PERSISTENCE AND PRODUCTIVITY OF NATIVE WARM-SEASON GRASS ECOTYPES AND CULTIVARS UNDER MANAGED GRAZING IN SOUTHERN WISCONSIN

by

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Chapter 1. General Introduction

"... you who farm and you who teach land use hold the key to either the continuing destruction of the biosphere and its diversity, or to a birth of ecological sanity which will allow life and man a continuing evolution."
Hugh Iltis (1967)

Loss of the tallgrass prairie in the Prairie Peninsula

Temperate grasslands cover approximately 32 % of the earth's land surface (Jones et al. 2006), having vast ecological significance as they are known to help mitigate against global warming by acting as carbon sinks (Jones and Donnelly 2004) and serving as reservoirs for plant, animal and microbial biodiversity (Watkinson and Ormerod 2001). In addition, temperate grasslands have great social and cultural significance as they supplement human nutritional needs (Samson and Knopf 1994) and sustain agricultural and rural livelihoods worldwide (Reynolds et al. 2005). Yet, temperate grasslands are among one of the most threatened ecosystems in the world, as they endure persistent and increasing pressures from human impacts such as urbanization, agriculture and fragmentation (Hoekstra et al. 2005). Less than 4% of temperate grasslands worldwide are under some type of protection (Jenkins and Joppa 2009).

Prairie is a type of temperate grassland that once ranged across the central portion of the North American continent. It is composed of a vegetation matrix dominated by long-lived perennial grasses, many with the warm-season (C4) photosynthetic pathway. Prairie species composition and productivity were differentiated along a longitudinal gradient of precipitation, from east to west, with the eastern portions of the prairie experiencing fewer periods of drought and more total growing season precipitation than the central and western portions (Risser et al. 1981). Grasses native to the eastern prairie, such as big bluestem

(*Andropogon gerardii* Vitman) and Indiangrass (*Sorghastrum nutans* (L.)), often reached over 3 meters in height, which lent to these areas being identified as the tallgrass prairie (Anderson 2006). Tallgrass prairie is characterized by its high productivity aboveground (Knapp and Seastedt 1986) and belowground (Knapp et al. 1998), organic soils (Knapp et al. 1998) and the immense diversity of plants, animals and microbes that depend on this system for habitat (Samson and Knopf 1994). Further, tallgrass prairie has been characterized as a system dependent on periodic natural and anthropocentric disturbances including drought, fire and/or grazing by large ungulates, and in the absence of these disturbances would likely transition into a different system such as woodland or forest (Transeau 1935, Axelrod 1985).

Described as a 'sea of grass', the tallgrass prairie prior to European settlement covered 68 million hectares (Samson and Knopf 1994) ranging across the eastern Great Plains and Midwest (Allen and Fike 2009). The eastern most section of the tallgrass prairie formed a wedge that extended into coniferous forests to the north and deciduous forests to the east and south (Anderson 2006). This area, termed the Prairie Peninsula (Transeau 1935), historically encompassed 1.5 million hectares including tracts in Illinois, Iowa, Indiana, Minnesota, Missouri and Wisconsin with outliers in Ohio, Kentucky and Michigan (Samson and Knopf 1994).

European settlement of the Prairie Peninsula began in the early 1800s. Settlers arriving from the east came with the notion that lands beyond the Appalachian Mountains needed to be tamed with agriculture (Gates 1941). This notion and subsequent migration of people were fueled by the federal government and land speculators through promotional materials that romanticized life in the "Wild West" and legislation such as the 1862 Homestead Act that encouraged settlement by offering inexpensive tracts of land (Gates

1941, Undersander et al. 2009). Initially, settlers moving into the Prairie Peninsula were wary of the openness of the landscape as they interpreted the lack of trees to the infertility of the land (Shannon 1966, Smith 1990). In addition, settlers needed timber for building materials and it was found the prairie sod was too laborious and costly to break up for crop production compared to clearing the forest. For these reasons pioneering settlement of the tallgrass prairie in the Prairie Peninsula was concentrated along the prairie-forest border (Weaver 1954).

> "It is true the prairie mania has ever prevailed among the eastern farmers coming to settle in the West. This is the result of a fancied convenience among new settlers, and a wish to gratify that thirst for novelty which is inherent in the minds of those who have been reared among the hills and vallies of the New England and middle States, where Nature, in her prairie beauty, has never appeared. But that prepossession in favor of prairie farms is rapidly yielding to the formation of a more rational conclusion. The absence of many of the common conveniences of life, which are enjoyed in the timber – the want of health and the failure of crops from year to year, are obstacles in the path of prosperity, which exist upon the prairies, and which can never be entirely surmounted. These will henceforth prove a barrier to their settlement, and will have a tendency to direct emigration to a forest home."
>
> *Solomon Lombard*
> *Wisconsin and Iowa Farmer and Northwestern Cultivator, Vol 3, 1851*

The prevailing suspicion that prairie soils were infertile and the associated difficulty with breaking up the prairie sod were short-lived. Between 1840 and 1900, 98% of the tallgrass prairie in the Prairie Peninsula was lost (Robertson et al. 1997) as the extensive root systems of the native sod succumbed to the John Deere cast steel plow. The activities of the "sodbusters" echoed across the Prairie Peninsula as "… that of a fusillade of pistols, the pistol-shot cracks of roots breaking" (Manning 1995), as native vegetation was rapidly replaced by agricultural crops such as corn and wheat. In addition, the rise of the railroads afforded to settlers the mobility to move timber for housing and harvested crops for profit, allowing settlement to move beyond the prairie-forest ecotone (Robertson et al. 1997).

Settler familiarity with the native vegetation at this time, primarily the native grasses, was minimal as these "wild grasses" were mainly used as community pasture for working livestock, such as oxen (Hibbard 1904, Schafer 1922). These livestock were allowed to "rustle" for a living in both summer and winter (Schafer 1922) and it was observed in Dane County, Wisconsin that "prairie grasses… if pastured, soon disappears all together." (Hibbard 1904). In those areas of the tallgrass prairie that escaped cultivation, but were degraded by continuous pasturing of livestock, settlers often introduced exotic cool-season (C3) grasses, many of which still comprise the pasture systems of today, as the settlers were familiar with the planting, management and use of these grasses as forage (Maddy 1975).

Return of the tallgrass prairie

Little attention was focused on the ecological value or management of tallgrass prairie vegetation for productivity and persistence under grazing during settlement of the Prairie Peninsula, since the production of annual agricultural crops was the main settler motivation for migrating west. Further, the rapid extinction of tallgrass prairie in the Prairie Peninsula did not allow time for scientific inquiries to be made on the ecological functions or agricultural applications associated with the system. It was not until the 1930s, in the wake of the catastrophic soil loss that occurred during the Dust Bowl period in the Great Plains, that ecological values of tallgrass prairie, such as the potential for soil building and stabilization, gained recognition in the Prairie Peninsula (Jordan 1983). This recognition has primarily been manifested as tallgrass prairie restorations and preservations (Wilson 2002), where much research has been conducted on topics ranging from establishment and management practices, such as seeding methods (Middleton et al. 2010) and control of aggressive and/or exotic species (Blumenthal et al. 2005, Harrington and Kathol 2009).

Further, ecological functions associated with tallgrass prairie beyond soil building and stabilization, such as nutrient cycling (Brye et al. 2002) and the value of restorations for wildlife habitat (Fletcher and Koford 2002), have been the subjects of extensive research. More recently, tallgrass prairie has been targeted as a potential perennial biofuel feedstock creating novel values for this ecosystem and needs for more research (Tilman et al. 2006).

Most tallgrass prairie restorations in the Prairie Peninsula have been managed with a combination of mechanical and chemical methods including prescribed burns, mowing and herbicide applications. Each of these methods is employed to meet objectives such as reducing undesirable species encroaching into the prairie, promoting the establishment and recruitment of the native vegetation (Howe 1994) and maintaining productivity by preventing litter accumulation (Knapp and Seastedt 1986). One tallgrass prairie management tool that has been largely overlooked in the Prairie Peninsula is ungulate grazing. Native ungulates are thought to have played a "keystone role" in tallgrass prairie functional and structural ecology, through foraging patterns and habits that interacted with other important ecological processes, including fire and drought (Knapp et al. 1999). Grazing of prairie vegetation in the Great Plains, by both wild and domesticated ungulates, has been shown to increase species diversity as ungulates preferentially graze on the native grasses, releasing their competitive dominance by allowing more light to penetrate the grass canopy to forb species of lower stature below (Collins 1987, Bakker et al. 2003, Towne et al. 2005). Research has also shown an increase in the rate of carbon and nitrogen cycling within the ecosystem as ungulate urine and fecal deposits contain these nutrients in forms more readily available to plants (Johnson and Matchett 2001).

It has been suggested that the reluctance to use grazing to manage tallgrass prairie restorations in the Prairie Peninsula is attributed to the widely accepted notion that grazing leads to tallgrass prairie degradation (Williams 1997, Howe 1999, Papanastasis 2009). The rapid decline of native prairie vegetation as European settlers and their domestic livestock advanced westward seemed to indicate prairie and domestic ungulate grazing were incompatible. This assumed incompatibility was fueled by the relative ease with which livestock "destroyed" native vegetation when continually pastured; contributing to the conclusion that grazing by domestic livestock is intrinsically harmful to tallgrass prairie (Williams 1997). In a recent survey of tallgrass prairie restoration practitioners, only 20% of phone respondents used ungulate grazing (rotational grazing) as a tool to meet objectives such as reducing cool-season grass dominance or increasing native forb abundance (Rowe 2010). Yet, all of these respondents considered it to be effective for meeting restoration objectives.

Grazing systems and native warm-season grasses

The act of grazing is a complex process that combines the interactions between numerous biotic and abiotic factors, such as plants, grazers, climate and soil, which are further complicated by the grazing management regimen that determines the frequency, intensity and seasonality of grazing events (Papanastasis 2009). Early research on the effects of defoliation on native warm-season grasses in the Prairie Peninsula involved clipping treatments that removed much of the aboveground biomass at frequent intervals throughout the growing season. These treatments decreased the productivity, vigor and persistence of the grasses in subsequent years (Robocker and Miller 1955, Neiland and Curtis 1956, Ehrenreich 1959). Studies have shown grasses exhibit compensatory responses to tissue loss

such as increased photosynthetic rates (Wallace 1990). Additionally, reallocation of organic compounds and nutrients from the soil rhizosphere, as well as the root system (Hamilton et al. 2008) and storage organs (Richards and Caldwell 1985) of grasses, has been shown to aid in the regrowth of new aboveground plant tissue after defoliation. However, these responses have been found to be tightly coupled to the development stage of the grasses at the time of defoliation (Mousel et al. 2003). Further, if defoliations are too frequent and/or intense during the growing season the plants may be unable to compensate for the tissue loss over time (Woodis and Jackson 2008). These conclusions reinforce research conducted on the thin-soil prairies of southern Wisconsin in the late 1950s that found low "grazing pressure" did not decrease dominance of the native grasses relative to ungrazed thin-soil prairies, yet as grazing pressure increased native grasses were replaced by more grazing tolerant, exotic species such as bluegrass (Dix 1959).

Much of the recent research focused on the use of ungulates as a management tool for tallgrass prairie comes from the Great Plains where soils, climate, growing season, landscape configurations, ungulate species, and the grazing systems used to manage them can be quite different than those of the Prairie Peninsula. There are two main types of grazing systems, continuous grazing and management intensive grazing (MIG). Continuous grazing, a system by which livestock are allowed to freely graze a confined area for an extended period of time, predominates in the Great Plains where large tracts of contiguous grasslands still exist. Continuous grazing management evolved in the Great Plains when the free-range cattle industry transitioned into the fenced-ranch cattle industry in the late 1870s, which was largely a consequence of the invention of barbed wire (Kirschenmann et al. 2009). Under continuous grazing, livestock managers exert direct control only over the stocking rates or

densities of livestock allowed to graze within fenced areas. Research has shown that livestock select for plants most palatable to them and that frequently grazed plants of the same species are more preferred over those that have not been grazed, ultimately leading to uneven grazing and thinning of the most desired species (Heath et al. 1973). Overgrazing of native prairie vegetation on both public and private lands in the late 19th and early 20th centuries allowed non-native species of lower forage quality and palatability and competitive cool-season grasses to invade and degrade the prairie (Edwards 1948) creating speculation over the use of continuous grazing to manage native grasslands. Enhanced understanding of plant responses to defoliation and how these responses are related to ecological conditions, such as precipitation amounts and distributions across a growing season, has increased the capacity to manage for the long-term health and productivity of rangeland vegetation under continuous grazing systems (Briske et al. 2008). However, the capacity to promote sustainable rangeland plant communities is ultimately controlled by land managers' perceptions of detrimental management practices, which are largely responsible for rangeland degradation under continuous grazing systems (Briske et al. 2008).

Management intensive grazing differs from continuous grazing systems in that livestock are actively rotated through subdivided pastures, with the intent to optimize the productivity, quality and persistence of pasture forage in order to meet livestock nutritional needs throughout the growing season (Taylor and Neary 2008). Since livestock are being rotated from paddock to paddock under MIG, the potential for overgrazing is reduced relative to continuous grazing systems, as graziers exert more control over the frequency, intensity, selectivity and spatial distribution of individual grazing events (Gerrish 2004). Briske et al. (2008) suggested that rotational grazing systems require more intensive management than

continuous grazing systems. Intensive management leads to enhanced capacities by land managers to manage for the long-term productivity and profitability of grazing lands (Paine et al. 1999, Taylor and Foltz 2006, Briske et al. 2008, Oates et al. 2011). Studies in cool-season grass dominated systems observed that MIG resulted in higher seasonal yields and quality of forage, which the authors attributed to managing for rest periods and forage regrowth (Paine et al. 1999), as well as sustaining the development phase of the vegetation in a juvenile state throughout much of the growing season (Oates et al. 2011). Likewise, a study comparing continuous and MIG grazing systems of tallgrass prairie in Oklahoma observed that end-of-season standing biomass was greater under MIG, which the authors concluded could have positive effects on pasture persistence as a result of greater soil protection and decreased impact of defoliation on plant vigor (Cassels et al. 1995). In addition, the movement of livestock through MIG rotations is intended to mimic the patterns of bison (*Bison bison*) grazing tallgrass prairie. Bison forage by establishing grazing patches across the landscape, areas characterized by heavy defoliation events interspersed with regrowth periods over a growing season to meet the nutritional needs of the herd (Knapp et al. 1999). Thus, bison foraging patterns meet the needs of both the animals (forage quality) and vegetation (rest period between defoliations) within a growing season. This research is intended to determine what grazing patterns are needed to maintain the vigor of native warm-season grass pastures in the long-term under MIG in the eastern tallgrass prairie.

Native grasses and MIG in the upper Midwest

Management intensive grazing attracted the attention of grass-based livestock farmers in the late 1980s (Paine et al. 2000) and the use of MIG among Wisconsin dairy farmers to manage pastures increased from 7.3% in 1993 to 26% in 2005 (Brock and Barham 2009).

This increasing trend corresponds to an increase in the number of grazing networks and network memberships in the state (Paine et al. 2000) implying that grass-based farmers are engaged to learn and adopt or adapt to new methods that can promote the health of their pastures and livestock. The willingness to engage in new forms of management may also relate to graziers' growing interests in the agronomic applications of native vegetation (Wiltshire et al. 2010). A 2006 survey distributed to grass-based farmers in the state found that 35% of the respondents were generally interested in incorporating native grasses into their grazing systems, and if native grasses were incorporated, approximately half of the respondents stated they would use them as pasture forage (Doll and Jackson 2009). Further, these same respondents were also concerned with how native grasses positively affect other ecosystem services, such as soil quality and wildlife habitat, concerns that mesh effectively with the interests and research of academic, conservation and natural resource professionals. In spite of this documented interest, little adoption of native grasses for use as forage has occurred, as farmers lack experience in native grass establishment and a source of knowledge of how to manage native grasses for long-term persistence and productivity under MIG in the upper Midwest (Doll and Jackson 2009). A recent study conducted on a bison farm in south central Wisconsin observed native warm-season grasses, intended to be used as pasture forage, rapidly declined in cover when an intense and frequent grazing management regimen was applied during the summer months (Jackson et al. 2010), highlighting the need for more studies on management of native grasses with grazing in the Prairie Peninsula.

Beyond the lack of technical knowledge over how to establish and manage native grasses with MIG in the upper Midwest, there are likely social barriers preventing the widespread adoption within the grazing community. For instance, two watersheds in Ohio

that received different levels of conservation outreach, technical and financial assistance, had similar farmland management practices, prompting the authors to conclude that the combination of information, technical assistance and economic subsidies was not enough to motivate farmers to implement conservation farming practices (Napier and Bridges 2002). It has been found that demographic factors such as the age of farmers, current financial situation, education level, and/or farm size also factors into activating farmer motivations to adopt new management practices that have a conservation focus (Prokopy et al. 2008). In addition, horizontal forms of networking have been shown to have a large influence on the potential for management changes among grass-based farmers (Hassanein and Kloppenburg 1995), since farmers largely rely on the knowledge of their peers as sources of information (Kahn et al. 2005). Thus, increasing knowledge concerning the mechanics of grazing native warm-season grasses will only partially satisfy motivations by grass-based farmers to incorporate new forage species into existing grazing systems, since farmer motivations to enact change are influenced by a complex set of demographic, social and technical interactions.

The following study was initiated by a grass-based farm family interested in increasing knowledge concerning how native grasses can be used in agroecosystems that practice sustainable grazing management. These same farmers are very active in local grazing networks, participating in horizontal forms of knowledge transfer by engaging with a group of peers in activities such as pasture walks, which allow graziers the opportunity to visually perceive and communicate about the management practices taking place on certain farms (Paine et al. 2000). In addition, the study was completed as part of a collaborative effort between farmers and university faculty and students, creating partnerships that have

potential to reach a larger group of individuals with diverse backgrounds, but common goals and interests. While the following study focused only on the technical aspects of grazing native warm-season grasses, the social networking and partnerships formed are critical if native grasses are to find a place within the agricultural landscapes of the upper Midwest.

Chapter 2. Persistence and productivity of local ecotype and cultivar warm-season grasses under early and late summer managed grazing in southern Wisconsin

ABSTRACT

Native warm-season grasses have potential to increase the ecosystem services associated with grazing lands, while simultaneously providing a source of quality forage for livestock. Yet, little information is available to livestock producers on how to manage native grass pastures for long-term productivity and persistence in the upper Midwest. Conservation agencies recommend native grasses should not be grazed until after July 15, based on the needs of grassland birds. In contrast, livestock producers practicing management intensive grazing (MIG) must meet both the needs of livestock (forage quality) and native grasses (late season rest period) in order to ensure a productive and profitable pasture system over time. Moreover, the type of seed to use for pasture establishment, cultivar or ecotype (non-cultivar), is unclear. Ecotype seed sources may not be adapted to repeated defoliations and cultivar seed sources may not survive or realize enhanced agronomic potential when planted outside their area of origin. We evaluated cultivar and ecotype native warm-season grass (big bluestem (*Andropogon gerardii* Vitman), Indiangrass (*Sorghastrum nutans* (L.)), and switchgrass (*Panicum virgatum* L.) persistence, vigor, productivity and quality under two contrasting graze schedules, production-based (grazed in June and July) vs. wildlife-based (grazed in July and September) using MIG. Overall, selected cultivars and ecotypes did not differ in persistence, production or quality under each graze schedule treatment. Total forage availability was greater when the initial graze cycle did not occur until mid-July. However, this resulted in a significant decrease in the quality of available forage (RFQ and crude protein content). Native grass cover was similar under each

graze schedule treatment. Vigor of the dominant native grasses big bluestem and Indiangrass, as measured by etiolated growth, was sustained or increased under each graze schedule relative to non-grazed plants of each species. These results indicate that native warm-season grasses can meet a variety of livestock producer management objectives (quality and quantity) and have capacity for long-term persistence and vigor in pasture systems of the upper Midwest using MIG. The overall lack of a consistent seed type effect suggests that both ecotype and the selected cultivar seed sources are suitable for pasture use in the upper Midwest, but this should be evaluated over a longer time period.

INTRODUCTION

As the sustainable agriculture movement grows, grass-based farmers are increasingly being targeted as the agents responsible for increasing the ecosystem services, or societal benefits, gained from grazing lands (Jensen 2001, Tilman et al. 2002). In the upper Midwest, grass-based farmers have addressed these challenges in part by renewing their interests in native sources of forage, which have the potential to increase the various provisioning, regulating, supporting, and cultural ecosystem services provided by current grazing agroecosystems (Center for Integrated Agricultural Systems 2009). In particular, farmers have expressed interest in incorporating the native warm-season grasses that once dominated the landscape of the region into their existing cool-season grass systems for use as livestock forage (Doll and Jackson 2009). However, if native grasses are to be used as sources of forage in the upper Midwest, management recommendations for when to initiate grazing within a growing season to meet nutritional needs of livestock and maintain stand persistence in the long-term need to be established.

Many species of grassland birds use native warm-season grass stands for habitat during their nesting season, leading to management recommendations that suggest native grasses be protected from ungulate defoliation until after mid-July, or the general end of the grassland bird nesting season (Renfrew and Ribic 2001, Perlut et al. 2006, Perlut et al. 2008). However, these recommendations may not be the best grazing management practices for the long-term productivity and sustainability of the native grasses (Vavra 2005). In addition, these recommendations are not suitable for grass-based livestock producers who must balance livestock forage quantity with forage quality needs throughout the growing season (Perlut et al. 2008). It has been well established that forage quality of warm-season grasses declines as grasses mature (Bruinenberg et al. 2002), If forage quality is a management goal, initial defoliations of native grasses need to occur earlier than mid-July in the upper Midwest (Tracy et al. 2010). Also, the regrowth rate of native grasses declines as the growing season progresses (Gillen and McNew 1987), implying that earlier defoliations could result in greater quantities of available native grass forage over a growing season. Further, production-based grazing recommendations for warm-season grasses urge caution against defoliation late in the growing season because grasses are in the process of replenishing and translocating carbohydrates and nutrients belowground for winter survival and initiation of spring growth in the following season (Mousel et al. 2006, Barnhart 1994). Deferring grazing until the middle of the growing season or later could have detrimental effects on long-term stand persistence (Jackson et al. 2010).

In addition to the question of when to initiate grazing within in a growing season, the type of native grass seed used to establish pastures remains uncertain. Most tallgrass prairie conservation practitioners and managers advocate the use of local ecotype seed (Jones 2003.

McKay et al. 2005), which is adapted to the local environmental conditions of a region (McMillan 1969) and maintains the genetic integrity of local plant populations (Bischoff et al. 2010). However, native grass ecotype seed may not be suited for agronomic applications such as repeated defoliations under MIG, and as a result may decrease in cover and productivity in the long-term. In contrast, cultivar seed types have been human-selected in field trials for enhanced agronomic qualities such as greater forage production (Brink et al. 2010). It was recently observed that cultivar seed sources of certain native warm-season grasses had greater root length, surface area and volume than ecotype seed sources during establishment, suggesting that cultivar seed types could be better suited for resource capture belowground (Klopf and Baer 2011), which would ultimately make them better adapted to defoliation by livestock. However, much of the native warm-season grass cultivar seed originates from areas west of the Mississippi River, where environmental and climate conditions are different than those of the sub-humid upper Midwest. Plant provenance has been found to be correlated with plant performance (McMillan 1969, Casler et al. 2007) such that if plants are moved too far from their area of origin, enhanced physiological traits may not be realized (Wilsey 2010). Within the Prairie Peninsula, results have been equivocal between what Wilsey (2010) termed the "cultivar vigor hypothesis" and the "local adaptation hypothesis", suggesting that more studies are needed to determine if enhanced agronomic traits of cultivar seed types can be realized when planted and defoliated outside their area of origin.

No studies have directly compared the suitability of ecotype and cultivar native warm-season grass seed types for pasture use under ungulate grazing in the upper Midwest. Objectives of the following study focused on evaluating the forage production, quality and

persistence of native grass seed types under two grazing schedules that reflect wildlife-based grazing recommendations against production-based management practices that emphasize a balance between plant regrowth and livestock nutritional needs using MIG. We hypothesized that grazing management practices based on the needs of both the native grasses and livestock would result in (1) greater total available forage yields with higher forage quality (2) greater persistence and vigor of native grass species. It was further hypothesized that cultivar seed would result in equal or greater pasture performance (production, persistence and vigor) than ecotype seed.

METHODS

Study Site

The study was conducted at the Paine Family Farm in Columbus, WI (43.310°N, -89.188°W), a beef cattle farm practicing MIG on ~32 ha of non-native, cool-season upland and lowland grass pastures. Hot/wet summers and cold/dry winters characterize the climate of the region. Average monthly temperatures range between -7 °C to 21°C, with lows occurring in January and highs in July. Total annual rainfall averages ~850 mm, and of this amount, ~65% falls during the main growing months, April through September. Climate data for the study area was recorded at the Arlington Agriculture Research Station (43.310°N, -89.380°W), which is part of the Automated Weather Observation Network (AWON) for the state of Wisconsin. Rainfall totals for each year of the study were 856 mm and 888 mm, respectively (Figure 1A). Of the total rainfall, 60% in 2009 and 85% in 2010 fell between April and September. Annual temperature ranges during the study period averaged between -12°C to 18°C (Figure 1B). The study area is comprised of two soil types,

St. Charles silt loam and Lapeer sandy loam, both classified as mixed, mesic Typic Hapludalfs.

Treatments

In the summer of 2007, 0.8-ha of cool-season grass pasture in the southeastern section of the farm was sprayed with PLATEAU® herbicide to kill existing vegetation. Two warm-season native grass seed mixes, local ecotype (*Ecotype*) and non-local cultivar (*Cultivar*), were seeded in the fall of 2007, into a total of 12 (6 of each seed type), 0.063-ha strips, using a Truax no-till drill (Truax Company, Inc., Minneapolis, MN). Ecotype grass seed mix consisted of the "Medium Soil Amber Waves Prairie Grass Mix" purchased from Prairie Nursery in Westfield, WI, and is labeled as source-identified by the Wisconsin Crop Improvement Association (WCIA), which governs the standards for source-identified native seed produced in the state (Table 1). The cultivars 'Bison' big bluestem, 'Tomahawk' Indiangrass, and 'Sunburst' switchgrass were purchased from Albert Lea Seed House in Albert Lea, MN. Each cultivar was originally a wild accession observed to have preferred agronomic traits such as winter hardiness, leafiness (forage quantity) and/or favorable seed yields and was tested in field trials conducted at Agriculture Research Service (ARS) stations in North and South Dakota (Barker et al. 1990, Haas et al. 1990, Boe and Ross 1998). Selected cultivars were chosen because they are recommended for pasture use in the North Central region (Table 1).

The experiment was set up as a hierarchical (split-plot) design with 4 treatment combinations replicated in 3 blocks. Whole plot factors consisted of two graze schedule treatments (*Early* and *Late*) and were applied to split-plot factors of the two native grass seed types (Figure 2). Early graze schedule treatments were initiated in June of 2009 and 2010,

when the grass canopy reached a height of approximately 45 cm. Late graze schedule treatments were initiated after mid-July, based upon recommendations for the protection of grassland bird nesting habitat. All experimental paddocks received two graze cycles, *Cycle 1* (early June for early graze schedule and mid-July for late graze schedule) and *Cycle 2* (mid-July for early graze schedule and early September for late graze schedule) each growing season and the same graze schedule was applied to each experimental paddock during the entire study. Timing of graze Cycle 2 was based on the quantity of native grass regrowth and assessed by canopy height. Grazing intensity was visually assessed by livestock managers to remove no more than half of the biomass at each cycle. Table 2 includes specific grazing management information.

Experimental paddocks were separated by portable electric fencing while grazing treatments were applied. Prescribed fires were conducted on April 17, 2009 and March 26, 2010 to create uniform growing conditions in each experimental paddock, remove accumulated plant litter, and increase the growing season length as a result of earlier warming of the soil (Knapp et al. 1998). Within each experimental paddock, 1-m^2 grazing exclusion cages were erected to provide undefoliated plants for the spring 2010 etiolated growth experiment. All cages were erected in early spring of 2009 and remained in the same position throughout the study.

Estimating plant cover

To monitor changes in plant community composition, cover of plant species within each experimental paddock was estimated in late May of 2009 and 2010 using the line-point method (Heady et al. 1959). A total of nine, 10-m transects were located in each paddock, a sharpened point was dropped every half meter along each transect, and the first herbaceous

species to intercept the point was recorded for a total of 180 intercepts per experimental paddock. Vegetation cover of individual species was estimated by dividing the number of species intercepts by 180. Species cover was further aggregated into the following functional guilds: native grass, non-native grass, forb and bare ground.

Assaying belowground reserves

To capture the effects of graze schedule treatments on seed type responses belowground, the etiolated growth of the dominant native grasses big bluestem and Indiangrass was measured in the spring of 2010. Etiolated growth, or growth in the absence of light, is a method that has been used since the 1960s (Reece et al. 1997) on a variety of grass species to quantify the amounts of organic reserves that accumulate in storage organs of plants during the previous growing season (Matches 1969). Organic reserve quantities of grasses can be influenced by the timing of defoliations within a growing season (McKendrik and Sharp 1970) and the total amounts stored depend upon the balance between plant photosynthesis, respiration and growth (White 1973). Information concerning how organic reserves are affected by different grazing management systems can provide insights into how these systems may affect native grasses in subsequent growing seasons (Reece et al. 1988), since accumulation of organic reserves is an indication of potential plant vigor (Cuomo et al. 1998).

A total of 3 plants of each species, with similar basal areas, were selected in each experimental paddock in the fall of 2009. Additionally, individual plants of each species were selected in each grazing exclusion cage so comparisons could be made between grazed and ungrazed plants. Selected plants were covered in early April 2010, prior to the emergence of spring growth, with #10 tin cans (438.309 cm^3). All cans were painted white

to reflect heat, and each can was drilled with 6 holes ~ 0.05cm in diameter, to allow air to freely flow between the inside and outside of each can. A groove 8-cm deep was cut around each can as it was being installed, to sever shallow roots and prevent translocation of nutrients to the covered plants from attached rhizomes during the experiment. Etiolated biomass was periodically clipped under each can starting on May 6 with subsequent clippings on May 27, June 8 and June 21. Clipped tillers were counted, dried at 60°C for 48 h and weighed to estimate dry matter content. Etiolated biomass for each plant was summed across all spring 2010 clippings to estimate the total amount produced by each plant.

Estimating forage availability and quality

Accumulation of pre-graze available forage, defined as standing crop biomass above 10 cm, was the response variable chosen to evaluate the productivity of native warm-season grasses under grazing. In 2009 and 2010, available forage estimates were taken before each experimental paddock was grazed. A total of five, 0.25-m^2 quadrats were randomly placed and then clipped in each paddock to a residual height of 10 cm. Clipped biomass was then dried at 60°C for a minimum of 48 h and weighed for dry matter content. For each experimental paddock, there were a total of two pre-graze available forage estimates collected during the growing season, June and July under the early graze schedule and July and September under the late graze schedule. These estimates were then summed to calculate total accumulation of forage that was made available to livestock across the two graze cycles.

The quality of pre-graze available forage was also estimated prior to all grazing cycles under each graze schedule. On account of selective grazing, 3 grab samples consisting of a mix of native grass leaves and plant tops, rather than whole-plant samples, were

collected by hand to more accurately estimate the quality of forage livestock would be likely to consume (Anderson and Matches 1983, George and Obermann 1989). Grab samples were dried at 60°C for 48 h and then ground to pass through a 2-mm mesh screen using a Model 4 Wiley Mill (Thomas Scientific, Swedesboro, NJ). Quality of ground samples was estimated using Near Infrared Reflectance Spectroscopy (NIRS) with a Foss NIR Model 6500 (Foss NIRsystems, Inc., Laurel, MD). Individual quality parameters were derived with the grass equation from the NIRS Forage and Feed Testing Consortium[1]. Relative forage quality (RFQ), an index used to characterize potential voluntary intake and digestibility of forages, and crude protein content (expressed as a percent) were the forage quality parameters chosen to be statistically analyzed and reported.

Statistical Analyses

Linear mixed effects (LME) models were used to test for significance of the fixed effects, graze schedule and seed type, on the response variables available forage, forage quality, vegetation cover and etiolated biomass. All modeling and analyses were run using Tibco Spotfire S-Plus 8.1 software (Insightful Corporation, Seattle, WA). As a consequence of the hierarchal design of the experiment and to avoid spatial pseudoreplication, random effects were nested in order to partition variance for each level of randomization (Crawley, 2002). Sub-sample data was averaged for each experimental paddock and used as the unit for analysis.

For each response variable, a saturated model with an interaction term between the fixed effects was compared to a nested model without an interaction term using a Likelihood Ratio Test (LRT). If the two models were significantly different at $\alpha = 0.05$ significance

[1] (http://nirsconsortium.org/Documents/eqa.pkgs.Feb10.for%20web.pdf)

level, the model with the lower Akaike Information Criterion (AIC) was selected. If models were not significantly different, the more parsimonious model (fewest parameter estimates) was chosen and compared to another nested model with a dropped fixed effect again using LRT. This same procedure was performed until the simplest model that significantly minimized deviance was obtained or until it was determined there were no significant effects of experimental treatments on the various response variables. For models with a significant interaction term, treatment levels with similar treatment means were consecutively collapsed and compared against uncollapsed models using the same LRT procedures described above.

All analyses were separated by study years to minimize the nuisance variability associated with climate (precipitation and growing degree days) between years. Separate LMEs were used to test for differences between treatment means for all response variables. Forage quantity and quality data was analyzed separately at each graze cycle within each year. Vegetation cover was analyzed at the guild level (native grass, non-native grass, forb and bare ground) and those species that averaged > 5% cover were individually analyzed. Total etiolated biomass between grazed and non-grazed plants for each graze schedule was analyzed separately for each species.

RESULTS

Vegetation cover

Cover across all experimental paddocks in each year was dominated by the native grass guild followed by the forb and non-native grass vegetation guilds (Table 3). In 2009, native grass cover in cultivar paddocks averaged 50.4 ± 1.8%, which was significantly higher than cover in ecotype paddocks 48.0 ± 2.7%. In 2010, no effect of seed type was observed

with native grass cover across all paddocks averaging 54.8 ± 1.6%. The cover of bareground was significantly affected by seed type, as ecotype paddocks averaged higher cover of bareground in 2009 (6.1 ± 1.2%) and 2010 (3.4 ± 1.1%) than cultivar paddocks (Table 3). Seed type had no effect on cover of the non-native grass or forb guilds and graze schedule treatments had no effect on vegetation cover of any guilds in either year. Between 2009 and 2010 there were fluctuations in cover for each guild. Across experimental treatments the non-native grass guild decreased in cover by 4.9% and cover of bareground decreased by 2.5%. In contrast, the native grass guild increased in cover by 5.6% across all treatments between years and the forb guild increased by 2.1% (Table 3).

Within each guild, species that averaged > 5% cover were further analyzed to assess treatment effects on cover. Big bluestem, Indiangrass and switchgrass dominated cover in the native grass guild (Table 3). Big bluestem and Indiangrass were co-dominant averaging 19.7 ± 1.0% and 18.2 ± 0.9% across treatments and years. In 2009, Indiangrass cover was significantly higher in cultivar paddocks (18.7 ± 1.6%) than ecotype paddocks (15.3 ± 2.0%). This effect was not observed in 2010, as cover of Indiangrass in ecotype paddocks increased by 3% while cultivar paddocks only increased by 1.9%. Big bluestem cover in 2009 was similar in all paddocks averaging 19.3 ± 1.3% cover. Yet in 2010, big bluestem cover in cultivar paddocks (23.1 ± 1.3%) was significantly higher than cover in ecotype paddocks (17 ± 2.1%), an effect that was largely driven by a 4.6% cover increase in cultivar paddocks managed with the early graze schedule (Table 3). Cover of big bluestem and Indiangrass was not significantly affected by graze schedule treatments in either year. Switchgrass cover was unaffected by graze and seed treatments, averaging 9.4 ± 0.5% cover in 2009 and 11.5 ± 1.5% cover in 2010 across all treatments.

Quackgrass (*Elytrigia repens* (L.)), a non-native, cool-season perennial and rhizomatous grass dominated the non-native grass guild (Table 3). Quackgrass prior to maturity is considered high quality forage, but can compete with native grasses for light, space and nutrients early in the growing season (Brenly-Bultemeier et al. 2005). Cover of quackgrass was not affected by graze schedule or native grass seed type treatments in either year, averaging 20.5 ± 2.9% cover in 2009 and 15.2 ± 2.0% cover in 2010 across all paddocks.

The bulk of cover within the forb guild was Canada thistle (*Cirsium arvense* (L.) Scop.) and dandelion (*Taraxacum officinale* F.H. Wigg.) (Table 3). Both species are perennial, but differ in their growth habits, phenologies, and livestock palatability (Bergen et al. 1990, DeBruijn et al. 2010). They diverged in their responses to graze schedule treatments in 2010. Cover of Canada thistle was significantly greater in paddocks managed with the early graze schedule (14.1 ± 2.7%) than paddocks managed with the late graze schedule (8.4 ± 0.8%). In contrast, dandelion cover averaged 6.4 ± 1.5% in paddocks managed with the late graze schedule, which is 3.4% greater than paddocks managed with the early graze schedule. Dandelion cover across treatments decreased in cover by 3.5% between 2009 and 2010, while cover of Canada thistle was either maintained under the late graze schedule or increased under the early graze schedule (Table 3).

Etiolated biomass

The etiolated biomass estimates of non-grazed big bluestem and Indiangrass plants provide baseline data to compare with grazed plants of each species in order to test the effects of each graze schedule on accumulation of etiolated biomass. Across species, the early graze schedule had no significant effects on total etiolated biomass. Big bluestem

cultivar plants maintained higher etiolated biomass than ecotype plants when defoliated and these amounts were similar to quantities accumulated by non-grazed plants (Figure 3A). Likewise, the quantity of etiolated biomass accumulated by grazed plants of Indiangrass was similar to that of non-grazed plants and did not differ between seed types (Figure 3C). In contrast, both big bluestem and Indiangrass etiolated biomass quantities were significantly affected by the late graze schedule treatment. For big bluestem, a significant interaction was observed as ecotype plant etiolated biomass was significantly increased by grazing, while big bluestem cultivar plants maintained similar quantities of etiolated biomass as non-grazed plants (Figure 3B). Indiangrass etiolated biomass of plants subject to the late graze schedule was significantly increased across seed types (Figure 3D).

Available forage

Native grass forage availability was significantly affected by the timing of grazing under each graze schedule. In 2009 and 2010, total available forage was 42% and 27% greater when experimental paddocks were managed with the late graze schedule treatment (Figure 4C and F). The total amount of available forage accumulated under each graze schedule was largely influenced by the amounts of available forage at graze Cycle 1 in each year, as the difference between treatment means was largest at this graze cycle (Figure 4A and D). Available forage at Cycle 1 under the early graze schedule across years and seed types averaged 2.4 ±0.1 Mg ha $^{-1}$ and 8.6 ± 0.4 Mg ha^{-1} under the late graze schedule. Of note is the emergence of a significant graze schedule x seed type interaction between amounts of available forage at graze Cycle 1 in 2010 (Figure 4D). Cultivar plots had accumulated significantly more available forage than ecotype plots under the late graze

schedule, an interaction that was also significant for quantities of total available forage in the same year (Figure 4F).

Graze Cycle 2 represents the amount of forage standing at the end of graze Cycle 1 and any regrowth that occurred between cycles. In 2009, available forage at graze Cycle 2 was similar under each schedule averaging 5.1 ± 0.3 Mg ha $^{-1}$ (Figure 4B). However, this pattern was not repeated in 2010. Paddocks managed with the late graze schedule accumulated 2.4 ± 0.1 Mg ha ¯1 of available forage, which was significantly less than the 5.5 ± 0.2 Mg ha ¯1 of available forage that accumulated in early grazed paddocks at graze Cycle 2 in 2010 (Figure 4E).

Forage quality

Livestock have varying nutritional requirements based on factors such as class of livestock (beef vs. dairy), age and gender. To qualitatively assess forage quality in this study, forage values with a RFQ < 110 and a crude protein content <11% were generally considered below minimum nutritional requirements for most livestock classes across genders and age (Rankins 2001, Undersander 2003). In our study grazing at different times within a growing season had significant effects on native grass forage quality in both 2009 and 2010 (Table 4). Relative forage quality values averaged 147.3 ±2.9 in 2009 and 132.8 ± 0.8 in 2010 across seed types under the early graze schedule at graze Cycle 1. These values were significantly higher than those for the late graze schedule at Cycle 1, as RFQ values across seed types and years averaged 99.7 ± 2.6. There was a significant but inconsistent effect of seed type on crude protein content under each graze schedule at Cycle 1 between years that was not observed for RFQ values. However, this effect did not scale up to have biological significance, as seed type treatment means under each graze schedule only varied

by approximately 1%. Crude protein content at graze Cycle 1 under the early graze schedule averaged 15.4 ± 0.2% in 2009 and 12.4 ± 0.3% in 2010 across seed types. Crude protein content under the late graze schedule ranged between 6.8 - 8.6% at Cycle 1 across seed types and years.

Relative forage quality and crude protein content at graze Cycle 2 was inconsistent between graze schedules and years (Table 4). In 2009, RFQ values averaged 109.3 ± 2.2 and crude protein content 8.0 ± 0.2% under the early graze schedule across seed types. These values were significantly greater than the values observed under the late graze schedule, RFQ of 82.0 ± 3.3 and crude protein content of 5.4 ± 0.3%. This pattern was not observed in 2010 for graze Cycle 2. Late graze schedule forage quality parameters were greater than those measured for the early graze schedule and were above minimum suggested requirements across seed types (RFQ of 116.7 ± 1.6 and crude protein content of 11.5 ± 0.5%). Early graze schedule RFQ values in 2010 across seed types averaged 111.2 ± 1.7, but crude protein content was below minimum requirements averaging only 9.7 ± 0.2% (Table 4).

DISCUSSION

Native warm-season grasses maintain cover under grazing

Results addressing the persistence of native warm-season grasses under grazing in the Prairie Peninsula have been ambiguous, across a range of defoliation schedules and species assemblages. In the current study, although there were slight fluctuations in cover of the dominant native grass species between years, overall native warm-season grasses maintained cover across MIG schedules that differed in the seasonality of grazing cycles. These results support two studies in Missouri that observed no decreases in cover of big bluestem or

switchgrass monocultures, across clipping regimens that staggered initial harvest dates of various clipping intensities and frequencies (Anderson and Matches 1983, Forwood and Magai 1992). In contrast, a recent study conducted on a bison farm in south Central Wisconsin observed native warm-season grass species annually decreased in cover when repeatedly grazed during the summer months (Jackson et al. 2010).

The persistence of native warm-season grasses in the Prairie Peninsula under grazing has been attributed to a combination of propitious environmental and grazing management conditions. It has been suggested that favorable amounts of precipitation during the growing season (Gillen et al. 1991), such as those that generally occur in the Prairie Peninsula (Anderson and Matches 1983), combined with defoliations that are low in intensity (Forwood and Magai 1992, Trocsanyi et al. 2009), and rest periods that follow native grass growth rates (Gillen and McNew 1987, Mousel et al. 2003) can mitigate against potential injurious effects associated with defoliation. In this study the above listed conditions were met, as growing season precipitation was average to above average each year, defoliation intensity at each graze cycle was closely monitored to maintain half of the original canopy and rest period lengths were shorter in the first half of the growing season and longer during the second half. In the Wisconsin bison grazing study growing season precipitation was also favorable. However, the native warm-season grass paddocks were grazed frequently and intensively (low residual height) within a 3 month grazing period over the eight-year study (Jackson et al. 2010), indicating that the decreases in native grass cover were likely a result of inappropriate management. These results combined with those of the current study indicate native warm-season grass persistence, as assessed by cover, in pasture systems of the upper Midwest is largely a function of defoliation intensity and frequency and not necessarily the

timing of defoliations. Thus, native grasses may be suitable for pasture use in the region if grazing system management variables are designed to meet the regrowth needs of the grasses.

It is important to note that the Wisconsin bison grazing study could also be distinguished from our study and the two Missouri studies by the use of annual prescribed burns. Prescribed burns have been shown to promote the persistence of native warm-season grasses by increasing the grass "bud bank", or the population of belowground meristems that reside along grass rhizomes and other belowground organs (Benson et al. 2004). Further, grazing has been shown to increase stem densities of native warm-season grasses, by increasing the rate grass buds evolve into grass tillers (Dalgleish and Hartnett 2009). No prescribed burns were applied throughout the eight-year study under Jackson et al. (2010), while annual prescribed burns were applied in this study and the two Missouri studies. It is therefore important to compare studies that have similar prescribed burn regimens and grazing management systems, as fire and grazing can interact to maintain native warm-season grass cover in pasture systems.

Vigor of native warm-season grasses maintained under grazing

Assessing how plants are responding to disturbances aboveground may not be representative of responses occurring belowground. In this study, to better understand whole plant responses of the dominant native grasses big bluestem and Indiangrass to seasonal defoliations, the total quantity of etiolated growth that accumulated in spring was measured. Etiolated growth measurement quantifies amounts of excess organic reserves stored in the previous growing season and is an indicator of potential plant vigor (White 1973). Cuomo et al. (1998) observed that after a single season of clipping treatments total etiolated biomass of

big bluestem plants clipped 1 to 3 times in a growing season was reduced relative to plants that were not defoliated, while Indiangrass etiolated biomass was not significantly affected by grazing frequency treatments. In this study, no decreases in etiolated biomass yields were observed under either graze schedule for either species relative to ungrazed plants, suggesting that native grasses were tolerant to the growing season disturbances tested in this study.

It has been well established that grass plants will mobilize organic reserves for regrowth when the products from photosynthesis are unable to meet demands for tissue regrowth and respiration. Yet, White (1973) noted in a review on carbohydrate reserves of grasses that studies conducted on various cool-season grass species found that plant tissues remaining after defoliation, which are photosynthetically active, contribute carbon assimilates for regrowth of plant tissues. These results were further supported by Richards and Caldwell (1985) who observed that between 89-99% of carbon assimilates for regrowth were supplied from current photosynthesis. Grazing intensity in this study was monitored to ensure that no more than half of the existing native grass canopy at each grazing cycle was removed. Although the photosynthetic capacity of remaining plant tissues was not measured, it is likely that this tissue was able to contribute carbon assimilates for regrowth, thereby decreasing the need to mobilize organic reserves from plant storage organs for regrowth of aboveground plant tissue.

Additionally, it has been observed that uneven grazing (not all tillers defoliated) affects how plants mobilize carbon assimilates for regrowth (White 1973). Stout and Brooke (1985) observed that differences in total non-structural carbohydrate concentrations between clipped and unclipped pinegrass (*Calamagrostis rubescens* Buckley) plants with intact

rhizome connections were less than differences between clipped and unclipped plants with severed rhizome connections. The authors went on to conclude that ungrazed tillers can aid in sustaining the general vigor of pinegrass stands. These same conclusions were supported by a study conducted on tall fescue (*Festuca arundinacea* Schreb.), in which it was observed that total etiolated biomass was reduced between 76 to 84% in plants where all tillers were defoliated relative to plants where at least 10 to 30% of plant tillers remained intact (Matches 1966). Although this study did not measure the extent to which ungrazed tillers remained after each graze cycle, an earlier study on tiller defoliation patterns in a tallgrass prairie restoration found that no more than 74% of big bluestem or little bluestem tillers were defoliated during any single graze cycle under varying short duration grazing regimens (Gillen et al. 1990), suggesting that intact tillers of native grasses incidentally play a role in sustaining plant vigor. In this study, maintenance of organic reserves in grazed plants relative to ungrazed plants suggests that the above two mechanisms likely resulted in plants needing to mobilize minimal organic reserves for regrowth. These results indicate native warm-season grasses can maintain vigor across a variety of defoliation timings in the short-term and suggest grazing frequency and intensity likely control the persistence of native grasses in pastures of the upper Midwest.

A somewhat surprising result to come from this study was the increase in total etiolated biomass of grazed ecotype and selected Indiangrass cultivar plants relative to non-grazed plants under the late graze schedule. Hassan and Krueger (1980) found greater to equal amounts of organic reserves accumulated in plants of perennial ryegrass (*Lolium perenne* L.) that were grazed compared to those that were protected from grazing, concluding that protection from defoliation did not benefit perennial ryegrass. While the authors did not

provide a mechanistic explanation for why organic reserve levels were either maintained or increased under grazing, they did suggest that the lack of tissue removal of protected plants would eventually create sub-optimal growing conditions, yet they did not elaborate on what these conditions might be.

The quantity of organic reserves that perennial grasses store is directly related to photosynthesis, such that any time the rate of photosynthesis is altered the total accumulation of organic reserves is affected (Owensby et al. 1970). Photosynthesis of non-defoliated native grasses can be affected by two mechanisms – canopy closure (Schimel et al. 1991, Owensby et al. 2006) and leaf maturity (Gold and Caldwell 1990, Owensby et al. 2006), both of which decrease the rate of photosynthesis on either a per tiller or per plant basis within a growing season. In contrast, defoliation of grasses has been observed to increase the per-unit-plant rate of photosynthesis (Gold and Caldwell 1990, Wallace 1990, Knapp et al. 1999, Owensby et al. 2006). Removal of plant tissue lessens the constraints associated with canopy closure and plant maturity by decreasing light limitations, such as self-shading (Schimel et al. 1991), and increasing the amount of new plant tissue, which has higher photosynthetic capacity compared to mature or older tissues (Gold and Caldwell 1990, Owensby et al. 2006). In this study, the mid-summer defoliation under the late graze schedule likely extended the time and increased the rate that native grasses were photosynthesizing, which likely increased the capacity for excess organic reserve storage relative to non-defoliated plants that became constrained by light and tissue age limitations later in the growing season. These results have significant agronomic and wildlife conservation implications as they suggest that native warm-season grass stands may be enhanced by mid-summer livestock defoliations in the long-term.

Native warm-season grasses provide for a variety of livestock producer needs

In the Prairie Peninsula there have been few studies focused on how the timing of graze cycles with MIG affects the quality and productivity of native warm-season grasses. Results from this study suggest that native warm-season grasses are able to meet an assortment of livestock producer management objectives in the upper Midwest, providing forage quality and quantities that span a range suitable for a variety of livestock classes. The total quantities of native grass available forage that accumulated under each graze schedule in this study were largely controlled by when defoliations occurred within the growing season. It was originally hypothesized that greater amounts of native grass forage would be available across the growing season when initial defoliations occurred earlier in the growing season, but we found the opposite pattern. Other studies in the Prairie Peninsula, across various environmental gradients and grazing frequencies and intensities, have also observed that delaying initial defoliations resulted in greater cumulative yields of native grass forage (Anderson and Matches 1983, George and Obermann 1989). The greater accumulation of forage when initial graze cycles are delayed has been attributed to the rapid growth of native warm-season grasses during early summer (George and Obermann 1989) and the associated accumulation of plant tissue (leaves and stems) with advancing plant maturity (Moore et al. 1991). A study conducted on switchgrass monocultures in Iowa observed that ~ 70% more forage was available when initial clippings were delayed by 4 weeks, and across clippings ~17% more total forage accumulated (George and Obermann 1989). This same approximate greater total forage yield was also observed in a switchgrass clipping study in Missouri, which examined yields across 5 first harvest dates and two clipping intensities (Anderson and Matches 1983). In this study, native grass yield trends were similar to previous studies,

suggesting that native warm-season grass productivity is mainly controlled by the timing of the initial defoliation within the growing season in the upper Midwest.

The quality of native grass forage in this study was also associated with the timing of defoliations, since the digestibility, energy, and protein content of native grasses declined as the initial graze cycle was delayed. These results were expected since it has been well established that forage quality declines with advancing plant maturity (Bruinenberg et al. 2002, Newman et al. 2009). These results also confirm the findings of earlier warm-season grass grazing studies that observed the digestibility and/or protein contents of switchgrass and big bluestem declined as initial defoliations were delayed early in the growing season (George and Obermann 1989, Forwood and Magai 1992). Yet, the magnitude of differences in native warm-season grass forage quality in this study shows that native grasses can meet nutritional needs for a range of dairy and beef livestock classes (Rankins 2001, Undersander 2003). However, this depends on when they are initially grazed, since forage quality at several graze cycles in our study was below minimum requirements for all livestock classes. Ultimately, the forage quantity and quality results from this study offer evidence that native warm-season grasses provide sustainable sources of forage and have potential to meet the nutritional needs for a variety of livestock classes. This all suggests that native warm-season grasses have significant capacity to be incorporated as pasture species into the MIG systems of the upper Midwest.

It is important to note that beyond forage quantity and quality, the timing of defoliations can alter the interspecific competition between pasture plant species, which can have effects on pasture productivity and quality in the long-term (Edwards et al. 2000, DeBruijn et al. 2010). In this study it was observed that Canada thistle cover was greater in

experimental paddocks managed with the early graze schedule after a single season of grazing. These findings are important since Canada thistle has low palatability to livestock and can decrease the productivity of native pastures by forming dense monocultures and crowding out native species (Grekel and Bork 2004). In a study of cool-season grass pastures in Alberta, Canada, it was observed that the timing of initial defoliations significantly affected the cover of Canada thistle in pastures, as experimental paddocks defoliated earlier in the growing season had greater Canada thistle cover (De Bruijn et al. 2010). These results support those of this study and demonstrate how management decisions have larger agroecological implications, such as altering competitive abilities between native and non-native pasture species, which could have negative impacts on the persistence and vigor of native pasture species in the long-term.

Ecotype and selected cultivars suitable for pasture use in the Upper Midwest

Grass cultivars to be used for agronomic purposes are generally selected for traits that are associated with the vigor of the plant, such as greater yields of biomass or long-term persistence (Casler 2005, Wilsey 2010). However, results of the enhanced vigor of cultivated seed types when planted in areas outside of their provenance have been equivocal in the Prairie Peninsula (Gustafson et al. 2001, 2004, Williams et al. 2004, Wilsey 2010). For instance, a study conducted in Iowa observed that populations of switchgrass seed collected from remnant prairie sites across the state produced greater numbers of shoots per plant than cultivars of the same species that originated from Nebraska and South Dakota (Williams et al. 2004). Yet, Wilsey (2010) observed no differences in aboveground biomass estimates of native warm-season grasses between locally collected seed from sources in Iowa and cultivated seed with provenances outside of Iowa, when grown in either monocultures or

mixtures of species and seed types. Likewise, a study in Belgium comparing cultivated varieties of perennial ryegrass (*Lolium perenne* L.*)* to existing ecotypes collected from local pastures observed no differences in forage productivity or quality under varying clipping schedules (Limbourg and Lecomte 1997).

The effect of seed type treatments in this study on the response variables measured was minimal and inconsistent. Recent studies have observed that non-local cultivars of native warm-season grasses can have larger basal areas (Wilsey 2010), enhanced photosynthetic rates (Lambert et al. 2011), and/or greater total root biomass (Klopf and Baer 2011) than ecotypes of the same species. These results together suggest that cultivar seed sources should be better adapted to grazing and provide some support for the cover results of this study. Yet, overall ecotype and cultivar experimental paddocks had similar productivity within each graze schedule in our study, which would indicate that neither seed type was better suited for grazing. It was suggested by Wilsey (2010) that the lack of enhanced performance of cultivars over ecotypes suggests that human selected traits may not be realized when seed is propagated outside its area of origin, ascribed to the stress associated with having to adapt to new environmental (soil and climate) conditions. Local-cultivar and non-local ecotype seed sources were not included in our study, making it impossible to detect whether the general lack and inconsistencies in seed type effects was due to a weakening of cultivar performance, as a result of being poorly adapted to local environmental conditions. Further, there are many other native warm-season grass cultivars that could have been used in this study, so it remains unclear if results can be generalized across cultivars or if they are specific to the selected cultivars used in our study.

It addition, it has been suggested that study periods are often too short to test for local adaptation differences between plant populations (Bischoff et al. 2010). Extreme and irregular climatic events often drive local adaptation (Lesica and Allendorf 1999). These events, such as floods or early/late frosts do not often occur within the time frame of many scientific experiments (Bischoff et al. 2006). In a study on California oat grass (*Danthonia californica* Bol.), a grass species native to coastal California prairies, it was initially observed that non-local populations had greater survival across experimental treatments (Buisson et al. 2006). However, after only 1.5 years, survival rates of non-local populations at one study site decreased in number below those of local populations, prompting the authors to emphasize the use of caution when interpreting local adaptation results from short-term studies. In the current study, only two field seasons of data were collected and growing season conditions were favorable in both years, with no extreme climatic events occurring. Thus, ecotype vs. cultivar pasture performance conclusions from this study may be somewhat inconclusive in the short-term.

Beyond the agronomic implications of using native warm-season grass ecotypes or cultivars, there are other ecological implications and social constraints associated with their use. Non-local seed populations, such as the cultivars used in our study, create opportunity for poorly adapted genetic material to “pollute” local plant populations (ecotypes) through hybridization, which can result in succeeding populations of decreased fitness, a process known as outbreeding depression (Lesica and Allendorf 1999, McKay et al. 2005). Additionally, in plant populations that overlap in flowering periods, such as the native warm-season grass ecotypes and cultivars used in this study, the potential for hybridization and outbreeding depression is increased if populations are proximate to each other (Selbo and

Snow 2005). These ecological consequences are further exacerbated by differences in the cost and availability associated with each seed type. Cultivars in general are less expensive and easier to acquire than ecotype seed (Houseal and Smith 2000, McKay et al. 2005), which can greatly influence the choice of seed used to establish native grass plantings (Gustafson et al. 2005, Selbo and Snow 2005). As a result, the choice of seed to use when establishing native grass pastures is complicated by interactions that occur between agronomic, ecological and social factors.

Conclusion

Increased awareness of the ecological benefits associated with native warm-season grasses has renewed grass-based farmer interest in the capacity for native grasses to be incorporated into grazing systems for use as forage in the upper Midwest. Yet, native grasses remain largely absent across the agricultural landscapes of the region, in part due to the lack of technical information associated with their establishment and management. The goal of our study was to evaluate the persistence, vigor, productivity and quality of native warm-season grass ecotypes and selected cultivars under managed grazing schedules that reflected wildlife-based and production-based objectives.

We found that across seed types native grasses persisted and maintained vigor under each graze schedule, indicating that native grass tolerance to defoliation is likely controlled by grazing management variables other than defoliation timing, such as grazing frequency and intensity. Conversely, we observed that native warm-season grass productivity and quality was directly influenced by the timing of the first defoliation under each graze schedule. Together these results demonstrate that the suitability of native warm-season grasses for pasture use in the upper Midwest is ultimately controlled by the grazing

management system. While our study provides desired technical information associated with grazing native warm-season grasses, it is important to acknowledge that their widespread use will also depend on how this technical knowledge is disseminated and perceived by grass-based farmers. Overall, our project demonstrates that native warm-season grasses can be used as forage if properly managed in the grazing systems of the upper Midwest, which has the capacity to increase the ecosystem services offered by grazing lands in the region

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Table 1. Ecotype and cultivar seed mixes, provenance, and USDA hardiness zones.

Seed mix	Species - Common name/*Scientific name*	City/County, State	Lat, Long	USDA Hardiness Zone[1]
Local Ecotype	Big bluestem/*Andropogon gerardii*	Marquette County, WI	43.865 N, -89.322 W	4
	Indiangrass/*Sorghastrum nutans*	Marquette County, WI	43.865 N, -89.322 W	4
		Waushara County, WI	44.131 N, -89.208 W	4
	Switchgrass/*Panicum virgatum*	Marquette County, WI	43.865 N, -89.322 W	4
	Little bluestem/*Schizachyrium scoparium*	Marquette County, WI	43.865 N, -89.322 W	4
	Sideoats grama/*Bouteloua curtipendula*	Marquette County, WI	43.865 N, -89.322 W	4
	Canada wild rye/*Elymus canadensis*	Rock County, WI	42.625 N, -89.017 W	4
Cultivar	'Bison' Big bluestem	Prince, ND	47.084 N, -100.942 W	4
	'Tomahawk' Indiangrass[2]	Ludden, ND	46.008 N, -98.125 W	4
		Britton, SD	45.791 N, -97.750 W	4
		Hecla, SD	45.883 N, -98.152 W	4
	'Sunburst' Switchgrass	Union County, SD	42.862 N, -96.706 W	4

1 – www.usna.usda.gov/Hardzone/ushzmap.html

2 – 'Tomahawk' Indiangrass composite of 3 wild accessions

Table 2. Graze schedule treatment information.

Year	Graze schedule	Graze cycle	Month/Day grazed	Growing Degree Days	AUD ha^{-1}	Avg paddock rotation (hours)	Rest period between graze cycles (days)
2009	Early	1	06/08	748	70	12	45
		2	07/22	1918	76	12	
	Late	1	07/18	1832	1024	16	61
		2	09/18	3286	84	12	
2010	Early	1	06/09	1048	109	24	40
		2	07/20	2263	99	20	
	Late	1	07/14	2067	117	24	57
		2	09/10	3731	79	12	

Table 3. 2009 and 2010 vegetation cover (% Cov) by guild and individual species with cover > 1%. Treatment means ± 1 s.e. of mean (n=3) with different letters within rows are significantly different at α = 0.05. ***** Species with cover < 1%.

			2009							
			Early				Late			
Vegetation Guild	Species		Ecotype		Cultivar		Ecotype		Cultivar	
	Common name	Scientific name	% Cov	± 1 s.e.	% Cov	± 1 s.e.	% Cov	± 1 s.e.	% Cov	± 1 s.e.
Native C4 grass			51.3[a]	4.9	50.7[b]	3.6	44.9[a]	1.3	50.2[b]	1.8
	Big bluestem	*Andropogon gerardii* Vitman	19.1	2.2	19.1	2.6	15.9	3.4	23.1	1.8
	Indiangrass	*Sorghastrum nutans* (L.) Nash	17.6[a]	3.7	20.7[b]	2.8	13.0[a]	0.4	16.7[b]	0.6
	Little bluestem	*Schizachyrium scoparium* (Michx.) Nash	5.2	1.9	0.6	0.3	8.1	1.3	0.2	0.2
	Switchgrass	*Panicum virgatum* L.	9.3	0.7	10.4	1.0	7.8	1.6	10.0	0.6
Non-native grass			20.9	3.6	18.9	10.0	24.6	3.8	21.5	5.5
	Orchardgrass	*Dactylis glomerata* L.	1.1	0.8	0.2	0.2	0.0	0.0	0.4	0.4
	Quackgrass	*Elymus repens* (L.) Gould	19.6	4.5	18.2	10.4	24.4	3.8	20.0	5.8
Forbs			21.9	5.6	26.5	6.7	23.9	3.3	25.0	4.8
	Canada goldenrod	*Solidago canadensis* L.	1.3	0.8	0.4	0.4	0.9	0.7	1.9	1.0
	Canada thistle	*Cirsuim arvense* (L.) Scop.	8.9	3.6	10.4	2.4	7.0	1.6	6.7	3.0
	Common ragweed	*Ambrosia artemisiifolia* L.	0.0	0.0	1.1	0.6	0.7	0.4	0.0	0.0
	Curly dock	*Rumex crispus* L.	0.6	0.3	2.4	1.3	0.4	0.2	1.5	0.7
	Dandelion	*Taraxacum officinale* F.H. Wigg.	7.0	3.7	6.1	2.0	9.8	3.5	10.0	4.7
	Horseweed	*Conyza canadensis* (L.) Cronquist	1.9	1.1	2.4	1.4	3.7	3.1	2.4	1.3
	White campion/cockle	*Silene latifolia* Poir.	0.7	0.4	1.9	0.8	0.2	0.2	0.4	0.4
Bareground			5.7[a]	1.9	3.5[b]	1.9	6.5[a]	2.0	3.3[b]	1.2

***Native C4 grass**: Side oats grama (*Bouteloua curtipendula* (Michx.)),

***Non-native grasses**: Foxtail spp. (*Setaria* spp.), Kentucky bluegrass (*Poa pratensis* L.), Reed canarygrass (*Phalaris arundinacea* L.), Smoothbrome (*Bromus inermis* Leyss.)

***Forbs**: Bull thistle (*Cirsuim vulgare* (Savi) Ten.), Alfalfa spp. (*Medicago* spp.), Common burdock (*Arctium minus* Bernh.), Mouse-ear chickweed (*Cerastium fontanum* Baumg.), Sow thistle (*Sonchus oleracues* L.), Yellow conflower (*Ratibida pinnata* (Vent.)), Clover spp. (*Trifolium* spp.)

Table 3 cont'd.

			2010							
			Early				Late			
Vegetation Guild	Species		Ecotype		Cultivar		Ecotype		Cultivar	
	Common name	Scientific name	% Cov	± 1 s.e.	% Cov	± 1 s.e.	% Cov	± 1 s.e.	% Cov	± 1 s.e.
Native C4 grass			53.5	4.5	55.7	2.7	57.0	2.4	53.0	4.1
	Big bluestem	*Andropogon gerardii* Vitman	18.3[a]	3.3	23.7[b]	2.5	15.7[a]	3.0	22.6[b]	1.3
	Indiangrass	*Sorghastrum nutans* (L.) Nash	17.8	2.6	21.5	2.5	18.5	1.5	19.8	2.3
	Little bluestem	*Schizachyrium scoparium* (Michx.) Nash	6.9	1.2	0.0	0.0	8.0	0.5	0.4	0.2
	Switchgrass	*Panicum virgatum* L.	10.6	4.7	10.6	1.0	14.8	2.9	10.2	3.2
Non-native grass			15.6	3.4	13.5	5.6	16.5	1.6	20.4	6.0
	Quackgrass	*Elymus repens* (L.) Gould	14.6	3.5	12.2	5.9	15.6	1.6	18.3	5.5
Forbs			28.5	5.1	29.3	4.4	22.4	1.5	25.6	3.3
	Birdsfoot trefoil	*Lotus corniculatus* L.	1.1	0.6	0.0	0.0	0.4	0.4	0.2	0.2
	Canada goldenrod	*Solidago canadensis* L.	2.6	1.5	1.3	0.7	2.6	1.4	3.9	2.2
	Canada thistle	*Cirsuim arvense* (L.) Scop.	12.2[a]	2.0	15.9[a]	5.5	7.8[b]	0.6	8.9[b]	1.6
	Clover spp.	*Trifolium* spp.	5.7	3.6	3.0	1.4	0.9	0.4	3.5	2.5
	Dandelion	*Taraxacum officinale* F.H. Wigg.	2.8[a]	0.3	3.1[a]	0.7	6.9[b]	2.0	6.0[b]	2.6
	Fleabane spp.	*Erigeron* spp.	0.9	0.7	3.3	2.0	0.0	0.0	0.7	0.4
Bareground			2.4[a]	0.7	1.5[b]	0.5	4.4[a]	2.1	0.9[b]	0.2

*__Non-native grasses__: Orchardgrass (*Dactylis glomerata* L.), crabgrass spp. (*Digitaria* spp.), Foxtail spp. (*Setaria* spp.), Kentucky bluegrass (*Poa pratensis* L.), Reed canarygrass (*Phalaris arundinacea* L.)

*__Forbs__: common ragweed (*Ambrosia artemisiifolia* L.), horseweed (*Conyza canadensis* (L.) Cronquist), white cockle/campion (*Silene latifolia* Poir.), curly dock (*Rumex crispus* L.), alfalfa spp. (*Medicago* spp.), black eyed Susan (*Rudebekia hirta* L.), common plantain (*Plantago major* L.), bull thistle (*Cirsuim vulgare* (Savi) Ten.), common burdock (*Arctium minus* Bernh.), mouse-ear chickweed (*Cerastium fontanum* Baumg.), purple coneflower (*Echinacea purpurea* (L.) Moench.), yellow coneflower (*Ratibida pinnata* (Vent.) Barnhart), Sow thistle (*Sonchus oleracues* L.)

Table 4. Relative forage quality (RFQ) and crude protein content (% CP) for 2009 and 2010. Treatment means ± 1 s.e. of mean (n=3) with different letters within columns separated by year, graze cycle and forage quality parameter are significantly different at $\alpha = 0.05$. Cycle 1 defoliations under the early graze schedule occurred in early June and under the late graze schedule in mid-July, and Cycle 2 defoliations occurred in mid-July for the early graze schedule and in mid-September under the late graze schedule in each year.

Year	Graze cycle	Graze schedule	Seed type	RFQ ± 1 s.e.	% CP ± 1 s.e.
2009	Cycle 1	Early	Ecotype	147.1 ±5.0[a]	15.1 ±0.1[a]
			Cultivar	147.4 ±4.2[a]	15.7 ±0.2[b]
		Late	Ecotype	100.7 ±1.8[b]	7.9 ±0.2[c]
			Cultivar	97.0 ±0.6[b]	6.8 ±0.2[d]
	Cycle 2	Early	Ecotype	112.7 ±1.1[a]	8.4 ±0.1[a]
			Cultivar	105.8 ±3.3[a]	7.5 ±0.2[a]
		Late	Ecotype	82.9 ±6.4[b]	5.3 ±0.5[b]
			Cultivar	81.0 ±3.6[b]	5.4 ±0.4[b]
2010	Cycle 1	Early	Ecotype	132.8 ±1.3[a]	11.9 ±0.3[a]
			Cultivar	132.7 ±1.2[a]	12.9 ±0.3[b]
		Late	Ecotype	104.6 ±8.4[b]	8.8 ±1.3[c]
			Cultivar	96.6 ±7.5[b]	7.8 ±1.3[c]
	Cycle 2	Early	Ecotype	110.0 ±3.3[a]	9.3 ±0.3[a]
			Cultivar	112.4 ±1.5[a]	10.0 ±0.2[a]
		Late	Ecotype	115.6 ±2.9[b]	11.4 ±0.9[b]
			Cultivar	117.7 ±1.9[b]	11.6 ±0.7[b]

Figure 1. Monthly precipitation totals (A) and average monthly temperatures (B) for 2009 and 2010. Data was recorded at the Arlington Agriculture Research Station in Arlington, WI.

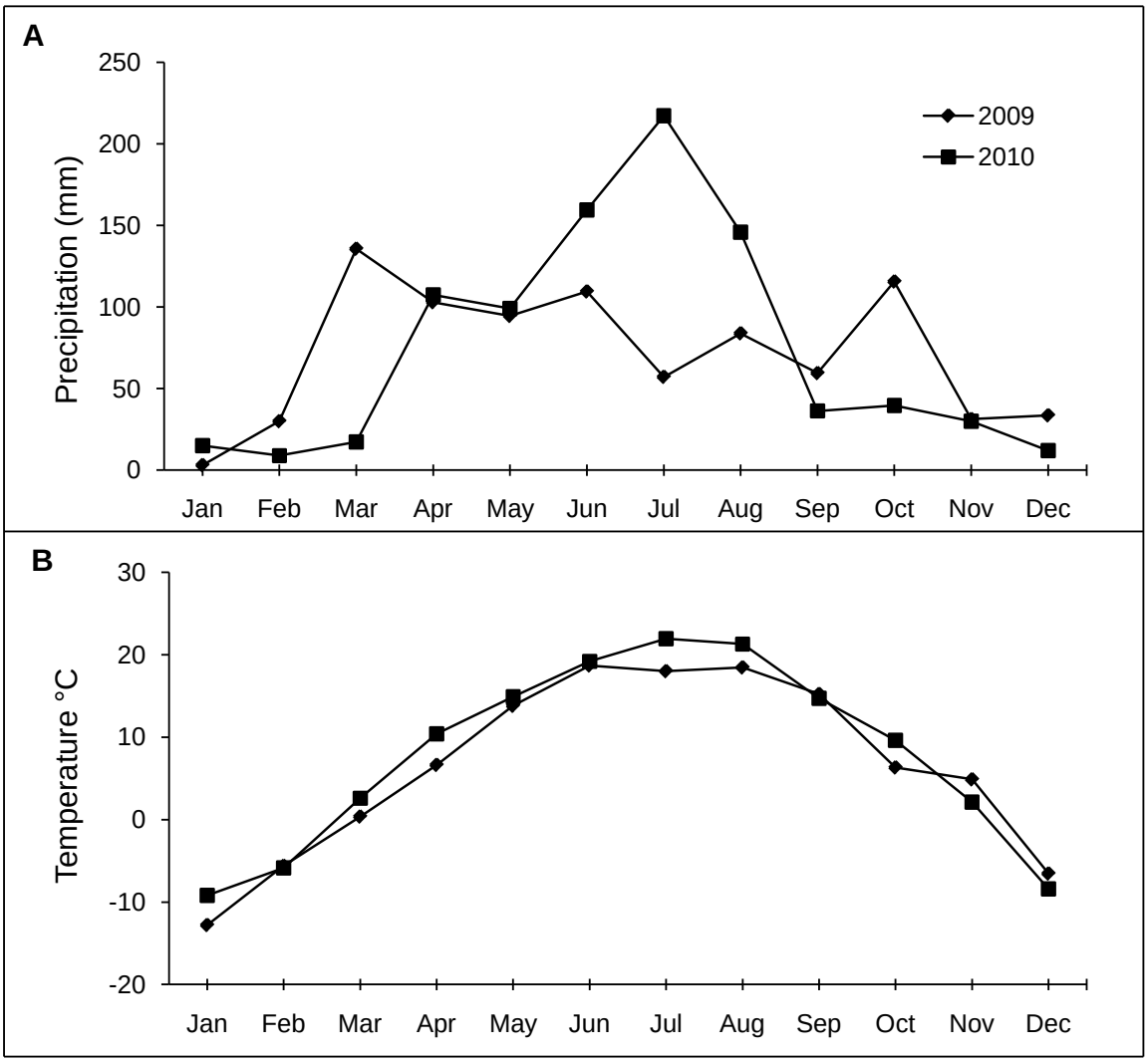

Figure 2. Hierarchical layout of experimental paddocks. Graze schedule treatments (Early and Late) were randomized within each replicate and seed type treatments (Ecotype and Cultivar) were randomized within each graze schedule within each replicate.

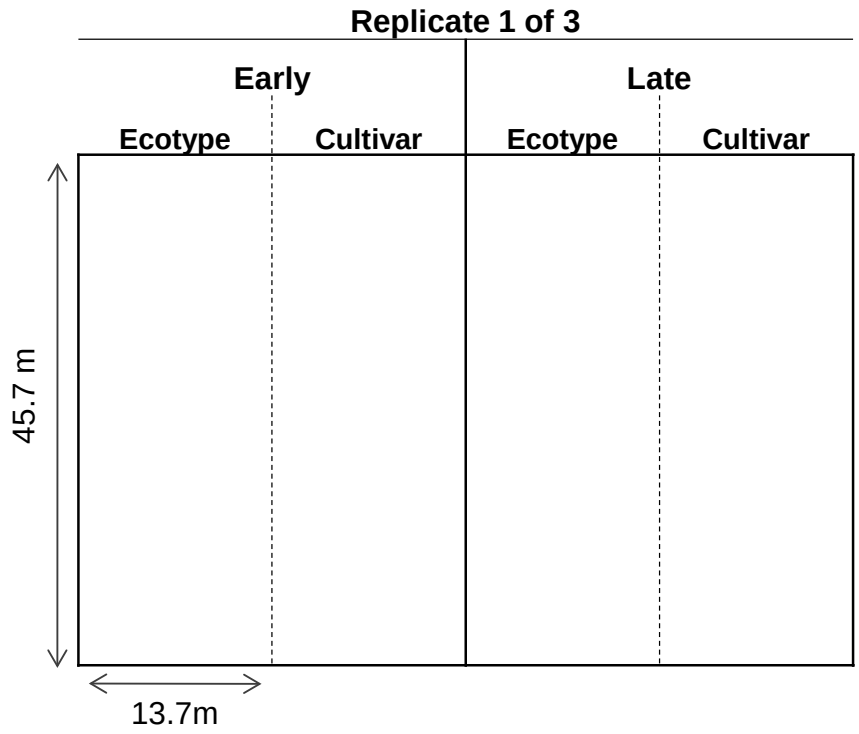

Figure 3. Total etiolated biomass growth (April to June 21, 2010) of non-grazed and grazed big bluestem (Panels A and B) and Indiangrass (Panels C and D) plants by seed type within each graze schedule. Early grazed plants were defoliated in early June and mid-July and Late grazed plants were defoliated in mid-July and mid-September. Bars represent treatment means with ± 1 s.e. (n = 3). Bars within graze schedule and species with different letters are significantly different at $\alpha = 0.05$

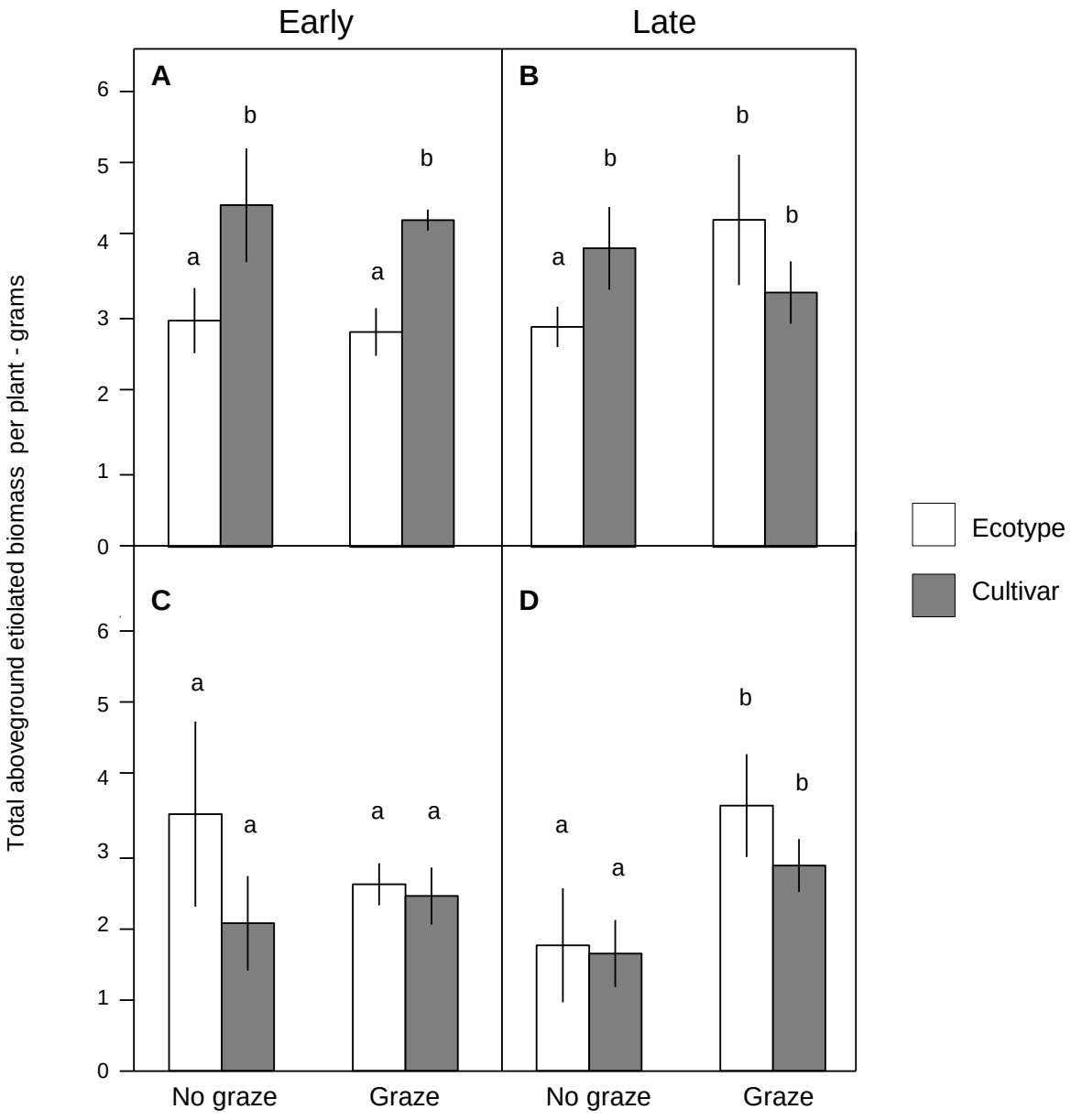

Figure 4. Available forage at each graze cycle and total accumulation across graze cycles in 2009 (Panels A – C) and 2010 (Panels D – F). Cycle 1 defoliations under the early graze schedule occurred in early June and under the late graze schedule in mid-July, while Cycle 2 defoliations occurred in mid-July for the early graze schedule and in mid-September under the late graze schedule in each year. Total accumulation is the sum of available forage at Cycle 1 and Cycle 2 under each graze schedule treatment. Bars represent seed type treatment means ± 1 s.e. of mean (n = 3). Bars within graze cycles and the total with different letters are significantly different at $\alpha = 0.05$.