

THE FIRE ECOLOGY OF KENTUCKY BLUEGRASS
(*POA PRATENSIS*)

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ABSTRACT

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Kentucky bluegrass (*Poa pratensis*) is a serious invader found throughout the Central and Northern Great Plains. This paper is a review of prescribed fire effects on Kentucky bluegrass (*Poa pratensis*). The general approach of the paper is to look for a mechanistic understanding of its response to fire. The first portion of the paper describes the biology of Kentucky bluegrass. The next section of the paper provides an overview of fire ecology in the Great Plains. The changes to the abiotic environment during and post-fire are discussed which identifies several processes that may be responsible for the plant response to fire. Water relations, light limitation, and soil temperatures are all identified as ecosystem components that are altered by fire. The abiotic environment is further altered post-fire by biotic responses. These effects include temporal fluxes in available N, increased evapotranspiration, and increased rhizome production. Species and community responses are highly variable, depending on timing of fire, fire intensity, species identity and plant community composition. Finally, two experiments are proposed that are designed to provide mechanistic explanation for the fire response of Kentucky bluegrass. Understanding the mechanism behind its response will enable the science of prescribed burning to move forward by reducing the confounding factors associated with the use of fire.

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INTRODUCTION

Kentucky bluegrass (*Poa pratensis*) is an introduced, cool-season (C₃), rhizomatous, perennial grass that has been widely planted in the eastern United States for pastures, lawns and golf courses. In order to meet these diverse uses, there are over 100 commercially available cultivars (USDA 2010). Unfortunately, Kentucky bluegrass is expanding into the native range and wildland areas of the Great Plains. While there are subspecies that are native to alpine regions, it is considered a naturalized exotic plant throughout the central United States. As an exotic invader, Kentucky bluegrass is a serious threat to native plant communities throughout the Great Plains. In fact, contemporary expansion and invasion of Kentucky bluegrass is altering plant community structure and function in native prairie throughout the Northern Great Plains (Murphy and Grant 2005, Miles and Knops 2009). Documented decreases in plant community diversity on US Fish and Wildlife Service lands have been associated with increases in Kentucky bluegrass invasions (Murphy and Grant 2005). Several studies have documented the widespread nature of this on-going invasion in multiple sites throughout the Great Plains (Ehrenreich and Aikman 1963, Hadley 1970, Towne and Ownesby 1984, Smith and Knapp 1999, Martin and Chambers 2001, Bowles et al. 2003, Cully et al. 2003, Travnicek et al. 2005, Hendrickson and Lund 2010). In addition to the inherent concerns with loss of diversity, forage production and quality can suffer when diversity is lost (Foster et al. 2009).

In the Northern Great Plains as well as other temperate prairie systems, public and private land managers are beginning to take note that Kentucky bluegrass invasion into native plant communities is associated with passive management (i.e., little to no grazing or prescribed fire) (Towne and Ownesby 1984, Bowles et al. 2003, Murphy and Grant 2005). Likewise, Kentucky bluegrass is a known increaser under heavy grazing pressure because of its relative tolerance to intense grazing (Ehrenreich 1963, Waddington et al. 1999, Patton et al. 2010). This emphasizes the need to understand site history when interpreting ecosystem properties and plant community dynamics.

In an attempt to control Kentucky bluegrass and other invaders, land managers in the Northern Great Plains use prescribed fire. Much research has been conducted on plant community response to spring fires in the Tallgrass prairie region (Hartnett et al. 1996). However, less work has been conducted in the Northern Mixed Grass prairie which is characterized by a shorter growing season and lower average precipitation than prairies to the east and south (Higgins et al. 1989). The Northern Mixed Grass prairie is also characterized by higher levels of cool-season grasses that have similar phenology to Kentucky bluegrass and thus compete more directly (Barker and Whitman 1988).

Previous fire research has investigated the season of fire (e.g., early spring, late spring, summer, and fall) effects on plant community responses, however, plant phenological data or measures of fire intensity are rarely

provided (Engle and Bultsma 1984, Biondini et al. 1989). Thus, annual climatic variability and climatic gradients across the entire Great Plains confound the results when referenced only to the day of the year. Other confounding factors include measures of fire intensity and landscape position which may have important influences on mechanisms providing the desired result.

Plant community composition and dominant species identity are essential considerations when using prescribed fire (Silletti and Knapp 2002, Brudvig et al 2007), however, seed bank dynamics and individual plant response are less often investigated because of the time and difficulty of capturing this information. Interactions between plants within a community take place both above and below ground with multiple components operating within the context of ecosystem processes. Nitrogen dynamics (and other plant nutrients), water relations, light interception and physical limitations due to spatial arrangement are all factors influencing the outcomes of any plant community experiments. These ecosystem and plant community processes provide vital information to develop management plans for use in restoring the diversity and productivity of native prairie ecosystems.

Driscoll et al. (2010) recently identified several key factors in expanding the knowledge base associated with prescribed fire. Specifically, they call for studies that (1) emphasize the mechanistic response of individual species; (2) elucidate the spatial and temporal fluxes in prescribed fire as they relate to ecosystem processes and community dynamics; and (3) identify

the limitations of various experimental approaches. I expand on our current knowledge about the critical areas identified by Driscoll et al. (2010) as they apply to Kentucky bluegrass, and propose experimental approaches to various aspects of the fire ecology of Kentucky bluegrass.

BIOLOGY OF KENTUCKY BLUEGRASS

In order to understand possible mechanisms associated with ecosystem invasion and control by prescribed fire, it is essential to understand the basic biology and ecology of the target species. Kentucky bluegrass is a widely adapted species as evident by its successful introduction throughout the North American continent. The same key factors that make Kentucky bluegrass a good turf grass also account for its success invading native rangeland. Kentucky bluegrass propagates by two primary methods, rhizomes and seeds.

The rhizome biology of Kentucky bluegrass was extensively described by Etter (1951). What follows is an adaptation of pertinent aspects from Etter (1951). The rhizomes of Kentucky bluegrass allow established plants to spread clonally outward, often forming a dense sod over time. Rhizomes of Kentucky bluegrass are primarily produced during the cool-fall period. Overall, the rhizomes are shorter in more arid conditions and reflect the condition of the parent plant. Shorter rhizomes have shorter internodes and fewer nodes overall. Since bud production takes place at the nodes of rhizome, lower bud production in dry falls may ultimately reduce production the following year. The rhizomes begin to lengthen during the same time as inflorescence elongation. The actively growing tips of the rhizomes eventually turn upwards to establish new tillers by early fall. It appears that once a rhizome produces its first leaves, it receives little nutrition from the parent plant, instead depending on its own adventitious roots and

photosynthate to produce new growth. Each tiller typically gives rise to one or two intra-vaginal shoots that serve to maintain current population levels, while extra-vaginal shoots are environmentally regulated and are responsible for the spreading of the clone or increasing the density of the stand.

Adequate water supply during the summer months can cause depletion of rhizome buds by encouraging continued sprouting, and depletion of carbohydrate reserves caused by growth in supra-optimal temperatures. Conversely, late summer burning, close mowing, or excessive grazing can stimulate many short rhizomes. Additions of nutrients (N, P, K) do not increase rhizome sprouting, but may have a significant effect on number of shoots produced. In addition to increasing rhizome density, Kentucky bluegrass can increase stem density by the branching of existing tillers. In pasture and range situations, it is this branching of tillers that ultimately determines the amount of annual production in Kentucky bluegrass. Thus factors that damage the growing point or reduce branching can dramatically influence production levels. The branching of tillers is complex and depends on many factors including temperature, water, nutrition, and physiological development.

Kentucky bluegrass typically flowers in late spring. Since the main shoot dies after flowering, mowing or grazing below the flowering point can result in continued vegetative growth into summer. Floral induction in Kentucky bluegrass requires cool temperatures of fall and winter along with a short photoperiod (Carlson et al. 1995). Kentucky bluegrass has a long

induction period. In fact, increased induction time continues to produce an increase in reproductive tillers and subsequent seed production (Canode and Perkins 1977). Depending on the cultivar, 9-12 weeks can be required for vegetative tillers to make the transition to reproductive status (Moser et al. 1968). As in all grasses, the transition to reproductive status happens inside the primordia at the apex prior to elongating (Canode et al. 1972).

Although rhizomes and other sprouts give rise to clonal expansion and persistence, initial site introduction must take place by seed. Kentucky bluegrass normally produces seeds apomictically (Nielson 1946). Apomixis is an asexual form of reproduction where seed is produced directly from parthenogenesis of the gametophyte cells rather than undergoing meiosis and subsequent fertilization. Apomictic seed production is a facultative process where certain environmental conditions or cultivars can favor sexual reproduction (Grazi et al. 1961, Wieners et al. 2006). There are several consequences of apomictic seed production that may give Kentucky bluegrass a relative advantage in the invasion process. Apomictic seed production can take place with a single individual and still remain heterozygous (Matzk 1991, Mazzucato et al. 1996). Heterogeneity results in high levels of plasticity that allow Kentucky bluegrass to adapt to local conditions.

Seed production can be stimulated with late summer burns or through residue removal (Pumphrey 1965, Chastain et al. 1997). The mechanism for this is assumed to be greater fall re-growth. However, the removal of litter

alters the energy balance of the soil by changing the albedo and loss of the insulating effect of accumulated mulch and current growth. Cooler fall and winter soil temperatures could result in extended induction time. Incomplete vegetation removal results in lowered seed production over time (Johnson et al. 2003). Fire that takes place later in the fall can damage re-growth and consequently lower seed production (Pumphrey 1965). The mechanism or mix of mechanisms by which fire increases flowering in Kentucky bluegrass and other species warrants further investigation. Increased flowering following a fire is a widely documented phenomenon in many grass species (Curtis and Partch 1948, Kucera and Ehrenreich 1962, Ehrenreich and Aikman 1963, Hulbert 1988). Identifying individual controls for rhizome growth and induction could explain this relationship.

Kentucky bluegrass responds to increased litter by altering specific leaf area and leaf shape. In this way, Kentucky bluegrass avoids self-limitation by the dense mat of litter associated with this species or extended rest in other rangeland situations (Facilli and Pickett 1991, Lamb 2008). In fact, in Tallgrass prairie, Kentucky bluegrass was responsible for most of the new shoots found in rested areas (Benson and Hartnett 2006). Leaf plasticity may also serve to benefit Kentucky bluegrass when responding to drought or recovery following drought or grazing.

Although most perennial grasses have limited seed banks, Kentucky bluegrass can be an exception (Tracy and Sanderson 2004, Travnicek et al. 2005). Along with other factors that contribute to the existence of a seed

bank, Kentucky bluegrass seed remains viable for longer periods of time than native grasses (Garrison and Stier 2010). After 22 months, Kentucky bluegrass seed was 12-24% viable compared with 0-1% for natives *Andropogon gerardii*, *Panicum virgatum*, and *Elymus virginicus*. The existence of a large seed bank has serious long-term consequences when attempting to restore plant diversity to a compromised site. In fact, research has shown that this limitation may result in sites that are prone to re-invasion once exotic invaders are controlled (Carson and Peterson 1990, Travnicek et al 2005).

When harvested at full maturity, Kentucky bluegrass seed has little initial dormancy, however, when harvested with a high moisture content the seeds express variable levels of dormancy (Bangalore et al. 1978). Complete darkness or continual light appears to suppress germination in Kentucky bluegrass. Likewise, some Kentucky bluegrass cultivars needs diurnal temperature fluctuations to induce germination (Aamlid and Arntsen 1998). The ideal seeding depth was identified to be 1cm in northern latitudes. The base temperature for Kentucky bluegrass germination is 2.6° C and requires a mean thermal time of 97-134 growing degree days (Larsen and Bibby 2005). The time from 25% to 75% cumulative germination is 30-40 growing degree days (Larsen and Bibby 2005).

By harvesting the seed of Kentucky bluegrass from wild populations with culms intact, germination percentages can remain high even when harvested prior to optimum maturity (Canode et al. 1970). Dormancy can be

broken by storage at 5° C for a minimum of 14 days. Kentucky bluegrass germinates well on moist blotter paper in a germination chamber set to 16h light at 25° C and 8h dark at 15° C. A 0.2% KNO₃ solution on the blotter paper may enhance germination (Larsen and Andreasen 2004a). Cumulative germination should be assessed every day for 28 days (Canode et al 1970). Successful germination should be considered radical protrusion of greater than 2mm (Larsen and Andreasen 2004b). Since germination timing is a critical factor in seedling competition and establishment, cumulative germination percentage should be recorded and fitted to a Weibull curve for

analysis: $f(t; \lambda, k) = 1 - \exp\left[-\left(\frac{t}{\lambda}\right)^k\right]$ where t=germination time, and λ and k are

fitted parameters.

Another factor that contributes to Kentucky bluegrass survival in rangelands is its high tolerance of repeated defoliations. Typically, Kentucky bluegrass increases in response to grazing pressure in both the Tallgrass prairie (Ehrenreich and Aikman 1963, Towne and Owensby 1984) and Mixed-grass prairie (Waddington et al. 1999, Volesky et al. 2004, Biondini et al. 1998). Kentucky bluegrass achieves its grazing tolerance by maintaining a low growing point (shoot apical meristems) throughout its life cycle and decreasing leaf length after grazing. Recent evidence suggests that Kentucky bluegrass is capable of enhancing its own nitrogen supply when grazed or mowed (Hamilton and Frank 2001). The defoliation causes a flush of carbon rich root exudates that stimulate the local microbial biomass.

Increased microbial biomass results in a positive feedback that results in higher nitrogen availability. Likewise, Kentucky bluegrass litter has higher net mineralization rates for nitrogen than warm-season species (Wedin and Tilman 1990) due to lower litter C:N ratio than warm-season grasses. Increased nitrogen availability may favor Kentucky bluegrass over other perennial grasses (Waddington et al. 1999), particularly warm-season species (Tilman and Wedin 1991) because of its higher growth rate (Levang-Brilz and Biondini 2002). Kentucky bluegrass appears to have a higher nitrogen R^* than other native species (Tilman and Wedin 1991), R^* being the level to which a species is capable of reducing the nutrient content in the available soil pool. The R^* of grass species is inversely correlated to root mass, that is plants with high R^* allocate more biomass to photosynthetic or reproductive tissue. Cool-season grasses in general devoted a higher percentage of photosynthate to reproductive tissues rather than roots. This means that other native grasses will compete better against Kentucky bluegrass in a nitrogen limited environment. However, when the N soil pool is large, plants with higher growth rates and allocation to photosynthetic tissue (like Kentucky bluegrass) should be able to out-compete plants with lower photosynthetic tissue and higher roots (Levang-Brilz and Biondini 2002). Nitrogen relations are an important ecosystem component that is potentially altered spatially and temporally by prescribed fire.

In addition to being tolerant to grazing pressure, it appears that Kentucky bluegrass does well under extended rest (Towne and Ownesby

1984, Bowles et al. 2003, Murphy and Grant 2005). Accumulated litter underneath Kentucky bluegrass can reduce survival of other species (Foster and Gross 1998). Ex situ leachate from Kentucky bluegrass litter has reduced germination in several native species (Bosy and Reader 1995). However, this may not be a species specific response; litter in general has been shown to reduce species diversity (Carson and Peterson 1990). In addition to these direct influences, litter can affect soil-water relations, soil temperatures, and light interception (Weaver and Rowland 1952). Because of these relationships, accumulated mulch can result in decreased yield in Tallgrass and Mixed-grass prairie.

Long-term studies suggest that Kentucky bluegrass can reduce diversity, and that this influence does not decrease over time (Miles and Knops 2009). Diversity has been shown to increase yield stability in planted pastures and restored prairies (Tracy and Sanderson 2004; Biondini 2007). Other important factors influencing yield in rangelands include photosynthetic pathway, available moisture, nitrogen supply and dominant species identity (Miles and Knops 2009). Growth of warm season grasses during mid-summer when Kentucky bluegrass is dormant due to heat and water stress can result in increased primary productivity and forage quality (Towne and Owensby 1984).

Rangelands dominated by Rough fescue (*Festuca campestris*), a cool-season grass yielded more herbage than those areas co-dominated by Kentucky bluegrass in the same region of the extreme northwestern portion of

the Great Plains (Willms et al. 1996). Likewise, in study in the Aspen Parkland in the northwestern Great Plains yields of Kentucky bluegrass (4040-4490 kg/ha) were lower than other forage species except Red fescue (*Festuca rubra*) (Baron et al. 2004). In eastern Canada, Kentucky bluegrass yielded more than 8 t/ha (Durr et al. 2005), however the quality of Kentucky bluegrass drops off rapidly upon maturation. Consequently, harvest frequency can alter the forage quality of Kentucky bluegrass. Durr et al. (2005) compared 4 vs. 5 harvests a year. Results showed that a 4 harvest frequency resulted in: (1) lower N concentration (24.8 vs. 30.6 g/kg); and (2) higher neutral detergent fiber (NDF- 565 vs. 543 g/kg) and acid detergent fiber (ADF- 290 vs. 276 g/kg) than a 5 times a year harvest frequency. Kentucky bluegrass flowers and matures earlier (Ehrenreich and Aikman 1963, Mason and Lachance 1983) than other cool-season grasses. For example, Holman et al. (2007a) showed that in a fertilized system not limited by moisture, Kentucky bluegrass had a NDF of 435 g/kg, ADF of 196 g/kg and crude protein (CP) of 165 g/kg at the boot stage, and a NDF of 637 g/kg and ADF of 332 g/kg and CP dropping to 70 g/kg at seed ripe.

Since seasonal moisture is often limiting in Mixed-grass prairies, biotic factors that alter ecosystem processes can have an influence on forage production. Infiltration below Kentucky bluegrass has been shown to be lower than below other native grasses (Weaver and Rowland 1952). Mulch has been shown to increase infiltration by lowering rain drop energy and providing good soil structure and moisture, as dry soils without mulch can

have hydrophobic properties. During small rain events, however, the increase in infiltration can be balanced and even negated by moisture lost due to interception. Mulch is capable of intercepting 50-75% of the total rainfall. Intercepted precipitation can remain in the litter and evaporate without reaching the soil. Up to 30% of the annual precipitation can be lost in this manner. In addition to these effects, litter can trap snow during the dormant season which can provide early season moisture. Although Weaver and Rowland (1952) provided a good list of the effects of mulch, the mechanism for these changes remains somewhat confounded by these processes and other long-term ecosystem changes such as soil organic matter.

Many fire studies document consistent decreases in Kentucky bluegrass regardless of season of fire and dominant species identity (Higgins et al. 1989). Moisture relations and stimulation of warm season species have both been proposed as mechanisms for this. Another likely mechanism is the high amount of root tissue and rhizomes that Kentucky bluegrass has near the surface which would make it more prone to injury than other species (Weaver 1926). Tiller density and the ground hugging nature of Kentucky bluegrass litter could also locally increase fire intensity in areas associated with this dense sod (Durr et al. 2005).

FIRE ECOLOGY

Overview

The effects fire can have on a landscape are highly variable and complex. The use of prescribed fire to improve rangelands is widely acknowledged, however, ecologists still have much to learn about such management. Because fire influences so many factors simultaneously it is difficult to disentangle the various effects from each other. In addition to the heat effects of fire on biotic processes, the chemical signals caused by smoke and ash can have an impact (Wright and Bailey 1982). In a study of 37 native species, 30% were stimulated to germinate with ex situ smoke added to the soil (Jefferson 2008). Many of the changes associated with fire are temporal in nature and typically only last a season or two (Archibold et al. 2003, Redmann et al. 1993). Despite the wide array of variables impacted by periodic fire, the plants of the Great Plains are well adapted to this disturbance and tend to respond rapidly with renewed vigor (Engle and Bultsma 1984).

One way to categorize the effects of fire is to consider abiotic and biotic processes. The abiotic processes are independent of plant responses and include soil temperature, soil water availability, and soil nitrogen fluxes. The biotic processes include the plant reaction to the abiotic processes as well as physical injury to plants and any alteration in competitive ability in the post-fire environment.

Abiotic Environment

Fire influences soil temperatures directly during the fire and indirectly by influencing the post-fire environment. Direct impacts cause soil temperatures to be slightly elevated due to conduction and radiation of heat from the fire itself. The soil environment is not exposed to the extreme levels found above ground because of the insulating effects of soil and convective loss of heat (Wright and Bailey 1982). Despite the insulating effects of soil, temperatures can reach lethal levels during extremely intense fires (Archibold et al. 1998). Generally speaking, fire intensity and heat dosages are given as temperature and duration (Engle et al. 1989).

Several sources cite Rosenberg et al. (1971) in stating that the temperature required for instantaneous death in plant cells is 60° C based on protein denaturation of essential enzymes and other cell components, however, Rough fescue (*Festuca campestris*) survived up to 16 seconds at this temperature (Bogen et al. 2002). Heat induced damage to Kentucky bluegrass has been found as low as 43° C and lethality was achieved at 49° C for 30 minutes (Wehner and Watschke 1981). Busso et al. (1993) identified dehydration as a lethal factor for the rhizomes of *Stipa tenuis* in Argentina. Dehydration of live tissue provides a second possible mechanistic explanation for rhizome death associated with prescribed fire. Clearly this demonstrates the need to report heat dosage or fire intensity as a time and temperature related phenomenon. Research conducted on other grass species has found this relationship (the thermal-death-time curve) to be an

exponential function (Wright 1970). The thermal-death-time curve is species specific and has been shown to change over the course of the growing season. Moisture percentage in the plant tissues appears to be a key factor, but other factors including solute and protein content have not been ruled out. Another possible explanation for plant injury is direct damage to actively growing meristem tissues that are elevated above the soil surface during the growing season. This mechanism can only be identified on a species by species level and requires recognition of the variable effects of fire on different plant stages (Stueter 1987, Benning and Bragg 1993, Pfeiffer and Stueter 1994). Other research has reported fire intensity as an energy flux (kW/m) which is estimated by fire behavior and flame length (Howe 1995). This measurement is limited by the ability of the observers to properly and consistently estimate the flame length and the variability explained by this relationship. Another way of estimating energy flux is given by Bryam's fire-line intensity, where the energy is calculated by using the heat of combustion of the fuel, the weight of the fuel, and the rate of spread (Bidwell and Engle 1992). This estimation is limited by the variability in rate of spread and fuel load. There are advantages to recording fire intensity as an energy flux rather than a time-temperature phenomenon. Using an energy flux allows the process to be modeled and various temperature changes can be predicted based on initial site conditions which can aid transfer of laboratory findings to field responses.

In most grassland fires, the fire intensity is not sufficient to raise soil temperatures to critical levels for any significant time period (Choczynska and Johnson 2009). Thermal conductivity of soil is a function of bulk density, texture (quartz fraction) and soil moisture content (Lu et al. 2007). Thus the measurements associated with fire research must take into consideration the spatial variability associated with these soil properties. The fire intensity of several different plant communities was measured in the Northern Great Plains. Soil temperatures in Rough fescue, Smooth brome (*Bromus inermis*), and Needle-and-thread (*Stipa comata*) communities remained below average ambient air temperatures at 5cm depth in spring fires (Archibold et al.1998). However, in communities dominated by Western snowberry (*Symphiocarpus occidentalis*), lethal temperatures were approached and occasionally exceeded at the 5cm depth during the same study. The greater fire intensity associated with higher fuel loads and the woody nature of the fuel would account for this disparity. Increasing fuel size from grass to wood increases the duration of the fire. Wood also typically exhibits a higher heat of combustion associated with higher lignin content. In another study conducted in Fescue prairie, soil temperatures at 1cm depth were not elevated significantly during spring or fall fires, however, during summer fires the mean maximum temperature was 44° degrees C (Archibold et al. 2003). Fuel load, ambient air temperature, wind and fuel moisture are all ingredients influencing the fire intensity associated with these fires.

In spring fires in Tallgrass prairie with an average fuel load of 357 g/m^2 and fuel moisture of 31%, the mean fire line intensity was 543 kW/m (Bidwell and Engle 1992). These fires produced a fire intensity measured as a time-temperature function of 10,711 degree-seconds (Celsius) above ambient temperature at the soil surface. In this study, fire intensity showed a strong relationship to growing season standing crop. Another study indicated dormant season fires with almost entirely dead litter were more intense than growing season fires with large amounts of green material (626 kW/m vs. 157 kW/m) (Howe 1995). Late-summer fires in Oklahoma Tallgrass prairie produced 10,400 degree-seconds (Celsius) in low fuel fires (443 g/m^2) and 43,600 degree-seconds in the high fuel fires (1032 g/m^2) at the soil surface. Fire intensities at 30cm above the soil surface were approximately 40% lower (Ewing and Engle 1988).

Recent research has shown fire intensity to be a linear function of fuel load in laboratory settings and that this single factor explains 98% of the variability in the fire (Vermeire and Rinella 2010). However, it must be noted that the fuel load was dried to standardize the moisture content and a fan was used to manipulate air supply. Fuel moisture is normally a function of air temperature and fuel size with daily and seasonal fluctuations occurring. The fine fuels associated with grass fires rapidly dry after wetting and return to equilibrium with respect to the ambient temperature. Most fire research focuses on head-fires, but essential differences occur in back burned areas (Bidwell et al. 1990) because back burned areas spread more slowly and

result in higher fire intensities. Higher fire intensities are associated with less cover which results in decreased competition and increased seedling survival of forbs.

In addition to the direct effect fire has on short term soil temperatures, soil temperatures are indirectly influenced by fire as well. Surface albedo drops from 0.18-0.20 to 0.03-0.10 post-fire, which dramatically influences the solar energy balance (Archibold et al. 2003, Knapp 1984). This effect can remain for up to 3 months depending on weather and vegetation recovery (Archibold et al. 2003). Along with the change in albedo, the soil surface is no longer shaded by litter and standing growth. This too changes the energy flux associated with the soil surface. In spring and summer conditions changes in albedo associated with charring and exposed soil serve to increase soil temperatures. Increases of up to 9° C in leaf temperatures have been found in spring burns as compared to non-burned controls (Knapp 1984). Soil temperatures following spring burns at the surface were 4° C warmer than non-burned sites, and 2° C warmer at 10cm depth (Hulbert 1988). This fact along may be a key factor in stimulating warm season grasses post fire. Peet et al. (1975) found that the soil surface averaged 10.7° C higher in burned areas into July, and that diurnal fluctuations in temperature were higher as well (17.4° vs. 5.3° C). During winter conditions, however, soil temperatures may be colder than unburned sites. This is because litter and standing crop insulates the soil (Archibold et al. 2003).

Standing vegetation and mulch trap snow from blowing and drifting, which increases the insulation being provided, but serves a much more important function of increasing moisture supply. Throughout much of the Great Plains, productivity is moisture limited (Knapp et al. 2001). In a study of range productivity across the Great Plains, it was found that yield increased linearly with precipitation up to 500mm (Sims and Singh 1978). Above 500mm several other factors appear to be limiting. However, because of seasonal deficits or periodic droughts the timing of precipitation can have important impacts on productivity. Snowmelt can serve as a significant source of soil moisture in the early spring season (Redmann 1978). Other studies have shown that carry-over moisture from a wet fall can be important in the Northern Mixed-grass prairie (Rogler and Hass 1947). Either soil moisture at depth or bud bank response could explain these findings.

Besides being important for providing snow capture, the shading effects of litter can reduce evaporation from the soil surface (Archibold et al. 2003). Weaver and Rowland (1952) reported that less than 5% of the ambient light reached the soil surface with as little as 2.5 cm of mulch. They also found that 50-76% of precipitation was intercepted by the mulch and that 1/3 of this was rapidly lost to evaporation rather than being retained or moving to the soil surface. These complex and opposing interactions significantly alter the soil water flux over the course of the growing season which has the potential to alter plant competition dynamics. In addition to these abiotic factors, soil water may also be driven down later in the growing season by the increased

vigor of the grasses compared to non-burned controls. However, late spring fires can result in increased water availability early in the growing season due to defoliation and loss of production from the cool-season grass component (Knapp 1984).

Biotic Changes Associated with Fire

Complex interplay between seasonal and yearly precipitation patterns, alteration of hydrologic factors such as infiltration rate, and modifications to the evaporation-transpiration rates all can influence the actual response of a plant community to the post-fire environment. In general, plant communities in the Great Plains are adapted to periodic fire and the native grasses tend to recover rapidly (Tester 1996).

However, in the western Great Plains, production may drop off significantly following a fire, for as many as three growing seasons (Archibold et al. 2003, Redmann et al. 1993). The gradual build up of litter restores soil moisture to unburned levels over time (Redmann et al. 1993). This difference suggests that certain portions of the Great Plains are much more sensitive to moisture stress than others. A comprehensive review of forage production indicates that yield is limited by moisture when the yearly average is below 500mm, which includes the Mixed-grass prairie, short-grass steppe and most of the Northern Great Plains (Sims and Singh 1978). Obviously lowland and overland sites would not be included in this area as they receive water from adjacent areas (Redmann 1975). Likewise, any site with an aquic soil moisture regime is less likely to be affected by moisture limitations. Soils can

also directly affect moisture relations by changing the available water content based on soil texture and associated soil organic matter. Better quantification of soil moisture status and influences is clearly needed as these not only contribute the soil-plant relations but also have the ability to alter nitrogen cycling and other ecosystem processes.

Recent work done in the Tallgrass prairie region of the Great Plains has shown that fire stimulates production of additional axillary buds in grasses (Dalglish and Harnett 2009). This change along with short term nitrogen flushes may be responsible for the increased production seen in the eastern Great Plains following a fire where precipitation is less limiting. Other factors that may contribute to an increase in production following fire includes increased length of growing season by altering soil temperature and increased light interception early in the growing season caused by lack of litter. Spring burning in Tallgrass prairie resulted in a 23.3% increase in season long ET (Bremer and Ham 1999). Likewise a season long increase in photosynthetic available radiation was 13.8% more than non-burned control areas, with most of this increase taking place early in the growing season (Knapp 1984).

The axillary bud reserve has been suggested as a primary driver behind primary production in the Great Plains (Benson et al. 2004). This is consistent with a general decline in bud bank density moving westward across a precipitation gradient from the mesic Tallgrass prairie in the east to the arid short-grass prairie in the west. What remains a mystery though is

how fire stimulates production of additional axillary buds when fire serves to lower soil water. While large scale investigations have characterized plant community levels of bud bank (Dalglish and Hartnett 2006), species-specific data are not available with respect to changes related to fire. Turf grass research has identified bud bank changes as a primary mechanism of fall fire stimulation of seed production in Kentucky bluegrass (Chastain et al 1997). Other residue removal mechanisms such as grazing or haying have reduced seed yield compared to fall fire, however, grazing and haying have greater seed yield compared to no removal of residual litter (Holman et al 2007b).

Fires are known to impact nutrient cycling, however, ash micronutrient content does not appear to be the primary driver of this. Studies have shown that ash added to the soil does not significantly change production or nutrient status of the plant, which indicates that biocycling remains an important factor in the post-fire environment (Old 1969, Byre et al. 2002). Fires are also known to alter nitrogen cycling and have been implicated in the control of other plant nutrients such as P, K, Ca and Mg.

Nitrogen mineralization is lower in burned areas compared to non-burned sites. In Tallgrass prairie, N mineralization is five times higher on uplands than lowlands (Turner et al. 1997). Because N mineralization can take place as a multi-step process, this results in short-term increases in available ammonium followed by a rise in available nitrate (Wang et al. 2001). Research has shown that altering species composition can rapidly alter (2-3 years) N mineralization by altering the belowground biomass, the

belowground lignin content, and the N content in the belowground tissues (Wedin and Tilman 1990). The mechanism explaining rapid changes in N mineralization is based on a model where 2-3% of the total N is rapidly cycled in a labile pool that is based on individual species metrics, and that the rest of the nitrogen pool is largely recalcitrant and is based on historic site conditions (Wedin and Pastor 1993). The magnitude of change between species after three years results in a 10 fold difference in mineralization.

Fire results in a large loss of above ground N due to volatilization which begins at 200° C (White et al. 1973). These temperatures are easily reached when fuel loads exceed 3370 kg/ha (Stinson and Wright 1969). Over 90% of the above-ground N is lost during fires, and the magnitude of this loss is proportional to the above-ground biomass (Brye et al. 2002). During spring burns in Tallgrass prairie 1.8gN/m² were lost during the fire, however, in grazed sites that were also burned, the N losses were half this (0.9gN/m²) (Hobbs et al 1991). This indicates that by creating burned and grazed patches, nitrogen can be conserved. The loss of nitrogen is compensated by atmospheric deposition in 3 to 5 years. More frequent burning results in higher C:N ratios, which will ultimately result in lower soil N because of increased immobilization (Ojima et al. 1994). Long-term annual burning results in increased N use efficiency (NUE). The mechanism for this is increased root mass and deeper roots. Under annual burning the fine roots are increased by 47% over non-burned controls (Kitchen et al. 2009).

In dormant season early spring burns, immediate N availability did not change, but was enhanced during summer (June-July), and then reduced by net immobilization later in the season (Augustine et al. 2010). In Short-grass steppe the flush of N resulted in enhanced in-vitro digestibility of Blue grama (*Bouteloua gracilis*) by 11% due to higher CP content.

In Tallgrass prairie, the response of N appears to follow the transient maxima hypothesis where nitrogen and light availability are limiting in a non-equilibrium dynamic (Blair 1997). This phenomenon is explained by gradual build up of available soil nitrogen under non-burned conditions, where light is limiting early production. Following a burn where available light is increased (through removal of litter), the plants take advantage of this nitrogen and gradually return to a light limited system.

Research in other systems (coastal sand prairie) has shown that burning results in a short-term enhancement of available N, but that it is rapidly lost to leaching (Dudley and Lajtha 1993). This may be a function of the coarse soil texture and the increased precipitation that results in more leaching. Changes in the N availability appear to be related to seasonal microbial biomass in Argentina pampas (Picone et al 2003). Increased microbial biomass results in increased N mineralization compared to non-burned sites. The higher soil temperatures following a fire may stimulate existing microbes to increase mineralization rates. Ammonifying bacteria can survive soil temperatures of up to 100° C and nitrifying bacteria can only survive 53-58° C (Raison 1979). The microbial biomass is generally lower at

the beginning of the growing season in this system, which may reflect diminished C supply or seasonal water deficits. Fluxes in microbial biomass could explain the flushes of N found under burned conditions in other prairie ecosystems.

In addition to altering N mineralization by changing species composition, burning can also result in greater ecosystem level N by stimulating legume production (Towne and Kemp 2003). Forb production is shown to increase with early spring burning (Towne and Owensby 1984, Biondini et al 1989). Thus, fire has the potential to alter plant communities over time through a variety of mechanisms. This change in plant communities has been well documented in the Tall-grass prairie (Towne and Owensby 1984), and limited documentation exists elsewhere in the Great Plains (Engle and Bultsma 1984, Higgins et al. 1989).

Species and Community Responses to Fire

While limited work has been done to identify mechanisms explaining plant community dynamics in the post-fire environment, much work has been done identifying specific species response and overall plant community response to prescribed fire (Wright and Bailey 1982, Hartnett et al. 1996). Complicating the interpretation of these findings are the different plant communities and dominant species involved, as well as inadequate information regarding the timing and intensity of the fire. Differential response of individual species has been documented when changing the date of the fire by as little as two weeks (Benning and Bragg 1993). Due to yearly and

regional differences associated with plant community growth patterns, recording only the calendar date is inadequate. Plant phenology is likely a key factor in the differential responses to prescribed fire. Identifying the plant stage of dominants and the target species would aid in transferring fire related research across the Great Plains. This will also ease the transfer of knowledge obtained in laboratory settings to the field. Understanding the documented responses of dominant and subdominant species in a plant community context will aid land managers in interpreting and planning the use of prescribed fire.

Long-term ecological research conducted on Tallgrass prairie has consistently shown an increase of big bluestem during spring, fall and dormant season burns (Towne and Ownesby 1984, Towne and Kemp 2003). Likewise, the stimulation of forb production and diversity has been widely documented throughout the Great Plains regardless of the season of fire. A study in Nebraska Tallgrass prairie noted no response of big bluestem to early spring fires (before May 12) (Benning and Bragg 1993), while later spring fires showed a clear increase in big bluestem. In another study where big bluestem was dominant, no response to spring fire was noted (Abrams and Hulbert 1987). The stimulation of big bluestem in spring fires is often cited as a primary driver behind increases in yield seen in Tallgrass prairie. This suggests that a shift in species composition is responsible for the increased production. Hulbert (1988) compared clipped, burned, and warmed soil treatments in Tallgrass prairie. The warmed soil resulted in a 34%

increase in yield compared to non-burned controls, but the burned areas resulted in a 151% increase in yield. Addition of ammonium nitrate increased yield 41%, while just clipping the dead mulch resulted in over a 50% increase in flowering. This would indicate that burns combine the effects of increased light interception, increased soil temperatures, and temporary nitrogen fluxes. In analysis of long-term changes, big bluestem was correlated with decreasing cover, decreasing summer maximum temperature, and diversity (Silletti and Knapp 2002). In summer fires, big bluestem can have a variety of responses. Late summer fires in Oklahoma showed no change in big bluestem to a low fuel fire (440g/m^2) in late summer (August) compared to controls, but a significant decrease in a high fuel fire (1030g/m^2) compared to controls (Ewing and Engle 1988).

While other warm season co-dominants are often assumed to follow a similar pattern to big bluestem, recent research has shown this to not be the case. Indian grass (*Sorghastrum nutans*) increased only in response to spring (April) fires in Kansas compared to winter (February) or late fall (November) (Towne and Kemp 2003). Other studies show similar results with Indian grass increasing following spring fires (Towne and Owensby 1984; Abrams and Hulbert 1987). Regression analysis suggests that inter-annual variability in Indian grass is best explained by precipitation patterns (Silletti and Knapp 2002). Interestingly, Switchgrass (*Panicum virgatum*) biomass increased as a result of fire in any season on lowland sites, but did not respond to fires in upland positions in Tallgrass prairie (Towne and Kemp

2003). In a similar study, Switchgrass cover was not different from in spring burned sites vs. non-burned sites (Abrams and Hulbert 1987).

Studies looking at the warm season mid-grass little bluestem (*Schizachyrium scoparium*) have shown confounding results. In Tallgrass prairie, little bluestem decreased during winter or late spring fires, but was increased by mid spring and early spring fires (Towne and Ownesby 1984). Late April fires stimulated little bluestem production in other Tallgrass studies (Abrams and Hulbert 1987). In an infertile Mixed-grass prairie, a spring fire resulted in no net change in little bluestem (Knops 2006). Similarly, on an infertile sand prairie in Wisconsin, little bluestem failed to respond to fire on dry sites, but cover increased on mesic sites after spring fire (April 16) (Zedler and Loucks 1969).

In prairie of the Loess Hills in Iowa, the frequency of side-oats grama (*Bouteloua curtipendula*) in burned plots increased compared to grazed sites or burned and grazed sites (Brudvig et al. 2007). In planted monocultures, side-oats grama production was decreased by summer fire compared to controls and winter fire. In this same study, buffalograss (*Buchloe dactyloides*) showed no significant response to the fires (Castellano and Ansley 2007). In the Flint Hills of Kansas, buffalograss decreased in late spring fires, while Blue grama (*Bouteloua gracilis*) increased in early and mid spring burns (Anderson et al. 1970). Blue grama grass increased cover in a Northern Mixed-grass prairie (Manitoba) after spring burns (late May and early June) (Shay et al. 2001).

There is less documentation for cool-season grasses, and they are often lumped together by life cycle traits. In a seeding study, nearly pure stands of Reed Canary grass (*Phalaris arundinacea*) were reduced in May fires in Wisconsin and replaced with big bluestem and Switch grass (Howe 2000). However, August fires resulted in a mix of cool-season/warm-season species that was not different than non-burned controls. In a prairie remnant, midsummer (July 15) fire increased Reed Canary grass (Howe 1995).

Smooth brome (*Bromus inermis*) is another exotic cool season grass that is frequently invading native prairies and is often found in association with Kentucky bluegrass. Smooth brome response to fire is often neutral (Grilz and Romo 1994). In Illinois Tallgrass prairie, spring burns (April 27) reduced Smooth brome (Old 1969).

In eastern Montana, western wheatgrass (*Elymus smithii*) was unaffected by spring burns (White and Currie 1983). However, in similar northern Mixed-prairie, western wheatgrass decreased with fall burns (Redmann 1978). In Northern Mixed-prairie, Green needle grass (*Stipa viridula*) decreased significantly after spring and summer fire (Engle and Bultsma 1984). In the Northern Mixed prairie water stress was identified as a mechanism leading to lower yields following fire in Junegrass (*Koeleria macrantha*) (Redmann 1978).

All this information serves to highlight the complexity of plant community dynamics which serves to point out the need to better identify the mechanisms behind the plant responses both on individual species and within

a community context. In a recent review of investigations of the season of fire, Engle and Bidwell (2001) considered any guidelines as misleading. The variability associated with environmental factors, plant community dynamics and long-term effects of fire frequency combine to create an unpredictable species response to season of fire at this time. Future research may do this by approaching the questions to be answered in a mechanistic fashion.

Kentucky Bluegrass Response to Fire

In general, prescribed fire in any season decreases the amount of Kentucky bluegrass in favor of warm season grasses in the Tallgrass prairie region (Anderson et al. 1970, Towne and Owensby 1984, Towne and Kemp 2003). At this time, it is unclear whether fire damages Kentucky bluegrass, or whether the timing of the fire stimulates the warm-season components to be more competitive. However, at least one experimental treatment showed declines in Kentucky bluegrass without a concurrent increase of warm season components (Knops 2006).

An early investigation of spring burning in the Tallgrass prairie revealed that Kentucky bluegrass was rapidly expanding in the non-burned areas and the burned areas where mowing and raking were used to simulate grazing (Hensel 1923). Annual spring fires decreased Kentucky bluegrass from about 20% cover in unburned sites cover to zero in Tallgrass prairie (Abrams and Hulbert 1987). In Wisconsin old fields, Kentucky bluegrass was reduced by 80% after 6 years of annual burns regardless of season of burn (Curtis and Partch 1948). In Iowa Tallgrass prairie, Kentucky bluegrass was

reduced from 55% frequency-abundance to 18% after one burn, 6% after two burns and 3% after three burns (Ehrenreich and Aikman 1963). Later research in Iowa Tallgrass prairie showed Kentucky bluegrass was reduced by 20% in frequency for the burned treatments compared to grazed treatments (Brudvig et al. 2007). In the Mixed-grass prairie of eastern North Dakota, Kentucky bluegrass frequency was reduced the year of the fire, but rebounded to pre-burn levels after one year (Hadley 1970).

CONCLUSION

Prescribed burning is one of many tools that land managers have to manipulate the ecology of rangeland. The use of other tools such as mowing, grazing, and herbicide use must be carefully considered as well. When planning a prescribed burning regimen, it is important to evaluate the need economic considerations as well as the interaction between other tools being used on the landscape. In particular, the interaction between grazing and fire is an important aspect of future research needs. Economic considerations may outweigh the benefits associated with increased diversity following prescribed burning. Allowing mulch to accumulate enough to carry a fire could be seen as a loss of production. Likewise, in more arid regions prescribed fire depresses forage yields due to moisture stress. These factors limit the potential application of prescribed fire across the landscape.

The state of prairie fire research is rapidly developing, but still needs periodic assessments to ensure progress continues to be made. A clear research agenda will identify current and future needs. In particular, the need to provide sound scientific advice to working land managers should figure into all rangeland research. In order to best achieve this result, the following items need to be addressed in future research:

- Providing clear and consistent measurements of fire intensity
- Identifying the mechanism behind individual plant responses (from seeds to adult plants)

- Linking fire intensity and plant phenology to variable plant responses
- Using individual species biology to predict plant community responses
- Evaluating the effects of using multiple land management techniques on results

PROPOSED RESEARCH AGENDA

Driscoll et al. 2010 indicated a need to carefully plan out an agenda to investigate specific species response to fire and the mechanisms underlying these responses. Plant community response to prescribed fire is highly sensitive to timing, particularly when determining impacts to desirable native components (Engle and Bultsma 1984). With higher proportions of cool-season grasses in the plant communities of the Northern Great Plains, it is critical to identify the appropriate timing of fire treatments to achieve management objectives (Pylypec and Romo 2003). Fire intensity effects have been noted in woodland and savanna plant communities, but are generally not recorded in grassland environments. What follows are two proposed experiments designed to address how fires affects: (1) the seed bank dynamics; and (2) the rhizome and clonal response of Kentucky bluegrass.

Proposed Seed Bank Dynamics

Recent fire intensity research demonstrates that even modest fire intensity (corresponding to a fuel load of 200 g/m^2) is enough to reduce germination to less than 1% on surface deposited seeds of four weed species (Vermeire and Rinella 2010). However, the effects of heat and fire on buried seed banks are poorly documented. Even though clonal reproduction accounts for 99% or more of the ramets produced in a typical prairie, seed banks are important storehouses for site diversity (Benson and Hartnett 2006). For exotic invaders that share a common photosynthetic pathway and

large seed banks such as Kentucky bluegrass, Canadian thistle, and Leafy Spurge (Travnicek et al. 2005, Larson and Larson 2010), it is essential to understand the seed bank dynamics of these species. Most of the experimental procedures outlined here could apply to many exotic invaders besides Kentucky bluegrass. In areas that Kentucky bluegrass has invaded, restoration may involve artificial enhancement of the available species pool via seeding and continued maintenance until restoration goals are achieved. Ex situ germination cues should be measured for a much wider variety of native plants to determine which species are likely to respond by germinating in a post-fire environment

In order to study the seed response, specific measurements should be undertaken. Specifically, time-temperature curves should be developed in a laboratory setting to determine the lethal temperature for Kentucky bluegrass seeds. In addition to determining the lethal temperature, germination cues mimicking the post-fire environment should be investigated. Smoke, ash, and nutrient manipulations (especially nitrogen) all have the potential to alter germination (and survival) rates. Finally, the effect of different fire intensities should be investigated on different soil depth and moisture combinations. The fire intensity should be measured by a thermocouple both at the soil surface and at depth. Fire intensity can be manipulated over a wide range by altering fuel loads. Fuel loads should include the range found in various natural settings where Kentucky bluegrass has invaded. At the lower end of fuel ranges, establishing and maintaining the fire becomes difficult. While

much of the Great Plains would be included in the lower end of the range, Kentucky bluegrass is also a known invader in old fields and other areas associated with encroachment of woody species such as Western snowberry, Sumac (*Rhus spp.*) and Aspen (*Populus tremuloides*). A maximum fuel load of 1500 g/m² would encompass the range of fuel loads found on Tallgrass prairie with several years of accumulated mulch and within the range commonly found in areas invaded by Western Snowberry and Sumac (Weaver and Rowland 1952).

Because previous research has shown that surface deposited seeds rapidly lose viability during low intensity fires (Vermeire and Rinella 2010), I predict low cumulative germination percentages for all surface deposited seeds. Because soil has a moderating effect on temperature, I predict that buried seeds will have higher germination percentage than unburied seeds, and that the cumulative germination rate will decrease with increasing fire intensity. Even though a heat-transfer model has shown limited sensitivity to soil moisture (Choczynska and Johnson 2009), the specific heat of the soil will be altered with increased moisture. Therefore, I predict increasing soil moisture during the fire will have a neutral to positive response to fire on cumulative germination percentage. In addition to recording fire intensity as a temperature/time phenomenon, wind speed, air temperature, and relative humidity should be monitored.

Proposed Experiment

An example of an experiment to address seed germination problem would be factorial design consisting of 2 seeding depths at 2 soil moisture levels and 6 fuel loads (Table 1). The controls would be non-burned samples at the 2 seeding depths and 2 soil moisture combinations. The fuel loads would be varied between 140 g/m² to 1500 g/m² for the reasons explained in the overview section. Each replicated fire would have a total of 4 experimental units (germination trays) one from each of the seed depth/soil moisture treatments (surface dry, 1cm dry, surface wet and 1cm wet) (Larsen and Bibby 2005). A total of 40 fires would take place within the fire cage design shown in Figure 1a-b.

Table 1: Example of Experimental Treatments

Fuel Load g/m ²	Oven Dry		Field Capacity	
	Surface	1cm	Surface	1cm
0	8 reps*	8 reps	8 reps	8 reps
140	8 reps	8 reps	8 reps	8 reps
275	8 reps	8 reps	8 reps	8 reps
550	8 reps	8 reps	8 reps	8 reps
1000	8 reps	8 reps	8 reps	8 reps
1500	8 reps	8 reps	8 reps	8 reps

*Each replication will contain 100 viable seeds.

In preparation for the experiment, soil should be sieved to pass through 2 mm, oven dried at 60° C, and homogenized. Presence of weed seeds in the soil should be assessed in a germination chamber. If necessary, the soil should be steam-sterilized. Soil texture should be determined using the hydrometer method. Based on soil texture, a known volume of water

should be added to simulate field capacity. Bulk density should be controlled using a standard packing procedure. Soil packing involves weighing a soil sample and fitting the sample to a known volume with appropriate tamping, if necessary.

a.



b.

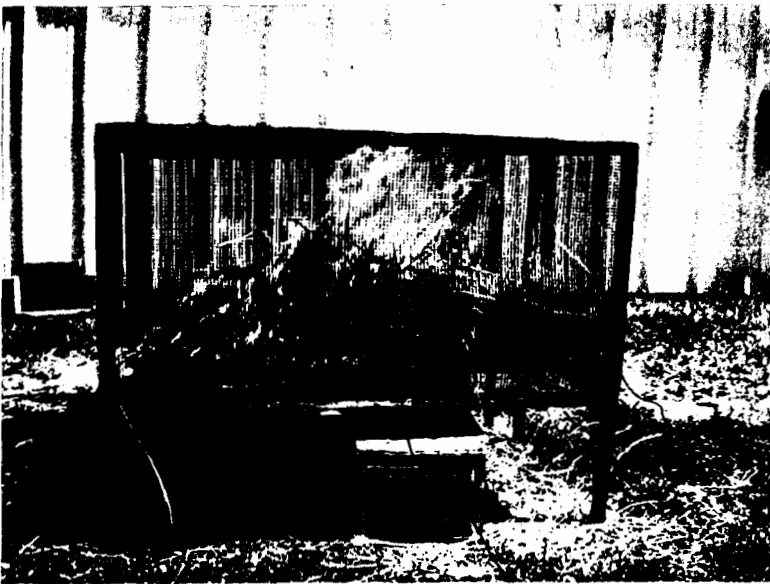


Figure 1a: Photo of Burn Cage & 1b: Photo of Fire Cage in Operation (photo credit Kim Haile).

The loading of trays should begin with the dry soil treatments followed by the wet soil treatments. Once the loading of dry trays is complete, the soil should be wetted by adding an appropriate volume of water to a known amount of dry soil and mixed before loading of trays. By using dry soil and soil approximately at field capacity, one should be able to capture the possible extremes of insulating values soil and water have on soil temperatures and seed death. The soil should be loaded into the trays in 1 cm increments to a total depth of 3 cm. Seeds then should be added to each germination tray at the appropriate seeding depth.

Seed should be hand harvested with culms intact (Canode et al. 1970) from wild populations. However, cultivars should be used if that is the target population. The seeds should be dried, cleaned, and stored at 5° C for a minimum of 14 days to alleviate any dormancy issues (Canode et al.1970). Viability of the collected seeds should be assessed using a germination chamber. Lots of 100 seeds should be randomly placed on moist blotter paper in a germination chamber set to 16h light at 25° C and 8h dark at 15° C (Canode et al. 1970). This procedure should be replicated 4 times. The blotter paper should be initially saturated with a 0.2% KNO₃ solution; any additional moisture required should simply be pure water (Larsen and Andreasen 2004a). Cumulative germination will be assessed every day for 28 days (Canode et al 1970). Successful germination will be considered radical protrusion of greater than 2 mm (Larsen and Andreasen 2004b). Germinated seedlings should be removed after counting. Cumulative

germination percentage should be recorded and fitted to a Weibull curve for analysis. Each experimental treatment should consist of 100 viable seeds, as adjusted by the cumulative germination percentage found in the viability test.

During the experimental treatments atmospheric conditions including wind speed, air temperature, and relative humidity should be monitored using weather device like a Kestral. To ensure an even fire front, a line of fuel should be poured on the edge of the cage and then ignited. A box fan should be used to maintain a constant rate of spread. The starting time of the fire and the end of the flaming should be recorded. In addition, the fire intensity should be monitored at seeding depth in soil using thermocouples. Fire intensity and heat dosage are temperature and time dependent. The fire intensity should be recorded by for example using four type K thermocouples at 1 second intervals by a data logger (Vermeire and Rinella 2010).

After the experimental treatments are applied, the germination trays should be placed in a germination chamber for monitoring. The environmental conditions should be the same as used in the initial viability test. The response variable, cumulative germination, should be monitored every day for 35 days. Emerged seedlings should be removed after counting. In addition to the fire treatments, unburned control samples should be germinated for each treatment to differentiate the fire effects from other germination factors associated with soil characteristics. The control should be replicated 8 times per treatment per standard germination protocol.

Rhizome and Clonal Plant Response

Differential rooting and rhizome depths can explain differential species response to fire and the post-fire environment. Shallower roots are more vulnerable to moisture stress in the post fire environment, and near surface roots and rhizomes are more prone to heat damage during the fire event. The fine-scale vertical profile of axillary buds, rhizomes and fine roots of Kentucky bluegrass should be determined under rangeland conditions (see experiment section for further details). Once the vertical distribution of axillary buds, and rhizomes is known, fire research could be conducted on similar cores. Using similar fuel loads as in the seed bank experiment should definitively answer the question whether fire can physically damage rhizomes buried at depth under normal fire conditions. The rhizome damage can then be plotted as a depth function with different fire intensities representing different depth functions. Expert analysis may be able to determine whether the dead rhizomes suffered from dehydration or protein denaturation as a primary factor in mortality. Although the thermal lethal limit of 60° C for plant tissue is rarely reached in grassland fires 2 cm below the soil surface, lower temperatures starting at 43° C may permanently damage important reproductive structures (Wehner and Watschke 1981). I predict that damage to the apical meristems will be greater during the 2-4 leaf stage than the dormant stage. Based on the nearly universal decrease experienced by Kentucky bluegrass to fire, I predict that damage will also be found in a high percentage of rhizomes during dormant season burns or simulations.

Increasing fire intensity should increase the damage to the apical meristems. Fires conducted during active growth are likely to set back production by removing apical dominance because the re-growth is slower when activating dormant rhizomes compared to intra-vaginal shoots associated with normal growth processes. Likewise loss of actively growing tissue may decrease carbohydrate reserves. This decrease in carbohydrate reserve combined with reduced growth rate could create a large competitive disruption for Kentucky bluegrass which may not be apparent without measurement of these characteristics in a laboratory setting where Kentucky bluegrass is the only species present.

Proposed Experiment

An example of an experiment to address the plant and rhizome response to fire could consist of a factorial design with 2 phenological stages and 5 fuel loads. The fuel loads will be the same used in the seed experiment (140, 275, 550, 1000 and 1500 g/m²). The phenological stages would be dormant and 2-3 leaf stage (Table 2).

Table 2: Example of Experimental Treatments

Fuel Load	Phenology	
	Dormant	2-3 Leaf
g/m ²		
0	12 reps	12 reps
140	12 reps	12 reps
275	12 reps	12 reps
550	12 reps	12 reps
1000	12 reps	12 reps
1500	12 reps	12 reps

To determine the fine-scale vertical profile of axillary buds and rhizomes of Kentucky bluegrass under rangeland conditions, samples should be taken in the field using a Soil Profiler (AMS, Inc. American Falls, ID) and separated by depth. Once the samples have been collected, axillary buds and rhizome characteristics should be quantified. Rhizome characteristics should include number, length and volume. The samples should be sliced into 1 cm increments for analysis. Previous research has indicated that this is the finest resolution possible while still maintaining accuracy (Chockzyska and Johnson 2009).

The core samples used for the fire part of the experiment should be of the same type used to characterize the vertical distribution of axillary buds, and rhizomes. To ensure minimal interference from other species, core samples of Kentucky bluegrass should be collected from populations displaying greater than 80% aerial cover when clipped to 7.5 cm. The cores should also all be taken from the same ecological site to minimize the variability caused by changes in the landscape. The core dimensions should be roughly 12.5 cm in diameter and 15 cm in depth. These are the cores to be transferred into PVC cylinders which will act as pots for the remainder of the experiment. Caps with three holes to allow free drainage should be fitted unto the bottoms of the PVC cylinders (Donkor et al. 2002). Any gaps between the soil core and the PVC cylinder should be filled with soil to prevent channeling of water along the outer edges. The sod should be trimmed to a standard 7.5 cm height once all cores have been collected. At

this time, field capacity should be measured by saturating 10 samples with water and allowing them to gravity drain. The weight of the soil cores at field capacity should be recorded. The cores should be maintained in a greenhouse for a minimum of 20 day to allow the plants to recover from the transplant.

In order to induce the desired phenological stage, the cores should be subjected to specific temperature, daylight, and moisture regimes in a growth chamber (Carlson et al. 1995). Dormancy should be induced by restricting moisture supply, providing a short photoperiod, and providing cool temperatures (less than 5° C) for a period of at least 9 weeks. Fires conducted at the dormant stage should simulate fall when the plant is not actively growing above ground, but may be continuing to produce rhizomes and buds belowground. Dormant plants should then be subjected to a warmer (15° C) and wetter environment with a longer photoperiod to initiate re-growth. The 2 to 3 leaf stage should be used to simulate fires conducted during the fall re-growth period or initial spring green up.

Similar to the seed bank experiment, the fire treatments would take place in a fire chamber. The fire chamber has holes in the bottom that allow the PVC pots to be level with the bottom of the chamber. By keeping the pots below the flame level, they are protected from heat damage. The fuel loading and ignition procedures should be the same as in the seed bank experiment (Fig. 1). Immediately prior to conducting the fire treatments, the soil moisture content should be estimated by weighing all the samples and comparing them

to the average field capacity as found above (Donkor et al. 2002). Each fire should be a block of 4 replicates of a single phenological stage. Fire intensity, wind speed, air temperature, and relative humidity would also be monitored in a manner similar to the one used in the seed bank experiment. The start of each fire and the end of flaming should be recorded.

After the fire treatment, the plants should be placed in a greenhouse and allowed to recover for 20-30 days. The response variable would be damage to apical meristems. The damage should be assessed visually for re-growth from individual tillers. In addition to tiller count, percent aerial cover should be recorded for each core. Half the samples should be destructively sampled to assess damage to rhizomes. Damage to rhizomes should be determined by adding a 1% tetrazolium solution to the collected rhizomes (Wright 1970). Each rhizome should be visually assessed for staining caused by the tetrazolium solution (i.e., red or pink for live tissues). The remaining samples should continue recovery for another 20-30 days and meristem and tiller development should be visually assessed. Number of flowering tillers should be recorded during this period as well. After visual inspection, the remaining samples should be destructively sampled to assess damage to rhizomes.

REFERENCES

- Aamild, T.S., and D. Arntsen. 1998. Effects of light and temperature on seed germination of *Poa pratensis* from high latitudes. *ACTA Agriculturae Scandinavica Section B- Soil and Plant Science* 48: 239-247.
- Abrams, M.D. and L.C. Hulbert. 1987. Effect of topographic position and fire on species composition in Tallgrass prairie in northeast Kansas. *American Midland Naturalist* 117: 442-445.
- Anderson, K.L., E.F. Smith, and C.E. Ownesby. 1970. Burning bluestem range. *Journal of Range Mangement* 23(2):81-92.
- Archibold, O.W., L.J. Nelson, E.A. Ripley, and L. Delanoy. 1998. Fire temperatures in plant communities of the northern Mixed prairie. *Canadian Field Naturalist* 112: 234-240.
- Archibold, O.W., E.A. Ripley, and L. Delanoy. 2003. Effects of season of burning on the microenvironment of Fescue prairie in central Saskatchewan. *Canadian Field Naturalist* 117: 257-266.
- Augustine, D.J., J.D. Derner, and D.G. Milchunas. 2010. Prescribed fire, grazing, and herbaceous plant production in shortgrass steppe. *Rangeland Ecology and Management* 63(3): 317-323.
- Bangalore, R.P., R.W. Duell, and C.R. Funk. 1978. Dormancy of Kentucky bluegrass seed in relations to the color of spikelets and panicle branches at harvest. *Crop Science* 18: 683-684.
- Barker, W.T. and W.C. Whitman. 1988. Vegetation of the northern Great Plains. *Rangelands* 6:266-272.
- Baron, V.S., A.C. Dick, M. Bjorge, and G. Lastiwka. 2004. Stockpiling potential of perennial forage species adapted to the Canadian western prairie parkland. *Agronomy Journal* 96: 1545-1522.
- Benning, T.L. and T.B. Bragg. 1993. Response of big bluestem (*Andropogon gerardii*) to timing of spring burning. *American Midland Naturalist* 130(1): 127-132.
- Benson, E.J. and D.C. Hartnett. 2006. The role of seed and vegetative reproduction in plant recruitment and demography in Tallgrass prairie. *Plant Ecology* 187: 163-177.

- Benson, E.J., D.C. Harnett, and K.H. Mann. 2004. Belowground bud banks and meristem limitation in Tallgrass prairie plant populations. *American Journal of Botany* 91: 416-421.
- Bidwell, T.G. and D.M Engle. 1992. Relationship of fire behavior to Tallgrass prairie herbage production. *Journal of Range Management* 45: 579-584.
- Bidwell, T.G., D.M Engle and P.L. Claypool. 1990. Effects of spring headfires and backfires on Tallgrass prairie. *Journal of Range Management* 43(3) 209-212.
- Biondini, M. E. 2007. Plant diversity, production, stability, and susceptibility to invasion in restored northern Tallgrass prairies (United States). *Restoration Ecology* 15:77-87
- Biondini, M.A., B.D. Patton, and P.E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern Mixed-grass prairie, USA. *Ecological Applications* 8: 469-479.
- Biondini, M.A., A.A. Steuter, and C.E. Grygiel. 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, J.M. 1997. Fire, N availability, and plant response in grasslands: A test of the transient maxima hypothesis. *Ecology* 78(8): 2359-2368.
- Bogen, A.D., E.W. Bork, and W.D. Willms. 2002. Rough fescue (*Festuca campestris* Rydb.) response to heat injury. *Canadian Journal of Plant Science* 82: 721-729.
- Bosy, J.L., and R.J. Reader. 1995. Mechanisms underlying the suppression of seedling emergence by grass (*Poa pratensis*) litter. *Functional Ecology* 9: 635-639.
- Bowles, M.I., M.D. Jones, and J.L. McBride. 2003. Twenty-year changes in burned and unburned sand prairie remnants in northwestern Illinois and implications for management. *American Midland Naturalist* 149: 35-45.
- Bremer, D.J. and J.M. Ham. 1999. Effect of spring burning on the surface energy balance in a Tallgrass prairie. *Agricultural and Forest Meteorology* 97: 43-54.

- Brudvig, L.A., C.M. Mabry, J.R. Miller, and T.A. Walker. 2007. Evaluation of central North American prairie management based on species diversity, life form, and individual species metrics. *Conservation Biology* 21(3): 864-874.
- Busso, C.A., R.M. Boo, and D.V. Pelaez. 1993. Fire effects on bud viability and growth of *Stipa tenuis* in semiarid Argentina. *Annals of Botany* 71: 377-381.
- Byre, K.R., J.M. Norman, S.T. Gower. 2002. The fate of nutrients following three- and six-year burn intervals in a Tallgrass prairie restoration in Wisconsin. *American Midland Naturalist* 148: 28-42.
- Canode, C.L. 1972. Grass seed production as influenced by cultivation, gapping, and postharvest residue management. *Agronomy Journal* 64: 148-151.
- Canode, C.L., and M. Perkins. 1977. Floral induction and initiation in Kentucky bluegrass cultivars. *Crop Science* 17: 278-282.
- Canode, C.L., A.G. Law, and J.D. Maguire. 1970. Post-harvest drying rate and germination of Kentucky bluegrass seed. *Crop Science* 10: 316-317.
- Carlson, J.M., N.J. Ehlike, and D.L. Wyse. 1995. Environmental control of floral induction and development in Kentucky bluegrass. *Crop Science* 35: 1127-1132.
- Carson, W.P. and C.J. Peterson. 1990. The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance. *Oecologia* 85: 8-13.
- Castellano, M.J. and R.J. Ansley. 2007. Fire season and simulated grazing differentially affect the stability and drought resilience of a C4 bunchgrass, C3 bunchgrass, and C4 lawngrass. *Journal of Arid Environments* 69:375-384.
- Chastain, T.G., G.L. Kiemnec, G.H. Cook, C.J. Garbacik, B.M. Quebbeman, F.J. Crowe. 1997. Residue management strategies for Kentucky bluegrass seed production. *Crop Science* 37: 1836-1840.
- Choczynska, J., and E.A. Johnson. 2009. A soil heat and water transfer model to predict belowground grass rhizome bud death in a grass fire. *Journal of Vegetation Science* 20: 277-287.

- Cully, A.C., J.F. Cully Jr., and R.D. Hiebert. 2003. Invasion of exotic plant species in Tallgrass prairie fragments. *Conservation Biology* 17: 990-998.
- Curtis, J.T. and M.L. Partch. 1948. Effect of fire on the competition between bluegrass and certain prairie plants. *American Midland Naturalist* 39(2): 437-443.
- Dalgleish, H.J., and D.C. Hartnett. 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: 81-88.
- Dalgleish, H.J., and D.C. Hartnett. 2009. The effects of fire frequency and grazing on tallgrass prairie productivity and plant composition are mediated through bud bank demography. *Plant Ecology* 201: 411-420.
- Donkor, N.T., E.W. Bork, R.J. Hudson. 2002. *Bromus-Poa* response to defoliation intensity and frequency under three soil moisture levels. *Canadian Journal of Plant Science* 82: 365-370.
- Driscoll, D.A., D.B. Lindenmayer, A.F. Bennett, M. Bode, R.A. Bradstock, G.J. Cary, M.F. Clarke, N. Dexter, R. Rensham, G. Friend, M. Gill, S. James, G. Kay, D.A. Keith, C. MacGregor, J. Russell-Smith, D. Salt, J.E.M. Watson, R.J. Williams and A. York. 2010. Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* 143: 1928-1939.
- Dudley, J.L. and K. Lajtha. 1993. The effects of prescribed burning on nutrient availability and primary production in sandplain grasslands. *American Midland Naturalist* 130(2): 286-298.
- Durr, G.H., H.T. Kunelius, R. Drapeau, K.B. McRae, and S.A.E. Fillmore. 2005. Herbage yield and composition of Kentucky bluegrass (*Poa pratensis*) cultivars under two harvest systems. *Canadian Journal of Plant Science* 85: 631-639.
- Ehrenreich, J.H. and J.M. Aikman. 1963. An ecological study of the effect of certain management practices on native prairie in Iowa. *Ecological Monographs* 33(2): 113-130.
- Engle, D.M., and P.M. Bultsma. 1984. Burning of northern Mixed prairie during drought. *Journal of Range Management* 37: 398-401.
- Engle, D.M. and T.G. Bidwell. 2001. Response of central North American prairies to seasonal fire. *Journal of Range Management* 54(1):2-10.

- Engle, D.M., T.G. Bidwell, A.C. Ewing, J.R. Williams. 1989. A technique for quantifying fire behavior in grassland fire ecology studies. *The Southwestern Naturalist* 34(1): 79-84.
- Etter, A.G. 1951. How Kentucky bluegrass grows. *Annals of the Missouri Botanical Garden* 38: 293-375.
- Ewing, A.L. and D.M. Engle. 1988. Effects of late summer fire on Tallgrass prairie microclimate and community composition. *American Midland Naturalist* 120(1): 212-223.
- Facelli, J.M. and S.T.A. Pickett. 1991. Plant Litter: its dynamics and effects on plant community structure. *Botanical Review* 57: 1-32.
- Foster, B.L., and K.L. Gross. 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology* 79: 2593-2602.
- Foster, B.L., K. Kindscher, G. Houseman, and C.A. Murphy. 2009. Effects of hay management and native species sowing on grassland community structure, biomass, and restoration. *Ecological Applications* 19: 1884-1896.
- Garrison, M.A., and J.C. Stier. 2010. Cool-season turfgrass colony and seed survival in a restored prairie. *Crop Science* 50: 345-356.
- Grazi, F., M. Umaerus, and E. Akerberg. 1961. Observations on the mode of reproduction and the embryology of *Poa pratensis*. *Communications from the Swedish Seed Association* 133: 489-540.
- Grilz, P.L. and J.T. Romo. 1994. Water relations and growth of *Bromus inermis* (Smooth brome) following spring or autumn burning in a Fescue prairie.
- Hadley, E.B. 1970. Net productivity and burning responses of native eastern North Dakota prairie communities. *American Midland Naturalist* 84(1): 121-135.
- Hamilton, E.W., and D.A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology* 82: 2397-2402.
- Hartnett D.C., K.R. Hickman, and L.E. Fischer-Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in Tallgrass prairie. *Journal of Range Management* 49:413-420.

- Hendrickson, J.R. and C. Lund. 2010. Plant community and target species affect responses to restoration strategies. *Rangeland Ecology and Management* 63(4): 435-442.
- Hensel, R.L. 1923. Recent studies on the effect of burning on grassland vegetation. *Ecology* 4: 183-188.
- Higgins, K. F., A.D. Kruse, and J.L. Piehl. 1989. Effects of fire in the northern Great Plains. U.S. Fish and Wildlife Service and Cooperative Extension Service, South Dakota State University, Brookings, South Dakota. *Extension Circular* 761:1-47.
- Hobbs, N.T., D.S. Schimel, C.E. Ownesby, and D.S. Ojima. 1991. Fire and grazing in the Tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* 72(4): 1374-1382.
- Holman, J.D., C. Hunt, and D. Thill. 2007a. Structural composition, growth stage, and cultivar affects on Kentucky bluegrass forage yield and nutrient composition. *Agronomy Journal* 99: 195-202.
- Holman, J.D., C. Hunt, J. Johnson-Maynard, L. VanTassell, and D. Thill. 2007b. Livestock use as a non-thermal residue management practice in Kentucky bluegrass seed production systems. *Agronomy Journal* 99: 203-210.
- Howe, H.F. 1995. Succession and fire season in experimental prairie plantings. *Ecology* 76(6): 1917-1925.
- Howe, H.F. 2000. Grass response to season burns in experimental plantings. *Journal of Range Management* 53: 437-441.
- Hulbert, L.C. 1988. Causes of fire effects in Tallgrass prairie. *Ecology* 69(1): 46-58.
- Jefferson 2008. Ex situ germination responses of Midwestern USA prairie species to plant-derived smoke. *American Midland Naturalist* 159: 251-256.
- Johnson, E.A. 1992. *Fire and vegetation dynamics*. Cambridge University Press, Cambridge, U.K.
- Johnson, R.C., W.J. Johnston, J.C. Golob. 2003. Residue management, seed production, crop development, and turf quality in diverse Kentucky bluegrass germplasm. *Crop Science* 43: 1091-1099.

- Kitchen, D.J., J.M. Blair, and M.A. Callaham Jr. 2009. Annual fire and mowing alter biomass, depth distribution and C and N content of roots and soil in Tallgrass prairie. *Plant Soil* 323: 235-247.
- 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.
- Knapp, A.K., J.M. Briggs, J.K. Koelliker. 2001. Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems* 4: 19-28.
- Knops, J.M.H. 2006. Fire does not alter vegetation in infertile prairie. *Oecologia* 150: 477-483.
- Kucera, C.L. and J.H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. *Ecology* 43(2): 334-336.
- Lamb, E.G. 2008. Direct and indirect control of grassland community structure by litter, resources, and biomass. *Ecology* 89(1) 21-225.
- Larsen, S.U., and C. Andreasen. 2004a. Light and heavy seeds differ in germination percentage and mean germination thermal time. *Crop Science* 44: 1710-1720.
- Larsen, S.U., and Andreasen, C. 2004b. Comparison of germination criteria in red fescue (*Festuca rubra* ssp *litoralis*), perennial ryegrass (*Lolium perenne*) and Kentucky bluegrass (*Poa pratensis*). *Seed Science and Technology* 32:341-354.
- Larsen, S.U., and B.M. Bibby. 2005. Differences in thermal time requirement for germination of three turfgrass species. *Crop Science* 45: 2030-2037.
- Larson, D.L. and J.L. Larson. 2010. Control of one invasive plant species allows exotic grasses to become dominant in northern Great Plains grasslands. *Biological Conservation* 143: 1901-1910.
- Levang-Brilz, N., and M.E. Biondini. 2002. Growth rate, root development and nutrient uptake of 55 plant species from the Great Plains grasslands, U.S.A. *Plant Ecology* 165:117-144
- Lu, S., T. Ren, and Y. Gong. 2007. An improved model for predicting soil thermal conductivity from water content at room temperature. *Soil Science Society of America Journal* 71(1): 8-14.

- Martin, D.W. and J.C. Chambers. 2001. Effects of water table, clipping, and species interactions on *Carex nebrascensis* and *Poa pratensis* in riparian meadows. *Wetlands* 21(3): 411-430.
- Mason, W. and L. Lachance. 1983. Effects of initial harvest date on dry matter yield, in vitro dry matter digestibility and protein in timothy, tall fescue, reed canary grass, and Kentucky bluegrass. *Canadian Journal of Animal Science* 63: 675-685.
- Matzk, F. 1991. New efforts to overcome apomixis in *Poa pratensis* L. *Euphytica* 55: 65-72.
- Mazzucato, A., M. Falcinelli, and F. Veronesi. 1996. Evolution and adaptedness in a facultative apomictic grass. *Euphytica* 92: 13-19.
- Miles, E.K., and J.M.H. Knops. 2009. Grassland compositional change in relation to the identity of the dominant matrix-forming species. *Plant Ecology and Diversity* 2: 265-275.
- Moser, L.E., S.R. Anderson, and R.W. Miller. 1968. Rhizome and tiller development of Kentucky bluegrass (*Poa pratensis*) as influenced by photoperiod, cold treatment and variety. *Agronomy Journal* 60: 632-635.
- Murphy R.K., and Grant, T.A. 2005. Land management history and floristics in Mixed-grass prairie, North Dakota, USA. *Natural Areas Journal* 25: 351-358.
- Nielson, E.L. 1946. The origin of macrogametophytes in *Poa pratensis*. *Botanical Gazette* 108: 26-40.
- Ojima, D.S., D.S. Schimel, W.J. Parton, and C.E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in Tallgrass prairie. *Biogeochemistry* 24(2): 67-84.
- Old, S.M. 1969. Microclimate, fire and plant production in an Illinois prairie. *Ecological monographs* 39(4): 355-384.
- Patton, B., P. Nyren, G. Mantz, and A. Nyren. 2010. Long-term grazing intensity research in the Missouri Couteau of North Dakota. Available at: <http://www.ag.ndsu.edu/centralgrasslandsrec/long-term-ecological-research>. Accessed 1 June 2010.
- Peet, M., R. Anderson, and M.S. Adams. 1975. Effect of fire on big bluestem production. *American Midland Naturalist* 94: 15-26.

- Picone, L.I., G. Quaglia, F.O. Garcia, and P. Laterra. 2003. Biological and chemical response of a grassland soil to burning. *Journal of Range Management* 56: 291-297.
- Pfeiffer, K.E. and A.A. Steuter. 1994. Preliminary response of Sandhills prairie to fire and bison grazing. *Journal of Range Management* 47: 395-397.
- Pumphrey, F.V. 1965. Residue management in Kentucky bluegrass (*Poa pratensis* L.) and red fescue (*Festuca rubra* L.) seed fields. *Agronomy Journal* 57: 559-561.
- Pylypec, B., and J.T. Romo. 2003. Long-term effect of burning *Festuca* and *Stipa-Agropyron* grasslands. *Journal of Range Management* 56: 640-645.
- Raison, R.J. 1979. Modification of the soil environment by vegetation fires, with particular reference to N transformations: a review. *Plant and Soil* 51: 73-108.
- Redmann, R.E. 1975. Production ecology of grassland plant communities in western North Dakota. *Ecological Monographs* 45(1): 83-106.
- Redmann, R.E. 1978. Plant and soil-water potentials following fire in a northern Mixed prairie. *Journal of Range Management* 31:443-445.
- Redmann, R.E., J.T. Romo, B. Pylypec, and E.A. Driver. 1993. Impacts of burning on primary productivity of *Festuca* and *Stipa-Agropyron* grasslands in central Saskatchewan. *American Midland Naturalist* 130: 262-273.
- Rogler, G.A. and H.J. Hass. 1947. Range production as related to soil moisture and precipitation on the northern Great Plains. *Journal of the American Society of Agronomy* 39: 378-389.
- Rosenberg, E., G. Kemeny, R.C. Switzer, T.C. Hamilton. 1971. Quantitative evidence for protein denaturation as cause of thermal death. *Nature* 232: 471-477.
- Shay, J., D. Kunec, and B. Dyck. 2001. Short-term effects of fire frequency on vegetation composition and biomass in Mixed prairie in south-western Manitoba. *Plant Ecology* 155: 15-167.
- Silletti, A. and A. Knapp. 2002. Long-term responses of the grassland co-dominant *Andropogon gerardii* and *Sorghastrum nutans* to changes in climate and management. *Plant Ecology* 163: 15-22.

- Sims, P.L. and J.S. Singh. 1978. The structure and function of ten western North American grasslands. *Journal of Ecology*: 573-597.
- Smith, M.D. and A.K. Knapp. 1999. Exotic plant species in a C4-dominated grassland: invisibility, disturbance, and community structure. *Oecologia* 120: 605-612.
- Steuter, A.A. 1987. C3/C4 production shift on seasonal burns- northern Mixed prairie. *Journal of Range Management* 40(1): 27-31.
- Stinson, K.J. and H.A. Wright. 1969. Temperatures of head-fires in the southern Mixed prairie of Texas. *Journal of Range Management* 22: 169-174.
- Tester, J.R. 1996. Effects of fire frequency on plant species in oak savannah in east-central Minnesota. *Bulletin of the Torrey Botanical Club* 123:304-308.
- Tilman, D., and D. Wedin. 1991. Plant traits and resource reduction for 5 grasses growing on a nitrogen gradient. *Ecology* 72: 685-700.
- Towne, G. and C. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas Tallgrass prairie. *Journal of Range Management* 37: 392-397.
- Towne, E.G. and K.E. Kemp. 2003. Vegetation dynamics from annually burning Tallgrass prairie in different seasons. *Journal of Range Management* 56: 185-192.
- Tracy, B.F., and M.A. Sanderson. 2004. Forage productivity, species evenness and weed invasion in pasture communities. *Agricultural Ecosystems and Environment* 102: 175-183.
- Travnicek, A.J., R.G. Lym, and C. Prosser. 2005. Fall-prescribed burn and spring-applied herbicide effects on Canada thistle control and soil seedbanks in a northern Mixed-grass prairie. *Rangeland Ecology and Management* 58(4): 413-422.
- Turner, C.L., J.M. Blair, R.J. Scharz, and J.C. Neel. 1997. Soil N and plant responses to fire, topography, and supplemental N in Tallgrass prairie. *Ecology* 78(6): 1832-1843.
- USDA, NRCS. 2010. The PLANTS database. Available at: <http://plants.usda.gov>. Accessed 1 June 2010.

- Vermeire, L.T., and Rinella, M.J. 2010. Fire alters emergence of invasive plant species from soil surface-deposited seeds. *Weed Science* 57: 304-310.
- Volesky, J.D., W.H Schacht, and D.M. Richardson. 2004. Stocking rate and grazing frequency effects on Nebraska Sandhills meadows. *Journal of Range Management* 57: 553-560.
- Waddington, J., D.H. McCartney, and L.P. Lefkovitch. 1999. Effects of management on species dynamics of Canadian aspen parkland pastures. *Journal of Range Management* 52: 60-67.
- Wang, S., D. Hui, and Y. Lou. 2001. Fire effect on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecological Applications* 11: 1349-1365.
- Weaver, J.E. 1926. *Root development of field crops*. MacGraw-Hill, New York.
- Weaver, J.E. and N.W. Rowland. 1952. Effects of excessive natural mulch on development, yield, and structure of native grasslands. *Botanical Gazette* 114(1): 1-19.
- Wedin, D.A. and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84(4): 433-441.
- Wedin, D.A. and J. Pastor. 1993. Nitrogen mineralization dynamics in grass monocultures. *Oecologia* 96: 186-192.
- Wehner, D.J., and Watschke, T.L. 1981. Heat tolerance of Kentucky bluegrasses, perennial ryegrasses, and annual bluegrass. *Agronomy Journal* 73: 79-84.
- White, E.W., W.W. Thompson, and F.R. Gartner. 1973. Heat effects on nutrient release from soils under ponderosa pine. *Journal of Range Management* 26: 22-24.
- White, R.S. and P.O. Currie. 1983. Prescribed burning in the northern great plains: yield and cover responses of 3 forage species in the Mixed-grass prairie. *Journal of Range Management* 36(2): 179-183.
- Wieners, R.R., S.Z. Fei, and R.C. Johnson. 2006. Characterization of a USDA Kentucky bluegrass (*Poa pratensis* L.) core collection for reproductive mode and DNA content by flow cytometry. *Genetic Resources and Crop Evolution* 53: 1531-1541.

- Willms, W.D., B.W. Adams, and J.F. Johan. 1996. Seasonal changes of herbage biomass on the Fescue prairie. *Journal of Range Management* 49: 100-104.
- Wright, H.A. 1970. A method to determine heat-caused mortality in bunchgrasses. *Ecology* 51: 582-587.
- Wright H. A., and A.W. Bailey. 1982. *Fire Ecology: United States and Canada*. John Wiley & Sons, New York.
- Zedler, J. and O.L. Loucks 1969. Differential burning response of *Poa pratensis* fields and *Andropogon scoparius* prairies in central Wisconsin. *American Midland Naturalist* 81(2): 341-352.