year cover of grasses was mediated by supplemental water, providing yet more evidence for interactions between disturbance events in Sandhills prairie. Soil disturbance in the form of disking alone had mostly negative effects on species cover. The difference in species response to disking

compared to disking followed by the seed drill, however, demonstrates the importance of specific soil disturbance methods. Total standing cover was unaffected regardless of treatment in both seasons showing the resilience of this ecosystem even to intense soil perturbation. Ultimately, Sandhills prairie uplands were formed under the interactions of various disturbance events, and the restoration of certain distinct disturbances has unique effects on species response with both grazing management and ecological implications.

Literature Cited

Anderson, H.W., 1976. Fire effects on water supply, floods, and sedimentation [forest fire]., in: Proceedings Tall Timbers Fire Ecology Conference, 15: 249–260.

Augustine, D.J., Cully, J.F., Johnson, T.L., 2007. Influence of Fire on Black-Tailed Prairie Dog Colony Expansion in Shortgrass Steppe. Rangeland Ecology & Management 60, 538–542.

Barnes, P.W., Harrison, A.T., 1982. Species Distribution and Community Organization in a Nebraska Sandhills Mixed Prairie as Influenced by Plant/Soil-Water Relationships. Oecologia 52, 192–201.

Barnes, P.W., Harrison, A.T., Heinisch, S.P., 1984. Vegetation Patterns in Relation to Topography and Edaphic Variation Nebraska Sandhills Prairie. Prairie Nat 16:145-158.

Barnes R. F., Nelson C. J., Moore K. J. et al., 2007. Wiley: Forages, Volume 2: The Science of Grassland Agriculture, 6th Edition.

Benedict, R.A., Freeman, P.W., Genoways, H.H., 1996. Prairie legacies-mammals, in: Prairie Conservation: Preserving North America's Most Endangered Ecosystem. Island Press, Washington, DC. pp. 149–166.

Benson, E.J., Hartnett, D.C., 2006. The Role of Seed and Vegetative Reproduction in Plant Recruitment and Demography in Tallgrass Prairie. Plant Ecol 187, 163–178. https://doi.org/10.1007/s11258-005-0975-y.

Benson, T.J., Dinsmore, J.J., Hohman, W.L., 2007. Responses of Plants and Arthropods to Burning and Disking of Riparian Habitats. The Journal of Wildlife Management 71, 1949–1957.

Biondini, M.E., Steuter, A.A., Grygiel, C.E., 1989. Seasonal Fire Effects on the Diversity Patterns, Spatial Distribution and Community Structure of Forbs in the Northern Mixed Prairie, USA. Vegetatio 85, 21–31.

Blankespoor, G.W., Larson, E.A., 1994. Response of Smooth Brome (Bromus inermis Leyss.) to Burning under Varying Soil Moisture Conditions. The American Midland Naturalist 131, 266–272. https://doi.org/10.2307/2426252.

Blewett, T.J., 1986. Eastern redcedar's (Juniperus virginiana L.) expanded role in the prairieforest border region. Canandian Journal of Forest Research 4, 222–228.

Bragg, T.B., 1998. Fire in the Nebraska Sandhills prairie, in: Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription. Tall Timbers Fire Ecol. Conf. Proc.(TL Pruden and LA Brennan, Eds.). pp. 179–194.

Briggs, J.M., Knapp, A.K., Brock, B.L., 2002. Expansion of Woody Plants in Tallgrass Prairie: A Fifteen-year Study of Fire and Fire-grazing Interactions. The American Midland Naturalist 147, 287–294. https://doi.org/10.1674/0003-0031(2002)147[0287:EOWPIT]2.0.CO;2.

Briske, D.D., Butler, J.L., 1989. Density-Dependent Regulation of Ramet Populations Within the Bunchgrass Schizachyrium Scoparium: Interclonal Versus Intraclonal Interference. Journal of Ecology 77, 963–974. https://doi.org/10.2307/2260816.

Brown, L., Trlica, M.J., 1977. Interacting effects of soil water, temperature and irradiance on CO2 exchange rates of two dominant grasses of the shortgrass prairie. Journal of Applied Ecology 197–204.

Case, R., Jasch, B., 1994. Pocket Gophers. The Handbook: Prevention and Control of Wildlife Damage.

Christiansen, P.A., 1994. Establishment of prairie species by overseeding into burned roadside vegetation, in: Proceedings of the 14th North American Prairie Conference. Kansas State University, Manhattan. pp. 167–169.

Coffin, D.P., Lauenroth, W.K., 1989. Spatial and Temporal Variation in the Seed Bank of a Semiarid Grassland. American Journal of Botany 76, 53–58. https://doi.org/10.2307/2444773.

Collins, S.L., Uno, G.E., 1983. The Effect of Early Spring Burning on Vegetation in Buffalo Wallows. Bulletin of the Torrey Botanical Club 110, 474–481. https://doi.org/10.2307/2996281.

Curtis, J.T., Partch, M.L., 1948. Effect of Fire on the Competition Between Blue Grass and Certain Prairie Plants. The American Midland Naturalist 39, 437–443. https://doi.org/10.2307/2421594.

Dalgleish, H.J., Hartnett, D.C., 2006. Below-ground bud banks increase along a precipitation gradient of the North American Great Plains: a test of the meristem limitation hypothesis. New Phytologist 171, 81–89. https://doi.org/10.1111/j.1469-8137.2006.01739.x.

Daubenmire, R., 1959. A canopy-coverage method of vegetational analysis. Northwest Sci 33, 43–66.

Detling, J.K., 1979. Processes controlling blue gramma production on the shortgrass prairie. Perspectives in grassland ecology: results and applications of the US/IBP Grassland Biome study 25–42.

Dollar, J.G., 2011. Responses of butterfly and forb communities to management of semi-natural grassland buffers. Ph.D. Dissertation. Mississippi State University.

Engle, D.M., Stritzke, J.F., Bidwell, T.G., Claypool, P.L., 1993. Late-Summer Fire and Follow-Up Herbicide Treatments in Tallgrass Prairie. Journal of Range Management 46, 542–547. https://doi.org/10.2307/4002869.

Ewing, A.L., Engle, D.M., 1988. Effects of Late Summer Fire on Tallgrass Prairie Microclimate and Community Composition. The American Midland Naturalist 120, 212–223. https://doi.org/10.2307/2425901.

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2003. Productivity responses to altered rainfall patterns in a C4-dominated grassland. Oecologia 137, 245–251. https://doi.org/10.1007/s00442-003-1331-3.

Foster, M.A., Stubbendieck, J., 1980. Effects of the Plains Pocket Gopher (Geomys bursarius) on Rangeland. Journal of Range Management 33, 74–78. https://doi.org/10.2307/3898233.

Frost, C.C., 1998. Presettlement fire frequency regimes of the United States: A first approximation, in: Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription, Ed. TL Pruden and LA Brennan. pp. 70–81.

Gibson, D.J., 1989. Effects of Animal Disturbance on Tallgrass Prairie Vegetation. The American Midland Naturalist 121, 144–154. https://doi.org/10.2307/2425665.

Glenn-Lewin, D.C., Johnson, L.A., Jurik, T.W., Akey, A., Leoschke, M., Rosburg, T., 1990. Fire in central North American grasslands: vegetative reproduction, seed germination, and seedling establishment. Fire in North American tallgrass prairies 28–45.

Groya, F.L., Sheaffer, C.C., 1981. Establishment of Sod-seeded Alfalfa at Various Levels of Soil Moisture and Grass Competition. Agronomy Journal 73, 560–565. https://doi.org/10.2134/agronj1981.00021962007300030036x.

Guretzky, J.A., Dunn, C., Hillhouse, H., 2016. Long-term Sandhills prairie responses to precipitation, temperature, and cattle stocking rate. Plant Ecol 217, 969–983. https://doi.org/10.1007/s11258-016-0622-9.

Hart, M., Waller, S.S., Lowry, S.R., Gates, R.N., 1985. Discing and Seeding Effects on Sod Bound Mixed Prairie. Journal of Range Management 38, 121–125. https://doi.org/10.2307/3899253.

Hartnett, D.C., Bazzaz, F.A., 1985. The Integration of Neighbourhood Effects by Clonal Genets in Solidago Canadensis. Journal of Ecology 73, 415–427. https://doi.org/10.2307/2260484.

Hartnett D.C., Keeler K.H., 1995. Population Processes, in: Joern A. Keeler K.H. (eds) The Changing Prairie: North American Grasslands. Oxford University Press, New York, pp. 82–99.

Heckathorn, S.A., Delucia, E.H., 1996. Restranslocation of Shoot Nitrogen to Rhizomes and Roots in Prairie Grasses May Limit Loss of N to Grazing and Fire during Drought. Functional Ecology 10, 396–400. https://doi.org/10.2307/2390289.

Heckathorn, S.A., DeLucia, E.H., 1994. Drought-Induced Nitrogen Retranslocation in Perennial C4 Grasses of Tallgrass Prairie. Ecology 75, 1877–1886. https://doi.org/10.2307/1941592.

Heiser, C.B., Smith, D.M., Clevenger, S.B., Martin, W.C., 1969. The North American Sunflowers (Helianthus). Memoirs of the Torrey Botanical Club 22, 1–218.

Higgins, K.F., 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains (Federal Government Series No. 161), Resource Publication. U.S. Fish and Wildlife Service, Washington, D.C.

Higgins, K.F., 1984. Lightning Fires in North Dakota Grasslands and in Pine-Savanna Lands of South Dakota and Montana. Journal of Range Management 37, 100–103. https://doi.org/10.2307/3898892.

HPRCC, 2017. High Plains Regional Climate Center. Climatological data (Nebraska). Lincoln, NE. https://hprcc.unl.edu. (accessed Oct 2017).

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, Diversity, and Invasion: Implications for Conservation. Conservation Biology 6, 324–337.

Hobbs, R.J., Mooney, H.A., 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. Oecologia 67, 342–351. https://doi.org/10.1007/BF00384939.

Hobbs, R.J., others, 1989. The nature and effects of disturbance relative to invasions. Biological invasions: a global perspective 389–405.

Hopkins, H., Albertson, F.W., Riegel, A., 1948. Some effects of burning upon a prairie in west-central Kansas. Transactions of the Kansas Academy of Science (1903-) 51, 131–141.

Houston, W.R., 1963. Plains pricklypear, weather, and grazing in the Northern Great Plains. Ecology 44, 569–574.

Hulbert, L.C., 1988. Causes of Fire Effects in Tallgrass Prairie. Ecology 69, 46–58. https://doi.org/10.2307/1943159.

Hulbert, L.C., 1969. Fire and Litter Effects in Undisturbed Bluestem Prairie in Kansas. Ecology 50, 874–877. https://doi.org/10.2307/1933702.

Keeler, K.H., Harrison, A.T., Vescio, L.S., 1980. The Flora and Sandhills Prairie Communities of Arapaho Prairie, Arthur County, Nebraska. Prairie Naturalist 12:65-78.

Knapp, A.K., 1984. Post-Burn Differences in Solar Radiation, Leaf Temperature and Water Stress Influencing Production in a Lowland Tallgrass Prairie. American Journal of Botany 71, 220–227. https://doi.org/10.2307/2443749.

Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., Towne, E.G., 1999. The Keystone Role of Bison in North American Tallgrass Prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. BioScience 49, 39–50. https://doi.org/10.1525/bisi.1999.49.1.39.

Knapp, A.K., Briggs, J.M., Koelliker, J.K., 2001. Frequency and Extent of Water Limitation to Primary Production in a Mesic Temperate Grassland. Ecosystems 4, 19–28. https://doi.org/10.1007/s100210000057.

Knapp, A.K., Hulbert, L.C., 1986. Production, Density and Height of Flower Stalks of Three Grasses in Annually Burned and Unburned Eastern Kansas Tallgrass Prairie: A Four Year Record. The Southwestern Naturalist 31, 235–241. https://doi.org/10.2307/3670564.

Knapp, A.K., Seastedt, T.R., 1986. Detritus Accumulation Limits Productivity of Tallgrass Prairie. BioScience 36, 662–668. https://doi.org/10.2307/1310387.

Kotliar, N.B., Baker, B.W., Whicker, A.D., Plumb, G., 1999. A Critical Review of Assumptions About the Prairie Dog as a Keystone Species. Environmental Management 24, 177–192. https://doi.org/10.1007/s002679900225.

Kral, K.C., Limb, R.F., Hovick, T.J., McGranahan, D.A., Field, A.L., O'Brien, P.L., 2015. Simulating grassland prescribed fires using experimental approaches. Fire Ecology 11, 34–44.

Lane, D.R., Coffin, D.P., Lauenroth, W.K., 2000. Changes in Grassland Canopy Structure across a Precipitation Gradient. Journal of Vegetation Science 11, 359–368. https://doi.org/10.2307/3236628.

Larson, D.L., Bright, J.B., Drobney, P., Larson, J.L., Palaia, N., Rabie, P.A., Vacek, S., Wells, D., 2011. Effects of planting method and seed mix richness on the early stages of tallgrass prairie restoration. Biological Conservation 144, 3127–3139.

Lauenroth, W.K., Dodd, J.L., Sims, P.L., 1978. The Effects of Water- and Nitrogen-Induced Stresses on Plant Community Structure in a Semiarid Grassland. Oecologia 36, 211–222.

Lindgren, D.T., Schaaf, D.M., 2004. Influence of Seed Stratification and Seed Age on Emergence of Penstemon. HortScience 39, 1385–1386.

Lippert, R.D., Hopkins, H.H., 1950. Study of Viable Seeds in Various Habitats in Mixed Prairie. Transactions of the Kansas Academy of Science (1903-) 53, 355–364. https://doi.org/10.2307/3626149.

Maret, M.P., Wilson, M.V., 2005. Fire and Litter Effects on Seedling Establishment in Western Oregon Upland Prairies. Restoration Ecology 13, 562–568. https://doi.org/10.1111/j.1526-100X.2005.00071.x.

Martin, C.E., Harris, F.S., Norman, F.J., 1991. Ecophysiological Responses of C3 Forbs and C4 Grasses to Drought and Rain on a Tallgrass Prairie in Northeastern Kansas. Botanical Gazette 152, 257–262.

Morrison, L.C., DuBois, J.D., Kapustka, L.A., 1986. The vegetational response of a Nebraska Sandhills grassland to a naturally occurring fall burn. Prairie Naturalist 18, 179–184.

Nippert, J.B., Knapp, A.K., 2007. Soil water partitioning contributes to species coexistence in tallgrass prairie. Oikos 116, 1017–1029.

NOAA, 2017. National oceanic and Atmospheric Administration. National Climatic Data Center. http://www.noaa.gov. (accessed Nov 2017).

Ojima, D.S., Schimel, D.S., Parton, W.J., Owensby, C.E., 1994. Long- and Short-Term Effects of Fire on Nitrogen Cycling in Tallgrass Prairie. Biogeochemistry 24, 67–84.

Packard, S., Masters, L., 2008. Interseeding with and without Raking (Illinois). Ecological Rest. 26, 113–114. https://doi.org/10.3368/er.26.2.113.

Peet, M., Anderson, R., Adams, M.S., 1975. Effect of Fire on Big Bluestem Production. The American Midland Naturalist 94, 15–26. https://doi.org/10.2307/2424534.

Petranka, J.W., McPherson, J.K., 1979. The Role of Rhus Copallina in the Dynamics of the Forest-Prairie Ecotone in North-Central Oklahoma. Ecology 60, 956–965. https://doi.org/10.2307/1936864.

Pfeiffer, K.E., Steuter, A.A., 1994. Preliminary Response of Sandhills Prairie to Fire and Bison Grazing. Journal of Range Management 47, 395–397. https://doi.org/10.2307/4002337.

Potvin, M.A., 1993. Establishment of Native Grass Seedlings along a Topographic/Moisture Gradient in the Nebraska Sandhills. The American Midland Naturalist 130, 248–261. https://doi.org/10.2307/2426125.

Potvin, M.A., 1988. Seed rain on a Nebraska Sandhills prairie. Prairie Naturalist 20, 81–89.

Potvin, M.A., 1984. Factors Affecting Native Grass Seedling Establishment Along Topographic Gradients In The Nebraska Sandhills: An Experimental Approach. Etd collection for University of Nebraska - Lincoln 1–165.

Potvin, M.A., Harrison, A.T., 1984. Vegetation and litter changes of a Nebraska sandhills prairie protected from grazing. Journal of Range Management 55–58.

Rabinowitz, D., Rapp, J.K., 1980. Seed Rain in a North American Tall Grass Prairie. Journal of Applied Ecology 17, 793–802. https://doi.org/10.2307/2402656.

Rice, E.L., Parenti, R.L., 1978. Causes of Decreases in Productivity in Undisturbed Tall Grass Prairie. American Journal of Botany 65, 1091–1097. https://doi.org/10.2307/2442326.

Rogers, W.E., Hartnett, D.C., 2001a. Vegetation Responses to Different Spatial Patterns of Soil Disturbance in Burned and Unburned Tallgrass Prairie. Plant Ecology 155, 99–109.

Rogers, W.E., Hartnett, D.C., 2001b. Temporal vegetation dynamics and recolonization mechanisms on different-sized soil disturbances in tallgrass prairie. Am. J. Bot. 88, 1634–1642.

Rogers, W.E., Hartnett, D.C., Elder, B., 2001. Effects of Plains Pocket Gopher (Geomys bursarius) Disturbances on Tallgrass-prairie Plant Community Structure. The American Midland Naturalist 145, 344–357. https://doi.org/10.1674/0003-0031(2001)145[0344:EOPPGG]2.0.CO;2.

Rowe, H.I., 2010. Tricks of the Trade: Techniques and Opinions from 38 Experts in Tallgrass Prairie Restoration. Restoration Ecology 18, 253–262. https://doi.org/10.1111/j.1526-100X.2010.00663.x.

Sala, O.E., Lauenroth, W.K., 1982. Small Rainfall Events: An Ecological Role in Semiarid Regions. Oecologia 53, 301–304.

SAS. Statistical Analysis System. 2017. Version 9.4. SAS Institute. Cary, N.C., USA.

Schacht, W.H., Volesky, J.D., Bauer, D., Smart, A., Mousel, E., 2000. Plant community patterns on upland prairie in the eastern Nebraska sandhills. Agronomy–Faculty Publications 339.

Schmeisser, R.L., Loope, D.B., Wedin, D.A., 2009. Clues to the medieval destabilization of the nebraska sand hills, usa, from ancient pocket gopher burrows. Palaios 24, 809–817. https://doi.org/10.2110/palo.2009.p09-037r.

Singh, J.S., Milchunas, D.G., Lauenroth, W.K., 1998. Soil Water Dynamics and Vegetation Patterns in a Semiarid Grassland. Plant Ecology 134, 77–89.

Smart, A.J., Derner, J.D., Hendrickson, J.R., Gillen, R.L., Dunn, B.H., Mousel, E.M., Johnson, P.S., Gates, R.N., Sedivec, K.K., Harmoney, K.R., Volesky, J.D., Olson, K.C., 2010. Effects of Grazing Pressure on Efficiency of Grazing on North American Great Plains Rangelands. Rangeland Ecology & Management 63, 397–406. https://doi.org/10.2111/REM-D-09-00046.1.

Sorensen, J.T., Holden, D.J., 1974. Germination of Native Prairie Forb Seeds. Journal of Range Management 27, 123–126. https://doi.org/10.2307/3896747.

Steuter, A.A., Steinauer, E.M., Hill, G.L., Bowers, P.A., Tieszen, L.L., 1995. Distribution and Diet of Bison and Pocket Gophers in a Sandhills Prairie. Ecological Applications 5, 756–766. https://doi.org/10.2307/1941983.

Towne, G., Owensby, C., 1984. Long-Term Effects of Annual Burning at Different Dates in Ungrazed Kansas Tallgrass Prairie. Journal of Range Management 37, 392–397. https://doi.org/10.2307/3899622.

USDA-NRCS, 2018. United States Department of Agriculture. Natural Resources Conservation Service. Ecological Site Description. https://esis.sc.egov.usda.gov. (accessed Jan 2018).

U.S. Drought Monitor, 2017. The National Drought Mititgation Center. University of
    Nebraska-Lincoln. http://droughtmonitor.unl.edu. (accessed Nov 2017).

Vogel, K.P., Masters, R.A., 2001. Frequency Grid: A Simple Tool for Measuring
    Grassland Establishment. Journal of Range Management 54, 653–655.
    https://doi.org/10.2307/4003666.

Vogel, K.P., Schmer, M.R., Mitchell, R.B., 2005. Plant Adaptation Regions: Ecological
    and Climatic Classification of Plant Materials. Rangeland Ecology &
    Management 58, 315–319. https://doi.org/10.2111/1551-
    5028(2005)58[315:PAREAC]2.0.CO;2.

Voigt, J.W., 1977. Seed Germination of True Prairie Forbs. Journal of Range
    Management 30, 439–441. https://doi.org/10.2307/3897806.

Volesky, J.D., Connot, S.B., 2000. Vegetation Response to Late Growing-Season
    Wildfire on Nebraska Sandhills Rangeland. Journal of Range Management 53,
    421–426. https://doi.org/10.2307/4003754.

White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: an
    introduction. Unknown Journal 3–13.

Wilson, S.D., Shay, J.M., 1990. Competition, Fire, and Nutrients in a Mixed-Grass
    Prairie. Ecology 71, 1959–1967. https://doi.org/10.2307/1937604.

Wolfe, C.W., 1973. Effects of fire on a sand hills grassland environment. Tall Timbers
    Research Station, pp. 241-255.

Wonkka, C.L., Twidwell, D., West, J.B., Rogers, W.E., 2016. Shrubland resilience varies
    across soil types: implications for operationalizing resilience in ecological
    restoration. Ecological applications 26, 128–145.

Zink, R.R., Schultz, H., Wright, R., Shurtliff. D., 1985. Soil survey of
    Rock County, Nebraska. U.S. Dept. Agric, Soil Conserv. Serv., Washington,
    D.C. 168 pp.

Tables and Figures

Table 2-1. Two-way interaction of mid-spring fire and early summer supplemental water on estimated June density (plants/m^2) of western ragweed in the first growing season post-disturbance in Nebraska Sandhills prairie.

Fire	Water	
	Unwatered	Watered
	———— Western Ragweed, plants/m^2 ————	
Unburned	15.7ab[1]	14.3b
Burned	15.6ab	17.6a

[1]Similar letters indicate no significant difference (P > 0.05) between treatment combination means.

Table 2-2. Three-way interaction of mid-spring fire, early summer supplemental water, and mid-spring soil disturbance on estimated June density (plants/m^2) of Canadian horseweed in the first growing season post-disturbance in Nebraska Sandhills prairie.

Fire	Water	Soil Disturbance		
		Undisked	Disked	Disked plus seeded[1]
		————— Canadian Horseweed, plants/m^2 —————		
Unburned	Unwatered	9.6b[2]	9.8b	12.6ab
	Watered	16.4a	10.4b	12.0b
Burned	Unwatered	3.1c	0.8c	2.1c
	Watered	3.9c	3.1c	2.6c

[1]Disked plus seeded treatments were mid-spring drill-seeded with a perennial forb mix (purple prairieclover, roundhead lespedeza, stiff sunflower, largeflowered penstemon) following disking.
[2]Similar letters indicate no significant difference ($P > 0.05$) between treatment combination means.

Table 2-3. Two-way interactions between year and mid-spring fire and between year and early summer supplemental water on estimated June density (plants/m^2) of purple prairieclover seedlings in the first growing season post-disturbance in Nebraska Sandhills prairie.

	Fire		Water	
Year	Unburned	Burned	Unwatered	Watered
	——— Purple Prairieclover Seedlings, plants m^2 ———			
2016	1.4b[1]	5.2a	1.9b[1]	4.7a
2017	0.1c	0.4bc	0.2c	0.2c

[1]Similar letters indicate no significant difference (P > 0.05) between treatment combination means within a respective interaction.

Table 2-4. Three-way interaction of year, mid-spring fire, and early summer supplemental water on estimated June density (plants/m^2) of roundhead lespedeza seedlings in the first growing season post-disturbance in Nebraska Sandhills prairie.

Year	Fire	Water	
		Unwatered	Watered
		—— Roundhead Lespedeza Seedlings, plants m^2 ——	
2016	Unburned	0.3bc[1]	0.4bc
	Burned	1.2b	3.0a
2017	Unburned	0.0c	0.2c
	Burned	0.1c	0.1c

[1]Similar letters indicate no significant difference (P > 0.05) between treatment combination means.

Table 2-5. Two-way interaction of year and mid-spring fire on percentage cover of litter in the first growing season post-disturbance in Nebraska Sandhills prairie.

Year	Fire	
	Unburned	Burned
	Litter, %	
2016	12.8b[1]	6.2c
2017	36.2a	15.7b

[1]Similar letters indicate no significant difference (P > 0.05) between treatment combination means.

Table 2-6. Two-way interaction of early summer supplemental water and mid-spring soil disturbance on percentage cover of warm-season (WS) bunchgrasses, fall rosette grass, and clammy groundcherry in the first growing season post-disturbance in Nebraska Sandhills prairie.

Water	Soil Disturbance		
	Undisked	Disked	Disked plus seeded[1]
	———————— WS Bunchgrasses, % ————————		
Unwatered	10.3a[2]	6.7b	7.9ab
Watered	4.9b	6.5b	7.3ab
	———————— Fall Rosette Grass, % ————————		
Unwatered	1.4a[2]	0.5ab	0.8ab
Watered	0.3b	1.1ab	0.8ab
	———————— Clammy Groundcherry, % ————————		
Unwatered	0.1b[2]	0.9ab	0.3ab
Watered	1.0a	0.1b	0.4ab

[1]Disked plus seeded treatments were mid-spring drill-seeded with a perennial forb mix (purple prairieclover, roundhead lespedeza, stiff sunflower, largeflowered penstemon) following disking.
[2]Similar letters indicate no significant difference ($P > 0.05$) between treatment combination means within a respective interaction.

Table 2-7. Three-way interaction of mid-spring fire, early summer supplemental water, and mid-spring soil disturbance on percentage cover of bare ground, prairie sandreed, cactus, and brittle cactus in the first growing season post-disturbance in Nebraska Sandhills prairie.

Fire	Water	Soil Disturbance		
		Undisked	Disked	Disked plus seeded[1]
		Bare Ground, %		
Unburned	Unwatered	11.3ef[2]	11.6ef	17.4efd
	Watered	7.0f	20.5cde	16.9ef
Burned	Unwatered	28.9bc	38.1ab	27.8bcd
	Watered	28.9bc	34.5ab	41.2a
		Prairie Sandreed, %		
Unburned	Unwatered	0.9abc[2]	0.5c	1.0abc
	Watered	1.7a	0.8bc	0.6c
Burned	Unwatered	1.2abc	1.5ab	1.3abc
	Watered	1.0abc	0.7bc	1.6a
		Cactus, %		
Unburned	Unwatered	1.5ab[2]	0.8abc	0.7abc
	Watered	0.8abc	1.2abc	1.6a
Burned	Unwatered	0.4c	0.5c	1.0abc
	Watered	0.6bc	0.3c	0.3c
		Brittle Cactus, %		
Unburned	Unwatered	1.5ab[2]	0.8abc	0.7abc
	Watered	0.8abc	1.2abc	1.6a
Burned	Unwatered	0.4c	0.5c	1.0abc
	Watered	0.6bc	0.3c	0.3c

[1]Disked plus seeded treatments were mid-spring drill-seeded with a perennial forb mix (purple prairieclover, roundhead lespedeza, stiff sunflower, largeflowered penstemon) following disking.
[2]Similar letters indicate no significant difference ($P > 0.05$) between treatment combination means within a respective interaction.

Table 2-8. Three-way interaction of year, early summer supplemental water, and mid-spring fire on percentage cover of bare ground in the first growing season post-disturbance in Nebraska Sandhills prairie.

Year	Water	Fire	
		Unburned	Burned
		Bare Ground, %	
2016	Unwatered	7.6c[1]	32.1ab
	Watered	15.8c	28.6ab
2017	Unwatered	19.3bc	31.1ab
	Watered	13.9c	41.1a

[1]Similar letters indicate no significant difference (P > 0.05) between treatment combination means.

Table 2-9. Three-way interaction of year, mid-spring fire, and mid-spring soil disturbance on percentage cover of warm-season (WS) grasses and sand bluestem in the first growing season post-disturbance in Nebraska Sandhills prairie.

		Soil Disturbance		
Year	Fire	Undisked	Disked	Disked plus seeded[1]
		———————— WS Grasses, % ————————		
2016	Unburned	16.8ab[2]	11.0b	13.8ab
	Burned	13.8ab	14.4ab	17.0ab
2017	Unburned	12.2b	17.0ab	16.6ab
	Burned	20.1a	18.2ab	16.3ab
		———————— Sand Bluestem, % ————————		
2016	Unburned	1.0bc[2]	0.9bc	1.3bc
	Burned	0.8c	1.5bc	3.1ab
2017	Unburned	1.7bc	2.0abc	2.4abc
	Burned	4.0a	1.3bc	1.1bc

[1]Disked plus seeded treatments were mid-spring drill-seeded with a perennial forb mix (purple prairieclover, roundhead lespedeza, stiff sunflower, largeflowered penstemon) following disking.
[2]Similar letters indicate no significant difference ($P > 0.05$) between treatment combination means within a respective interaction.

Table 2-10. Four-way interaction of year, mid-spring fire, early summer supplemental water, and mid-spring soil disturbance on percentage cover of cool-season (CS) bunchgrasses and Scribner's rosette grass in the first growing season post-disturbance in Nebraska Sandhills prairie.

			Soil Disturbance		
Year	Fire	Water	Undisked	Disked	Disked plus seeded[1]
			——— CS Bunchgrasses, % ———		
2016	Unburned	Unwatered	9.4abc[2]	13.8ab	9.7abc
		Watered	11.4abc	9.5abc	8.3abc
	Burned	Unwatered	10.3abc	7.6abc	10.5abc
		Watered	8.2abc	9.4abc	8.1abc
2017	Unburned	Unwatered	12.8ab	7.1bc	6.9c
		Watered	10.8abc	14.1a	6.1c
	Burned	Unwatered	11.3abc	9.5abc	10.8abc
		Watered	8.2abc	9.8abc	13.1a
			——— Scribner's Rosette Grass, % ———		
2016	Unburned	Unwatered	6.5abc[2]	11.4a	7.8abc
		Watered	9.8abc	6.6abc	5.1bc
	Burned	Unwatered	5.3bc	6.3abc	7.8abc
		Watered	6.1abc	7.4abc	6.4abc
2017	Unburned	Unwatered	9.7abc	4.8bc	5.3bc
		Watered	7.7abc	11.3a	4.2c
	Burned	Unwatered	8.8abc	7.6abc	9.3abc
		Watered	6.3abc	7.0abc	10.3ab

[1]Disked plus seeded treatments were mid-spring drill-seeded with a perennial forb mix (purple prairieclover, roundhead lespedeza, stiff sunflower, largeflowered penstemon) following disking.
[2]Similar letters indicate no significant difference (P > 0.05) between treatment combination means within a respective two-way interaction.

Table 2-11. Two-way interaction of mid-spring fire and mid-spring soil disturbance on estimated June density (plants/m^2) of forbs in the second growing season post-disturbance in Nebraska Sandhills prairie.

| Fire | Soil Disturbance | | |
	Undisked	Disked	Disked plus seeded[1]
	———————— Forbs, plants/m^2 ————————		
Unburned	15.0d[2]	18.4cd	20.2bc
Burned	26.0a	27.5a	24.0ab

[1]Disked plus seeded treatments were mid-spring drill-seeded with a perennial forb mix (purple prairieclover, roundhead lespedeza, stiff sunflower, largeflowered penstemon) following disking.
[2]Similar letters indicate no significant difference (P > 0.05) between treatment combination means.

Table 2-12. Two-way interaction of mid-spring fire and mid-spring soil disturbance on percentage cover of warm-season (WS) grasses and bunchgrasses in the second growing season post-disturbance in Nebraska Sandhills prairie.

Fire	Soil Disturbance		
	Undisked	Disked	Disked plus seeded[1]
	——————————— WS Grasses, % ———————————		
Unburned	19.3a[2]	12.3b	12.5b
Burned	17.5ab	16.9ab	19.8a
	——————————— WS Bunchgrasses, % ———————————		
Unburned	11.4a[2]	6.1b	6.3b
Burned	9.0ab	10.4ab	10.9ab

[1]Disked plus seeded treatments were mid-spring drill-seeded with a perennial forb mix (purple prairieclover, roundhead lespedeza, stiff sunflower, largeflowered penstemon) following disking.
[2]Similar letters indicate no significant difference ($P > 0.05$) between treatment combination means within a respective interaction.

Table 2-13. Two-way interaction of early summer supplemental water and mid-spring soil disturbance on percentage cover of grasses, warm-season (WS) grasses and bunchgrasses, hairy grama, and sand bluestem in the second growing season post-disturbance in Nebraska Sandhills prairie.

	Soil Disturbance		
Water	Undisked	Disked	Disked plus seeded[1]
	——————————— Grasses, % ———————————		
Unwatered	33.9a[2]	20.5b	26.3ab
Watered	26.5ab	26.3ab	26.5ab
	——————————— WS Grasses, % ———————————		
Unwatered	21.3a[2]	12.6b	17.3ab
Watered	15.5b	16.5ab	15.0b
	——————————— WS Bunchgrasses, % ———————————		
Unwatered	13.5a[2]	7.0b	9.0ab
Watered	7.0b	9.6ab	8.2b
	——————————— Hairy Grama, % ———————————		
Unwatered	4.1a[2]	0.9c	1.6bc
Watered	1.5bc	3.0ab	1.3bc
	——————————— Sand Bluestem, % ———————————		
Unwatered	1.1b[2]	0.7b	3.3a
Watered	1.5b	1.3b	1.3b

[1]Disked plus seeded treatments were mid-spring drill-seeded with a perennial forb mix (purple prairieclover, roundhead lespedeza, stiff sunflower, largeflowered penstemon) following disking.
[2]Similar letters indicate no significant difference ($P > 0.05$) between treatment combination means within a respective interaction.

Table 2-14. Three-way interaction of mid-spring fire, early summer supplemental water, and mid-spring soil disturbance on herbage mass (g / 0.5m^2) of cool-season (CS) grasses and percentage cover of clammy groundcherry in the second growing season post-disturbance in Nebraska Sandhills prairie.

		Soil Disturbance		
Fire	Water	Undisked	Disked	Disked plus seeded[1]
		———— CS Grasses, g / 0.5m^2 ————		
Unburned	Unwatered	24.7a[2]	18.6ab	16.8ab
	Watered	10.5b	18.3ab	23.6ab
Burned	Unwatered	14.2ab	14.8ab	19.4ab
	Watered	19.6ab	13.3ab	14.0ab
		———— Clammy Groundcherry, % ————		
Unburned	Unwatered	0.5b[2]	0.2b	0.0b
	Watered	0.0b	0.0b	3.8a
Burned	Unwatered	0.0b	0.3b	0.0b
	Watered	0.3b	0.0b	0.0b

[1]Disked plus seeded treatments were mid-spring drill-seeded with a perennial forb mix (purple prairieclover, roundhead lespedeza, stiff sunflower, largeflowered penstemon) following disking.
[2]Similar letters indicate no significant difference (P > 0.05) between treatment combination means within a respective interaction.
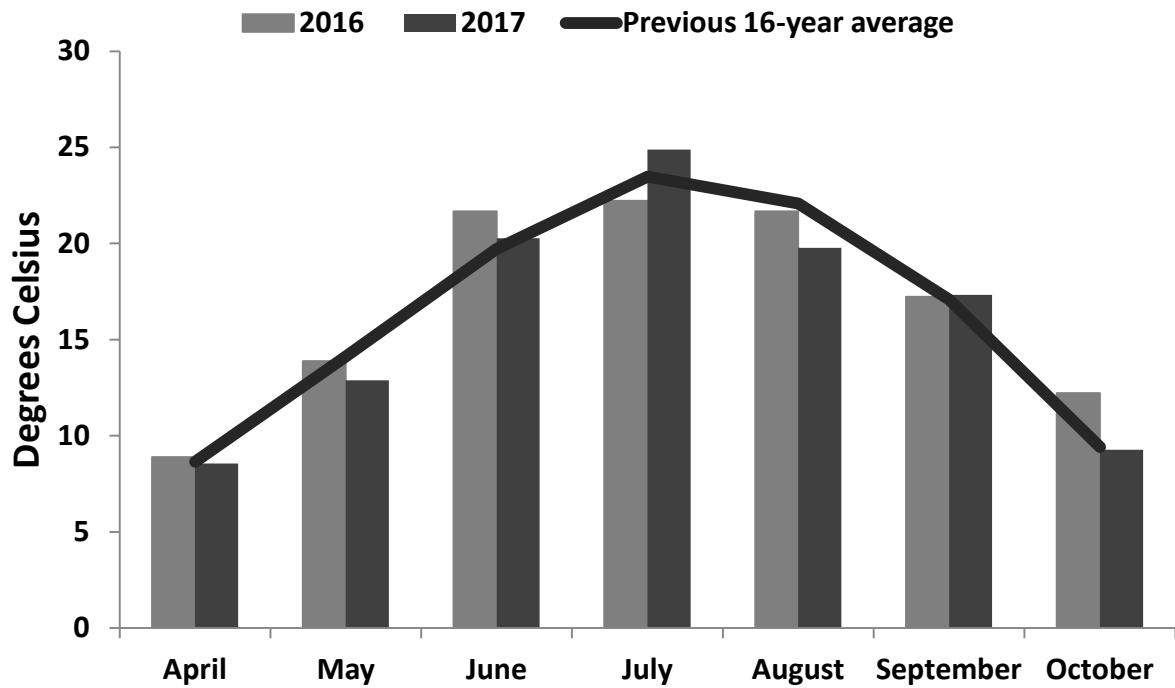
Figure 2-1. Monthly average temperature (degrees Celsius) from April through October for 2016, 2017, and the 16-year average at the University of Nebraska-Lincoln Barta Brothers Ranch in the eastern Nebraska Sandhills.
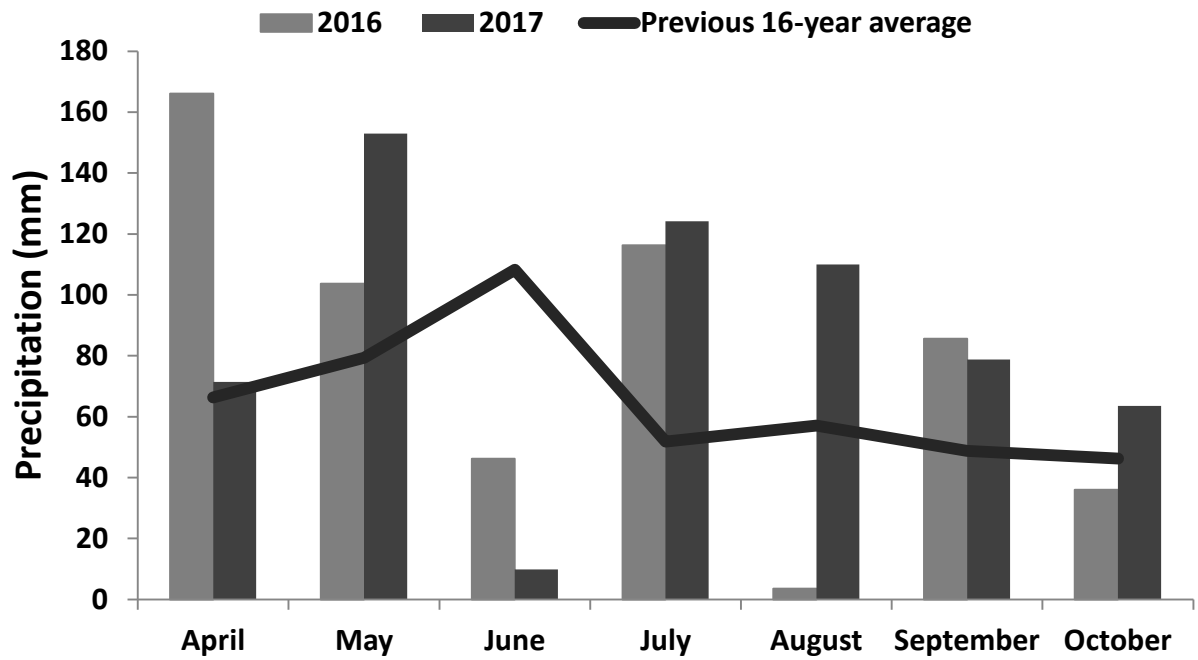
Figure 2-2. Monthly precipitation (mm) from April through October for 2016, 2017, and

the 16-year average at the University of Nebraska-Lincoln Barta Brothers Ranch in the

eastern Nebraska Sandhills.
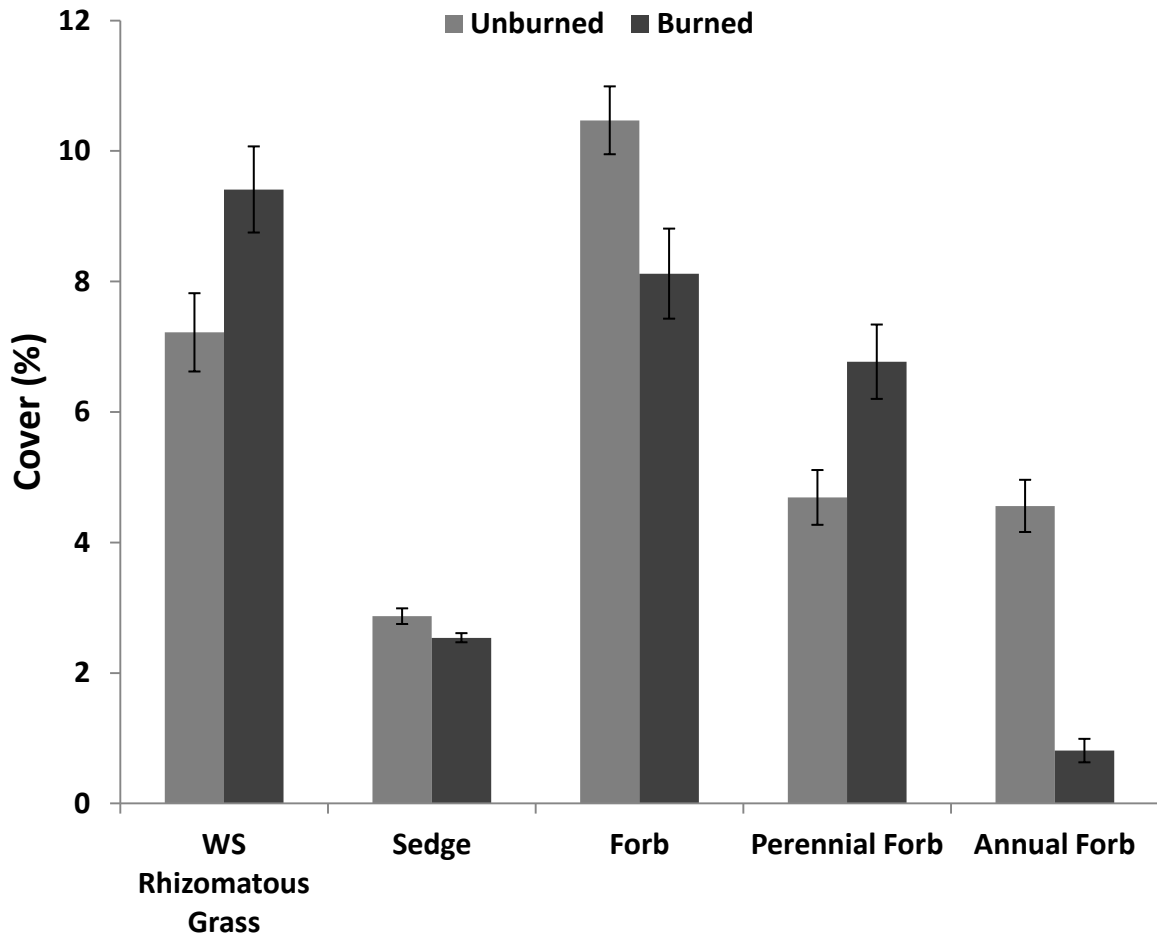
Figure 2-3. Significant (P < 0.05) main effects of mid-spring fire on percentage cover of plant groups in the first growing season post-disturbance in Nebraska Sandhills prairie. Standard error bars shown.
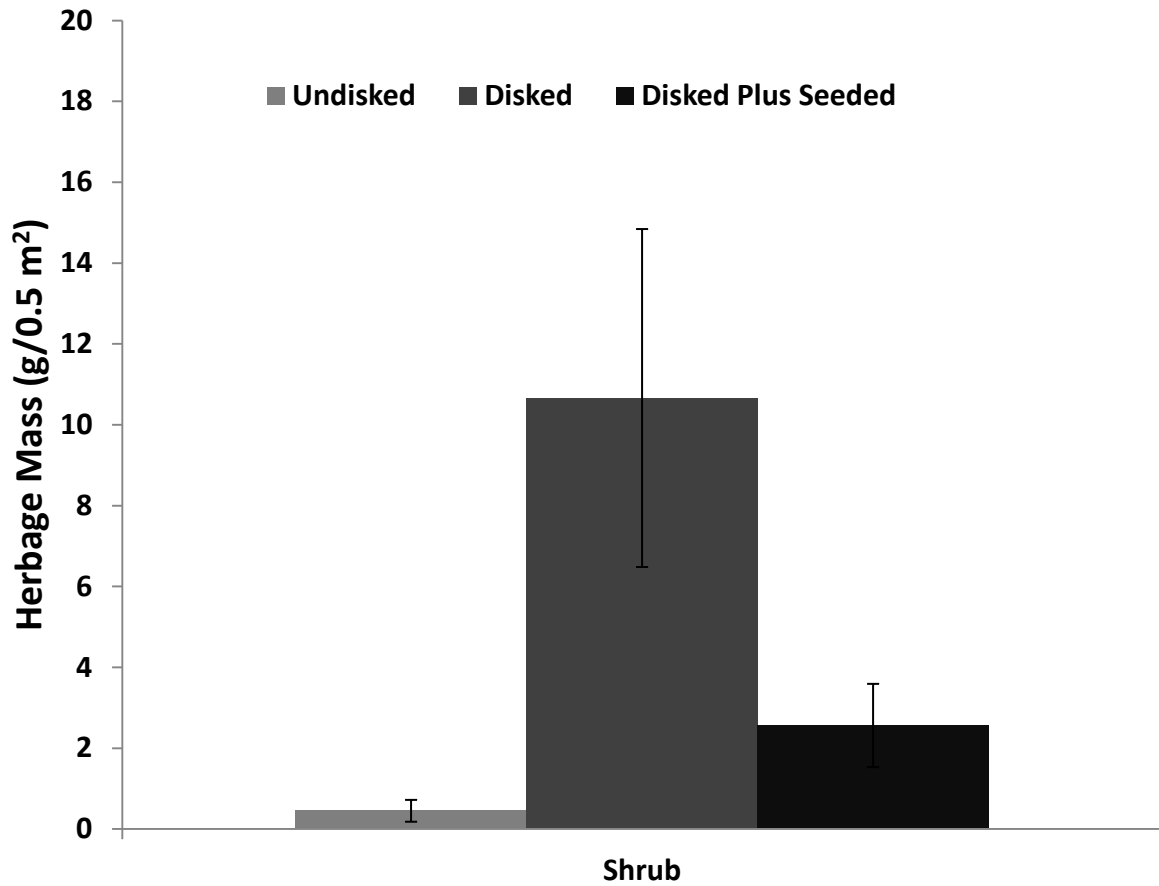
Figure 2-4. Significant (P < 0.05) main effect of mid-spring soil disturbance on shrub herbage mass (g / 0.5m^2) in the second growing season post-disturbance in Nebraska Sandhills prairie. Standard error bars shown. Disked plus seeded treatments were mid-spring drill-seeded with a perennial forb mix (purple prairieclover, roundhead lespedeza, stiff sunflower, largeflowered penstemon) following disking.