COWS IN THE PRAIRIES, PRAIRIES IN THE FIELDS: INTERACTIONS BETWEEN PLANT DIVERSITY AND ROTATIONAL GRAZING IN RECONSTRUCTED TALLGRASS PRAIRIES

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Thesis submitted to the faculty of the University of Wisconsin-Madison in partial fulfillment of the requirements for the degree of

Master of Science
In
Environmental Studies

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Acknowledgments

I could not have completed my course of study and this thesis without the assistance, guidance, and mentorship of many people. This research was supported by a competitive grant from the U.S. Department of Agriculture's Sustainable Agriculture Research and Education program (LNC08-299).

Many thanks to committee members Tom Eggert and Dan Undersander. Their perspectives and expertise have aided me immensely, as I must keep in mind that for agriculture to be sustainable, grass-based farmers need robust pastures and a profitable business model.

I was very lucky to work with Randy Jackson. Randy has accomplished a rare feat of fostering a lab group that combines high academic and scientific rigor with inspiring camaraderie and lots of humor.

The graduate students and post-docs in the Jackson Lab are good friends and contributed much to this research as they helped trouble shoot statistics and methods, accomplish field work, and always offered a great sounding board for ideas. My thanks go to Julie Doll, Gary Oates, Gregg Sanford, Herika Kummel, Andy Jakubowski, David Duncan, Sue Chamberlain, Laura Smith, Jessica Miesel, Nadia Alber, Carol Williams, and Maddy Raudenbush. Our undergraduates and research interns were a great crew to work with. I particularly owe thanks to Kraig Weber for his assistance during the summer of 2010. Many thanks go to Andrew Dean, James Tesmer, Gunnar Jepson, Logan Peterman, and David Williams, who endured many hot summer days (as well as plenty of cold and wet days in the field, too!).

Dr. Josh Posner and members of his lab proved to be close colleagues, as well. Many thanks to Josh for allowing me the privilege of introducing grazing and mowing to the restored prairies and switchgrass plantings at the Wisconsin Integrated Cropping Systems Trials. WICST was a great home for this research. Janet Hedtcke was an invaluable part of the team—her experience with managed grazing ensured the project stayed on the ground and kept moving smoothly. Many thanks to Nicole Tautges for assistance accomplishing field work and asking great questions.

Staff of the Arlington Agricultural Research Station and the Blaine Dairy provided much-needed help moving cattle to research plots and providing daily health checks, mowing plots as needed, and providing logistical support for farmer field days.

Thanks to Jim Miller, Tara Mohan, Paul Zedler, and many other staff and administrators who work behind the scenes at the Nelson Institute for Environmental Studies. Thanks to staff in the Agronomy office who help keep the department moving, including Sandy Bennett, Amy Cottom, and My Linh Do.

Outside of the UW, useful suggestions for managing prairies with grazing and re-introducing native legumes came from many people. I must thank John Ortmann, former manager of The Nature Conservancy's Niobrara Preserve in central Nebraska, for graciously spending a morning illustrating the effects of fire and grazing via a tour of Sandhills prairie and ponderosa pine savanna. Laura Paine, agroecosystem ecologist, grazing farmer, and Grazing and Organic Agriculture Specialist at the Wisconsin Department of Agriculture, Trade, and Consumer Protection, suggested we allow our cattle time to become acclimated to grazing in prairie paddocks before bringing them onto experimental units. Rich Henderson, terrestrial ecologist at the Wisconsin

Department of Natural Resources and champion of The Prairie Enthusiasts, vetted my suggestions for native legumes and helped me arrive at a mixture that represented a diversity of bloom times and life histories.

My final notes of thanks are reserved for my family. I was always encouraged in my curiosity and studiousness, and it wasn't until later that I understood that not every kid had a chance to get to know the garden and the wilder periphery outside of the home (picking hazelnuts and blackberries, or stopping to listen to the wind pass through the feathers of the wild geese on their way to Pine Island). My Caledonia family has been more welcoming and encouraging than anyone could ask for. It is an honor to live and work here with Amanda. As I've drafted these chapters, I've often had in mind what our neighborhood and our planet will look like through David-Alfred's eyes, thirty years from now.

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ABSTRACT

A major factor limiting the effort to reconstruct tallgrass prairies for ecological restoration is competition with agricultural land use. Demonstrating joint production of agricultural commodities and ecosystem services from restored tallgrass prairies could spur greater investment in prairie restoration as a form of natural capital that supports farmer goals for short-term profitability and long-term flexibility to adapt to environmental changes. In Wisconsin, the percentage of farmers using management intensive rotational grazing (managed grazing) is growing, and grasslands dominated by native, warm-season (C4) grasses may contribute to a managed grazing operation's economic and ecological sustainability by providing forage during hot, dry summers. In the central tallgrass prairie, grazing by cattle and bison has been shown to increase plant community evenness; selective grazing suppresses competition by highly-productive C4 grasses and facilitates increased abundance of subdominant forbs which make the greatest contribution to plant species diversity in tallgrass prairies. Whether or not grazing can demonstrate similar results east of the Mississippi River (where the cooler, wetter climate is less favorable for C4 grasses) has been contested but has not been experimentally tested. The objectives of this research included: evaluate how management-intensive rotational grazing (managed grazing) and mowing affect plant community composition in reconstructed native grasslands; evaluate forage availability and quality along a diversity gradient under managed grazing; and evaluate if native legume interseeding would have a significant effect on plant community composition and forage availability and quality. Experiments were conducted in a hierarchical split-split

plot design using existing diverse prairie and switchgrass monocultures in southern Wisconsin. Sub-plots were assigned managed grazing, mowing, or no defoliation (control) treatments, and defoliation treatments were applied in June and July of 2009 and 2010. Native legume interseeding was applied to sub-subplots. Multivariate comparisons of plant communities in fall 2010 indicated that undefoliated communities were significantly different from mowed communities—but not from grazed—in both switchgrass and prairies. Multivariate analyses of diverse prairies in June 2011 found similar patterns. Forage quality was generally adequate to meet the needs of non-lactating cattle across diversity levels. Forage availability was significantly lower in diverse prairies due to high abundance of native forbs that demonstrated traits for herbivory avoidance. Patches dominated by palatable plants (feeding stations) were significantly more frequent in switchgrass stands than in diverse prairies, and forage yield at feeding stations (0.5-m^2 scale) was higher in switchgrass stands than in diverse prairies; consequently, mean forage yield at the paddock scale was twice as high for switchgrass than for diverse prairies. Across all treatments, native legume frequency was too low to significantly affect plant community composition or forage quality and yield. These experiments indicate that reconstructed prairies can sustain managed grazing without shifting to alternative states of plant community composition. Conservationists may find these results useful for planning alternative management to suppress C4-grass dominance in reconstructed prairies, or for off-setting management costs by integrating managed grazing through rental or lease of grazing rights. The positive diversity-productivity relationship found elsewhere in experimental tallgrass prairie plantings was contradicted here— the relationship observed in unmanaged experimental grasslands was confounded

here due to invasion of non-native grasses and plant-herbivore interactions. Based on these results, farmers interested in using native species for sequential grazing may best meet their need for forage by using simple mixtures dominated by C4 grasses, with weed suppression provided by herbicide rather than species diversity. The positive biodiversity-ecosystem function relationships found in non-grazed native grasslands indicate that continued research employing varying combinations of plant species or functional group diversity in well-replicated experimental designs may bear fruit as knowledge of diversity × management × environment interactions improves.

Keywords: C4 grasses, native legumes, managed grazing, tallgrass prairie, ecological restoration, natural capital

General introduction

Integrating agriculture and conservation to produce food in ecologically diverse locales is one of many adaptive strategies appropriate to the challenge of sustaining human well-being via healthy relationships among people, land, water, and air. From local to global scales, citizens are increasingly recognizing that farming plays many roles in our communities, beyond producing food, providing jobs, and generating demand for goods and services. Agriculture can be valued for multiple functions, including preserving open space, providing habitat for native plants and animals, and yielding many beneficial ecosystem services by maintaining functional ecological communities.

Management intensive rotational grazing (managed grazing) is just one farming strategy that illustrates how multifunctional agriculture can be applied by diverse farmers in profitable businesses. Across the prairie-forest border region (where, historically, tallgrass prairie transitioned into eastern woodlands in Minnesota, Iowa, Wisconsin, and Illinois), farmers typically rely on grasslands dominated by non-native perennial grasses and legumes. These pasture plant communities are valued for their productivity, quality, and resilience. Advocates of managed grazing often purport that these pastures generate ecosystem functions similar to native tallgrass prairies, such as providing habitat for wildlife and improving soil structure and fertility. Ecological function generates ecosystem services that can flow to farmers and society: a perennial plant community promotes stability for a farm's resource base given increasingly intense precipitation and frequent periods of drought; building soil organic matter increases soil fertility (reducing the need for expensive artificial nitrogen or other fertilizers, and also offsetting other sources of greenhouse gases emitted by farm operations); perennial cover increases soil

stability, reducing soil erosion and preserving the productivity of the land; and improving soil structure can improve water infiltration and reduces stormwater runoff (improving water supplies, increasing base flow of coldwater to springs and streams, and dampening the magnitude and frequency of flash floods).

If reconstructed tallgrass prairies prove suitable for supporting livestock production, higher plant diversity at the field scale and greater ecological complexity at the farm and watershed scales may facilitate greater ecosystem function and increased ecosystem services for farmers and society. Restoring prairies to former cropland or non-native pastures could greatly benefit tallgrass prairie conservation by increasing the area of restored native grasslands and increasing connectivity, which would improve dispersal of native plants and the diverse invertebrates, herpetofauna, birds and mammals that depend on these habitats.

By conducting my research within a long-term cropping systems trial at a state land grant university's agricultural research farm, I was able to address important questions that bridge the disciplines of agronomy and ecology and provide information that is relevant for farmers, restoration ecologists, and policy makers. This research was supported by a competitive grant awarded by the U.S. Department of Agriculture's Sustainable Agriculture Research and Education (SARE) program: LNC08-299.

Thesis objectives

My objectives for this thesis included:

1) Illustrate important social and economic structures that shape how agriculture and biodiversity conservation are currently practiced (and typically segregated).
2) Evaluate how rotational grazing and mowing affects plant community composition and native legume recruitment in reconstructed native grasslands.
3) Evaluate the productivity and forage quality along a diversity gradient in a management-intensive rotational grazing system.

Organization

I have divided my thesis into three chapters that form the basis of manuscripts for publication. The first chapter is a work of literary non-fiction that is intended to reach an audience outside of peer-reviewed academic journals. This chapter illustrates some ways that agriculture is a socially- as well as ecologically-embedded practice. My goal is to publish this in a journal or magazine to reach readers who value biodiversity conservation but may lack first-hand knowledge of how rural livelihoods and land practices are shaped by broad cultural forces. I seek to foster knowledge and appreciation of several factors that limit the ability of private landowners to restore habitat for native species on working lands such as farms and woodlots. The second chapter presents the results of the first controlled experiment to evaluate how managed grazing with domestic cattle affects plant community composition in reconstructed tallgrass prairies in the Upper Midwest. This article is written for a journal that frequently publishes articles broadly relevant to ecological restoration or specifically relevant to tallgrass prairie restoration and management. The third chapter examines tradeoffs between plant community diversity and forage availability, and compares plant communities in grazed, mowed, and control

plots across a gradient of plant functional group diversity (switchgrass monocultures compared to diverse prairies). These factors are relevant to the delivery of a broad range of ecosystem services and the profitability and sustainability of native grasslands for grazing operations in the Upper Midwest. This chapter is written for a journal that addresses sustainable agriculture or management of pastures and rangelands.

Chapter 1. A view from Prentice Creek

Forty iron rectangles, each one blunt as a piano key, rotate into a blurring fury that hides the eight-foot-long shaft at the heart of the flail chopper. I am perched atop several tons of iron, with eighty horsepower at my command. This part of farming is easy—even a mechanically-challenged tree hugger like myself can manage to depress the clutch, shift into second, and ease the throttle forward. The tractor's tall, deeply-treaded tires churn easily, revolving into a smooth spin. Everything is spinning: fans, belts, alternator, drive shaft, axels. I don't understand the mechanism, fully, yet the tractor and chopper and I are propelled forward across the knee-high whiskers of a coarsely-bearded cornfield.

It is Indian summer in southern Wisconsin. My wife and I and our young son live here on her family's farm. Both of us are employed off the farm, but on weekends and many evenings I am an apprentice to my father-in-law David. Today, we are taking advantage of a brief period of warm, dry weather. Winter is approaching, and I could be spending the day beside our woodsplitter—the gasoline-sipping, hydraulically-heroic mechanism that makes it possibly to quickly put up several cords of firewood each year, but that is easy enough work to complete even when the cool, sunny days of fall are shoved aside by the relentless spin of the earth into darkness, sleet, snow and frozen ground.

The wall of tall green corn that stood here this summer has been transformed by fall and harvest. Little is standing after the field was stripped by a seed-combing combine. It is easy going, except that the mechanical tornado flails so loudly behind me: wailing against the air, grinding off the root-buttressed corn stalk stumps, sucking up

spent leaves and stripped cobs. In my wake, dry corn litter passes through the chopper like water compelled into frothy turbulence, falling again into an even, silent surface that hides so much activity below. I pass over the field like a speedboat crossing a glassy lake.

Ahead of me, the oak-covered hills are brown, and mare's tails are racing in from the north. No time to waste—the weather is expected to hold for another day, and I need to cover the field before the light fails this afternoon. Tomorrow David will rake this chewed-up detritus into windrows and then come back for another round to bale them up. The material left behind by the grain harvest is very coarse—high in fiber and low in nutrients. While it is good to leave some of this thatch on the field—to keep a roof over the soil and guard against erosion by wind and rain—on a flat cornfield that is part of a livestock producing farm, we can afford to borrow some of this thatch, which also makes good straw. Wherever livestock are gathered in close quarters, the concentrated waste can produce concentrations of ammonia and other gases that can be harmful to animals and people alike. Adding straw to the noxious mixture slows the breakdown of manure and urine, reducing the production of noxious gases and suspending valuable nutrients in a semi-solid mixture. The straw and excrement will come back to this field loaded with nitrogen, phosphorous and other nutrients that were removed when the grain was harvested.

The "barn-pack" is filled with readily available nutrients that can enter quickly into the soil, but it is also heavy with organic matter. The organic matter keeps a significant portion of the nutrients locked up for longer periods of time until it is broken down by the creatures who are at work beneath the calm surface of the field: literally tons of worms and beetles and other invertebrates; many miles of fungal hyphae; and

countless diversity of bacteria. The denizens of this particular foodshed work to decompose the thick cell walls of the straw, as well as of partially-digested grass stems and leaves that passed through the cattle and into their manure as the livestock fed on hay.

The creatures of the soil eat the dead bodies of many fellow microbes, too—the tribes of microbes who work in the guts of ruminants. The gut-borne microbes are a sort of apex herbivore in this system: the power of the sun is harnessed by plants and turned into grain or hay, transported to the barn by the farmers, and transported then to the habitat of the gut via a complex organism complete with coordinated brain, mouth, and esophagus. However, the microbes are short-lived, and quickly finish their shift at the top of the system. As they die, they pass through the threshold of hind gut and, finally, the anus. Shit.

Is it fair to call any of this waste? The spark of life in the stinking barn pack—the straw, the piss, the manure with its concentration of microbial corpses—is not yet exhausted, not yet lost to entropy. After the bedding is returned to the field, the constituent parts will be lifted into action when roots burrow deep in search of more phosphorous, nitrogen, and water to carry on the busy work of building ion transporters, enzymes, lignin and proteins—from root to stem to leaf to seed. Through spring, summer, and fall, the straw, plant fibers, and dead microbes that re-enter the field will take shifts in resurrection. Such is the life of the soil.

The end of the row breaks my reverie. Time to feather the lever and lift the heavy flail from chopping position. I turn the tractor in a half-circle and feather the lever again

until the tornado touches down just as I straighten out and catch the next row. Ready for another trip across the field, aimed down the rows, now due west. My route takes me just a few degrees north of where the late afternoon sun hangs in the soft yellow light of mid-latitude autumn.

The tractor runs smoothly and it feels like I could keep moving westward quite easily at latitude 43 degrees, 25 minutes North. Close by, I would crest and ease on over oak-dappled ridges—glacial moraines—which attest to the furthest advance of the recent Ice Age glaciers and the fire-centric economy of the people who covered this land with effigy mounds and who later began to grow corn and other crops in fields they weeded using the shoulder blades of bison. Further west, a narrow, rusty-girdered bridge threads over the Mississippi River, carrying water that fell as rain and snow on north country forests, coulee pastures in the tri-state Driftless Area, and the broad, flat corn-and-soybean lands of central and western Minnesota. Each fall, the skies above fill with white pelicans, bald eagles, and a paradise of waterfowl. Against this pattern of gathering and flow, I'd continue west, west: chopping through the dried stalks of compass plant and tall tassels of big bluestem at Hayden Prairie State Preserve in Iowa and fording the Big Sioux beneath the watch of yucca and side oats grama.

West, west: over the glacial rolling and prairie soils of eastern South Dakota farmland; ford the Missouri, climb a draw through dark shale cliffs of Cretaceous seafloor, and head into the Great Plains proper—that ramp of mountain-shed detritus in the rain shadow of the Rockies. Ford the White River beneath cottonwoods, chase the western meadowlarks out of the Badlands' shortgrass prairie. Perhaps a detour to see if buffalo are still good for the Broken Heart Ranch.

Across the west: climb the hogbacks near Hole-in-the-Wall and traverse Wyoming's dry Rockies. Meet metamorphic rocks shot through by pink granite in the deep gorge where the Wind River cuts paradoxically across the Owl Creek Mountains. Canyon. Across hard-baked bentonite, up over Union Pass, into Greater Yellowstone Country. Tempting to follow the sandhill cranes south down the Green River to seek winter refuge in the green lagoons of Sonora. West, west!

Follow the Snake through the overthrust belt, hence forward into gardens of the desert, reclaimed from Nature. Detour around the Craters of the Moon, where basalt awaits to shred tires. Meet the Snake again on its now northwestward route; then the Owyhee, grand river of the lovely loneliness of three corners country; further west through the sagebrush deserts of southeast Oregon. Up through pine forests and over the Cascade crest, down to the oak-shaded rangeland where the Umpqua meanders between the Cascades and Coast Range. Cross a continent, just to linger here in a black Angus savanna? West, west! *Ocian in view! O! the joy.*

End of the row—decision time again.

Finding a land ethic

I feather the hydraulics while turning again, back to the east, toward the oaks that mark the steeply-sloping hillside that falls to the Wisconsin River. The flail chopper roars a tune of simple physics, the oaks stand mute on a windless day, and the two-billion-year-old quartzite rock at the crest of the Baraboo Hills hums something of the rhythm of waves draping sands across a lifeless shore and peeling back again. The cultural

drumbeat persists—move on to pursue prosperity. Go get what's yours. Meanwhile, knowledge about how to dwell in any one place, and encouragement to do so, is harder to come by. I fear, too, that such knowledge is in danger of becoming irrelevant almost as soon as it might be gained—shredded by the fluxes of economies, cultures, and a disturbed biosphere and atmosphere as easily as the flail chopper shreds the stalks that accumulated so much life just this year. The only thing I am assured of, in staying, is a new world continuously unfolding around and within me.

Last September, I accompanied David to check out a field that lies due west of the stubble-chopping field, on the north bank of Prentice Creek. We were there to measure and mark a grass buffer that will separate row crops from the creek—a practice encoded in the conservation easement that is now a part of the deed to the property. Given the flash floods that have repeatedly swept across this low ground over the past few years, leaving this land in grass makes good economic and ecological sense. During the last major flood in 2008, David baled dusty hay from this field, while a substantial portion of his corn crop would have been completely lost. As we moved upstream to place more flags, I repeatedly plunged through the field-edge tangle of burdock, mulberry, eastern blackberry, woodland sunflowers and pointed leaf tick trefoil to find the eroded edge of the creek bank. It is not a pilgrim's creek, but a real one, cut deep into topsoil that has eroded off the long-planted fields and into its dynamic basin. David planned to follow this line of flags a few days later, while spraying the rest of the old hayfield with glyphosate to kill the grass and alfalfa and prepare for next spring's planting of herbicide-resistant corn.

We spent an hour flagging the buffer, and the heat of the day was lapsing as we reached the property line. To get back to the truck, we followed a strip of weedy foxtail grasses that waved yellow seed heads in a rolling sea of hay. We were moving due west, as the foxtail marked precisely where the soil had been disturbed when David's brother bulldozed the old fenceline a few years earlier. Halfway back to the truck, I was surprised when David stopped at a short, west-facing slope, where the field dropped along a slope that fell about ten feet over the course of thirty to forty feet.

"Let's flag this, too," he said. Though I couldn't see much of the soil beneath the late summer growth of alfalfa and grass, David said that he knew the soil on this slope was light—a band of sand and gravel. Probably where an outwash stream trickled from the collapsing glacier, I thought, as my geological training interrupted, unbidden. I kept quiet as we knelt down for a closer look. David pried up a few stones with his jackknife, and I turned a few rounded and smooth stones over in my hands. He quickly pointed out a pattern in the vegetation—"You can sort of see the change in soil in how the brome and alfalfa grows differently here. It's thinner. This won't be any good for corn, and it will erode away if the crop doesn't take hold, so I'm going to leave it in hay. I'll leave a broad enough strip so I can come in from the buffer to bale it. The neighbors might laugh at me, but it's the right thing to do."

In that moment, I was an elated farm ecologist—I sensed that we shared a respect for the soil and a sense of responsibility to hold this ground. "It makes sense to me," I said, and we spent some time walking that slope, looking closely at the grade, the vigor of the grasses and alfalfa, the density of stones, marking out the place to conserve in hay. His decision could limit if not reverse soil erosion and perhaps build thicker topsoil,

higher fertility, and greater yields in the long run. In the short run, too, holding this ground with hay will be more profitable than buying seed, fertilizer, and herbicide to plant hybrid corn. David uses all of those tools on his farm, yet they do not drive all of his farming decisions. He farms with a forethought that gives a fuller accounting of costs that come both out-of-pocket and at expense of the health of the land.

Out in the field, he expressed his knowledge of the system and loyalty to the land through the language of conversation rather than the rhetoric of seminar or sermon. His knowledge was hard-won—from long experience with a piece of land. He was now able to translate what he had observed in many a plow furrow to a subtle but discernible pattern in the field, which would otherwise appear as a uniform sea of green to the inattentive mind. He could make predictions, weigh costs and benefits, and chart a sustainable strategy without hardly pausing in his walk across the field. That kind of knowledge is not simply to be stored up, harbored, and lost; it can be relayed along in the evolution of a locally-adapted culture as he conveys the knowledge to following generations in situ.

With another year to add to my perspective, I have finally acknowledged what I could barely sense on that afternoon. My father-in-law was not talking to me as *farmer* to *ecologist* but as elder to apprentice. We agreed as professionals, but what was far more important than the congruence of our disciplined perspectives was the relationship we were building. When we choose to stay in place, we begin to feel the rub of constraints, responsibilities, and uncertainties now placed on us by the past and future, while simultaneously the process provides opportunities for stronger human connections. There is within this a deep joy, satisfaction, and hopefulness that is not readily available—

perhaps not comprehendible—when we are in the process of pulling up stakes and heading out on the open road. The time I've spent learning to work on this farm has reinforced the idea that a land ethic cannot spring from the mind but must live, renew, and evolve in the work and conversation that unfolds among families and communities.

Our antecedents derived the word "conversation" from the Latin *conversari*. The root is also related to *convertere*, "to turn around." On this level, the root of conversation may reflect how each participant takes a turn listening and speaking—and perhaps how we also tend to go beyond listening or exchanging and attempt to change, or turn, the belief or perspective of the other person. But *conversari* itself meant "to live with or associate with," resonating with how the lives, livelihoods, and well-being of people in a community ("together one") collectively turn around and depend on one another. This ancient truth remains valid as the scale of our mutual turnings stretches far beyond family and village and watershed to encompass national and global communities via economic and cultural exchanges and global cycles of carbon and nitrogen, dust and pollution. No matter the distance that separates us, the lives of urban and rural people turn around one another. An ethic grounded in this truth must be expressed in mutual interest in and concern for one another.

In the summer of 1947, the conservationist Aldo Leopold worked to integrate his thoughts on land use, working lands, wildness, and ethics in a single essay. As historian and conservationist Curt Meine recounted,[1] Leopold's efforts that summer produced his

[1] Meine, Curt. *Aldo Leopold: His Life and Work* Madison, WI: University of Wisconsin Press, 1988.

best known essay, "The Land Ethic," which became the capstone to *A Sand County Almanac*.

> A land ethic, then, reflects the existence of an ecological conscience, and this in turn reflects a conviction of individual responsibility for the health of the land. Health is the capacity of the land for self-renewal. Conservation is our effort to understand and preserve this capacity.[2]

The land ethic remains relevant in part because Leopold recognized his effort as a synthesis, as an articulation of the best of current understanding of people, land, and the connections between them, rather than as the final word. His deep understanding of his own place in the grand sweep of time and culture is reflected in the humility he brought to his argument, stating, "I have purposefully presented the land ethic as a product of social evolution," and he left his readers with clear guidelines for interpreting his message and for moving forward:

> …nothing so important as an ethic is ever 'written.' Only the most superficial student of history supposes that Moses 'wrote' the Decalogue; it evolved in the minds of a thinking community, and Moses wrote a tentative summary of it for a 'seminar.' I say tentative because evolution never stops.

We still have far to go in the attempt to encode a land ethic that is sufficiently strong to temper our appetite for the earth's resources and focus our work toward restoring land health. A land ethic, good land use, and an equitable and civil society arises from countless actions and conversations, constantly unfolding, as the nation's

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[2] Leopold, Aldo. "The Land Ethic." In *A Sand County Almanac and Sketches Here and There*. New York: Oxford University Press, 1949.

plain members and citizens go about their daily lives. To borrow from the environmental justice community, a land ethic is about how we live, work, play and eat. A land ethic evolves as we continuously interact with each other and the land—directly and indirectly.

My time on the farm has changed my perspective as a person and my stance as a conservationist, and I caution that proposed changes to farmer's production practices should not be offered lightly. Agriculture is an ecologically-embedded enterprise, and we should not tolerate actions that degrade our natural capital, the diversity and function of our ecosystems, or the health of the atmosphere, soils and waters that surround and support us. At the same time, we must recognize that agriculture is embedded in society—a farm practice that runs counter to society's goals is hard to maintain. I agree that a farm can and should be valued by its owners as a place to live, and as a source of pleasure in good farming, good eating, and engagement with both domestic and wild neighbors. Society continues to measure farms, and judge farmers, on their production of grain, meat, biomass, and other commodities. Farmers are caught up in a highly-competitive market system that typically allows only a slim margin between money coming in and money going out. Unlike a rural estate, a public wildlife area, or a non-profit's ecological preserve, a farm is a business—with taxes to pay on land and costs of production that must be surpassed by income if the business is to be sustainable. Furthermore, the farm enterprise is doggedly pursued without the financial safety net of a pension from a lucrative urban career, a broad public tax base, or an annual fundraising appeal to members. A majority of medium-sized family farms only stay in business today because off-farm income and benefits netted by one or more family members can be used to offset chronic unprofitability and economic insecurity. Farm families make such

sacrifices in order to keep the farm afloat for many reasons—often, because of connections to family history and community history, or to enjoy the amenities of a rural livelihood, such as close interactions with wild creatures and natural cycles.

While a particular farm may be hundreds of miles from an urban or suburban community, each farm is at the center of these non-farming communities due to the connections of food systems and ecological systems. Despite the clarity of these connections, the goal of public policy for agriculture remains to be guided by the desire for cheap food, as historian Donald Worster pointed out nearly two decades ago.[3] The narrow focus of public policy is changing, but slowly, and the shift is neither complete nor assured. Leopold suggested that the best definition of "What is a conservationist" is written with an axe rather than a pen, because in shaping the land directly through the application of plow, cow, and axe, we are writing our signature on the land.[4] I must counter that many valid definitions of what is a conservationist can be written with a vote, a conversation with a neighbor, or a call to a congressional representative, as well as with an axe. An international trio of ecologists recently concurred that politics is "…the practical social expression of our ethics…" [5] Each year, we leave our signature on the and via the land use and economic policies we support in our political silence or activism.

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[3] Worster, Donald. *The Wealth of Nature: Environmental History and the Ecological Imagination*: Oxford University Press, 1994.

[4] Leopold, Aldo. "Axe in Hand." In *A Sand County Almanac and Sketches Here and There*. New York: Oxford University Press, 1949.

[5] Milton, Suzanne J., James Aronson, and James Blignaut. "Restoring toward a Better Future." In *Restoring Natural Capital: Science, Business, and Practice*, edited by Suzanne J. Milton, James Aronson and James Blignaut, 313-18. Washington, D.C.: Island Press, 2007.

While the predicament of modern agriculture may appear to be so dire that we will inevitably adapt and organize a more sustainable system, Australian ecologists at Murdoch University came to a much different conclusion after analyzing the problems facing farmers in the semi-arid southwestern part of the continent. Farmers and policy makers continue to invest in production systems that do not fit the land because they are now tightly bound up in patterns of modern agribusiness and food production. Financial capital goes to conventional farmers more easily than alternative farmers, and social capital in the forms of agronomic research, technical assistance (for addressing issues with animal health, soil fertility, soil erosion and water pollution), and especially processing, distribution and retail, supports the energy- and natural-capital intensive system. The social structure has become highly resilient to change despite the fact that natural capital is being mined to support production. The authors describe this as a lock-in trap, "…which, in economics, describes an industry that has so much 'sunk-costs' that it may continue to degrade the resource it relies upon until the capital is totally removed."[6] Shifting the system to a more desirable state—one that is ecologically- as well as socially-resilient—will require us to forge new social connections in the quest to establish new and more sustainable patterns of land use.

The buy-local movement has helped bring many implications of abstract policy into focus via readily-visible examples. In sustainable agriculture, a few economically-

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[6] Allison, H.E., and R.J. Hobbs. "Resilience, Adaptive Capacity, and the 'Lock-in Trap' of the Western Australian Agricultural Region." *Ecology and Society* 9, no. 1 (2004): 3.

viable niches have opened up, thanks in part to growing public awareness about connections between healthy people, healthy ecosystems, healthy communities, and food production. Many members of the community have chosen to vote for better practices with their food dollars, as well as calling for better policies that as they talk to their neighbors and public representatives. While grass-based dairy farmers and organic vegetable growers were the original pioneers and innovators in reforming the food system, it is impossible to determine whether this movement is now being led by farmers or city dwellers. Fortunately, that distinction is irrelevant—like any complex system, there are intricate relationships and flows of energy and information between both groups. The key is that a new system is emerging.

In Search of a Keystone For Bridging Conservation and Agriculture

Can a community of well-connected but individually small actors hope to break Midwestern agriculture out of its lock-in trap? There is little room for optimism, but our prospects are not hopeless. As David Orr reminds us, "Hope is a verb with its sleeves rolled up."[7] When Professor Orr encouraged us to be hopeful in times like these, perhaps he was continuing a literary conversation with Wendell Berry who farms and writes in Kentucky hill country. Berry stated that he had no reason to be optimistic about the prospects of people becoming reconnected with the "wealth, health, knowledge and pleasure of their country," but he concluded still that "…hope is one our duties… The

[7] Orr, David W. "Optimism and Hope in a Hotter Time." *Conservation Biology* 21, no. 6 (2007): 1392-95.

health of nature is the primary ground of hope—if we can find the humility and wisdom to accept nature as our teacher."[8]

We may have much to learn from how nature's economy operates in the tallgrass prairie. By sharing examples like this, and from other ecosystems around the world, we can develop new rhetoric and build coalitions. We must find a frequency that can interfere with the dull roar of the rhetoric of efficiency and competition, rhetoric which threatens to supersede and drown out every American conversation about how land is to be used and how an economy might best be organized.

In the Flint Hills of Kansas, the prairies are truly dominated by tall grasses—all together, big bluestem, switchgrass, and Indian grass can account for more than 80 percent of the prairie's windswept greenery. The grasses are so dominant because they are remarkably efficient. Unlike many other grasses, these species build channels in their leaves to make the process of photosynthesis much more efficient than their competitors' process. The grasses need relatively few enzymes to carry out photosynthesis, so they need less of the element nitrogen, which is a building block for enzymes. This is a major advantage, as the amount of nitrogen in the soil is often the limiting factor for plant growth—hence the artificial nitrogen we are counseled to add to our gardens and crops as fertilizer, whether we pull a few pounds of Miracle Grow off the shelf or contract for tons through the local co-op. The tall grasses also lose less water thanks to their innovation, which helps put them ahead in dry climates with high evaporation rates.

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[8] Berry, Wendell. "Conservation and Local Economy." In *The Art of the Commonplace: The Agrarian Essays of Wendell Berry*, edited by Norman Wirzba. Berkeley, CA: Counterpoint, 2002.

In the language of microeconomics, the tall grasses have the lowest costs for construction and operations. As a result, theses ships in the prairie sea can cast huge nets of roots below the surface to capture water and nitrogen, and they can set huge sails of green leaves to catch the sun and propel photosynthesis. These photons and molecules are discrete and finite resources that plants cannot share and must compete for. The highly-efficient tallgrass fleets should rule the prairies. Paradoxically, the tallgrass prairies are blessed with an abundance of smaller, less efficient wildflowers and legumes, prospering from sub-boreal Manitoba to the sub-tropical coastal plains of Louisiana and Texas. As with the mystery of decay and renewal that abounds in the soil, microbes dwell at the heart of this paradox.

All of us mammals have microbes in our guts, facilitating and regulating digestion. Large-bodied herbivores take this to an extreme—huge body cavities accommodate an intricate digestive system that shelters, feeds, and harvests a community of microbes. Mouth, teeth, tongue, digestive tract, and brain are all organized to harvest and process grass, leveraging the ability of microbes to consume the fibrous grasses and excrete easily-digestible sugars.

In the tallgrass prairies, the American bison selects where to graze, to some extent, based on where they can maximize their intake of the plant resource they are best-adapted to. The ecological niche of an organism can best be translated as its *palace*, as the poet, translator and ecologist Gary Snyder has re-discovered, and interpreted for us, in

the work of the philosopher Dōgen.[9] In the cycles of evolution, the efficiency and dominance of the tall grasses built a palace of greenery. The bison evolved to dwell in this palace. Among the tall grasses, the bison are fully at home.

As the Kansas State University ecologists Alan Knapp and his colleagues have digested from their research in the Flint Hills,[10] the microbially-facilitated bison play a key role in making their home a palace for others, as well. As the bison fulfill their needs by feasting on leaves, they demolish the tall grasses' leafy superstructures. The rest of the prairie blushes and blooms in gratitude.

The leaves of, say, big bluestem, might have otherwise overshadowed a short-statured wild petunia seedling. Because the microbe-bison super-organism is shaped to make use of the abundant grass, the young flowering plant will now spend a good deal of the summer bathed in light, allowing the plant to take in carbon dioxide and expelling oxygen as it conducts photosynthesis and builds leaves and roots. Furthermore, nitrogen in the big bluestem leaves would have been locked up through the rest of the growing season, unless a passing band of grasshoppers landed for a meal and carried the nitrogen off, driven by the instinct to mate and lay eggs before the days become any shorter.

As the bison eat and excrete, the nitrogen and other nutrients that were in the leaves high overhead become more accessible to other community members. As a bison

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[9] Snyder, Gary. "Survival and Sacrament." In *The Practice of the Wild*. San Francisco, CA: North Point Press, 1990.

[10] Knapp, Alan K., John M. Blair, John M. Briggs, Scott L. Collins, David C. Hartnett, Loretta C. Johnson, and E. Gene Towne. "The Keystone Role of Bison in North American Tallgrass Prairie." *BioScience* 49, no. 1 (1999): 39-50.

cow pauses after scratching her belly on a compass plant, the nutrients she returns in a cascade of nitrogen-rich urine could be taken up by the wildflower right at the time it is beginning to send its flowering stalk skyward. The compass plant may have enough resources, in turn, to create one more flower on its stalk than it could have if the nitrogen had remained locked up in big bluestem. The compass plant's saucer-sized flowers attract and feed many native pollinators, and nutritious seeds are a staple for seed-eating birds—and the petals, pollen, and seeds are very expensive to build in terms of the nitrogen concentrated within the physical structures. The compass plant and wild petunia are simply two representatives of more than a hundred wildflower and grass species that can be outcompeted by the tall grasses. When the bison hone in on a patch of tall grasses, the dominance of the highly-efficient big bluestem, Indiangrass and switchgrass may be depressed such that the prairie's balance sheet may take a hit on the single measure of tons of biomass per acre, but

...what a good multitude

Is here in return… [11]

In the process of reorganization, trading of many currencies of importance to the community as a whole can be multiplied many times over, for many organisms dwell in the palace of wildflowers. Many herbivores and omnivores are smaller than a bison and lack the symbiotic microbial synergy that provides access to grass. Instead, they depend

[11] Jeffers, Robinson. "Bixby's Landing." In *The Selected Poetry of Robinson Jeffers*, edited by Tim Hunt. Stanford, CA: Stanford University Press, 2001.

upon the more digestible leaves, pollen, nectar, sugary fruit, starchy tubers and seeds, and protein-rich leaf buds that wildflowers and flowering shrubs produce. Badger, rabbit, mouse and vole, prairie chicken, grouse, turtles, and waterfowl can all benefit. The less efficient plants host many species of insect larvae, which in turn feed predatory insects, songbird hatchlings, and others on up the food web. Many more connections roll out and across the prairies in this fashion.

It will do no good to wait for the bison of federal policy reform to come trampling through the industrial agriculture complex. Each one of us is a microbe in the gut of the keystone species of policy reform. If you and I lay inert, this bison will stumble, and growth of the most ruthless competitors will run its course—to the degradation of soil, extinction of wild plants and animals, and the erosion of many resources our communities need to thrive. To restore agriculture to a more diverse and resilient community, each of us needs to express our individual land ethic in the markets for food and by expressing our values through speech and actions in the public sphere. There are deep congruencies between sustainable agriculture and conservation, and we cannot afford to lose the incremental but crucial gains that pioneers have made over the past few decades.

The Life of the Community

We are generating conversations and connections, and new attitudes and local economic connections are emerging. Those who practice sustainable agriculture on the farm, or as part of home economics, are beginning to understand the barriers to reforming the larger

food system. Environmentalists and conservationists must continue to throw their weight behind sustainable agriculture. We need to engage more and more people in understanding how current farm policies cascade into myriad costs and harms that undermine the health of people, economies, and ecosystems. We must continue to talk to one another about concerns over how our food is produced and paid for and seek out the mechanisms that keep the industrial machine lurching forward despite our protests. We need to clarify that there is indeed widespread support of alternatives, and, finally, we must be prepared to go about building them ourselves in spite of the governments and institutions which play deaf or actively resist such actions because agribusiness has purchased immense influence with their profits—thanks in no small part to our food dollars and other investments.

If we wish to strike at the root of the problem, we can find great satisfaction in devoting more of our time and capital to building mutually-beneficial relationships among farmers and consumers. Whether farmer or computer programmer, it is crucial that we continue the restoration of relationships between ourselves and neighbors across urban-suburban-rural boundaries. The anonymity and efficiency demanded by the global marketplace is sapping our communities of the vitality that springs from sincere interactions with one another—the kind of relationships that originally inspired Adam Smith's confidence in the virtuous outcomes of markets[12]—and from farmers' intimate knowledge of the soils, waters, plants and animals that comprise their land. Local,

[12] Evensky, Jerry. "Retrospectives: Ethics and the Invisible Hand." *The Journal of Economic Perspectives* 7, no. 2 (1993): 197-205.

alternative, and face-to-face commerce and trade in food and fuel can rebuild that vitality, which can emerge in the form of renewed community membership and healthy land.

The "key-log" which must now move to support the restoration of land health through rebuilding community and infrastructure around local food and energy is this: urban, suburban, and rural residents alike must be inspired to shift their time and money toward the effort. The farmers, ecologists, and other local food advocates must be willing to share the stories and examples that will help their critical allies understand, and feel, that they are part of the local landscape and part of the surrounding rural community.

Reviews of rural economies across the United States, including Iowa, Minnesota, and southwestern Wisconsin, have repeatedly shown that the amount of money the local community spends on importing food exceeds the value of the commodities and subsidies that comes to farmers in the region.[13] In other words, the current system of farming drains wealth from rural areas instead of creating prosperity for people who devote their lives to producing food and other values for society. It is no wonder that local farmers are undercapitalized.

By investing in local food and energy production, we are generating demand for more types of agriculture, leading directly to a renewal of diversity across the ecologically- and socially-impoverished landscapes promoted by industrial efficiency. Some of the easily met transformations have included: small, intensively cultivated fields and orchards producing vegetables and fruits for fresh consumption, preservation, and

[13] Meter, Ken. "Southwest Wisconsin Local Farm and Local Food Economy." 7. Minneapolis, MN: Crossroads Resource Center, 2008. Ken Meter has produced more than 30 similar local foods surveys for communities across the nation.

small-scale processing; rows of trellises growing locally-adapted hops to complement local brews and diversify farm income; perennial grasslands that produce healthy animal products from cattle, sheep, and poultry; corn, wheat, and other grains apportioned to small fields and incorporated into livestock production or sold to locally-owned flour mills; oak woodlots thinned to produce firewood and lumber. Our wetlands are often choked with reed canary grass and shrubs today, but the local economy could also improve wildlife habitat and restore the ecological function of these valuable lands through harvests for livestock hay and bedding or for renewable biomass that can heat homes, businesses, and schools during winter's deep freeze. By turning more of dollars away from large agribusiness and toward these small scale, locally-integrated systems, we will be rewarded with healthier soil, improved groundwater quality and quantity, fewer and less severe floods from intense rains, greater social capital in the form of skills for managing and enjoying biologically-complex farming systems, and greater security for a richer tapestry of semi-natural to wild habitats. Many semi-domestic parts of the rural landscape are important for the wild creatures that enrich our lives and who signify that we are indeed caring for the land. The touchstones of these partly-wild, partly-human landscapes are small pastures and sweeping grasslands, scattered woodlots and deep forests, shady valleys and sandstone-capped bluffs, clean and clear headwater springs and wetlands rich in waterfowl.

In the short run, for individuals and families, investing in such a landscape of food production can be more expensive than continued uneasy participation in the fraudulent prosperity that mainstream markets and industrial agriculture still proclaim to engender. In a less-mechanized, less-energy-intensive, less-concentrated system more people will

be directly involved in producing, processing and distributing food—providing more direct access food and a variety of decent-paying jobs that make food a reasonable portion of the household budget. Many urban agriculture initiatives are already improving access to food in areas where the industrial system has failed worst. Subsidies that currently promote cheap food on the production side can be shifted to ensure that the least among us have improved access to healthy food.

Furthermore, a diverse rural landscape, shaped by goals of complexity, contingencies, and resilience (rather than maximum production and minimal accounting) will be invaluable to our communities in the coming years. The landscape of diverse farming systems that rely much less on fossil fuels for energy and fertility are much more likely to remain productive despite shocks like intense rains, flooding, drought, high fuel and fertilizer costs, decreasing soil structure and fertility, and limited access to credit and financial capital. Such shocks to our systems are predicted to become increasingly severe as a result of the globally-driven trends of climate change, continued population growth, increasing demand for resources, and economic and social unrest.

Building relationships across the urban-suburban-rural divides will be as critical to weathering change as the aspects of reduced energy demand and increased ecological function. In today's anonymous economy, the large-scale industrial farmer has very little incentive to lend help to neighboring urban communities—the industrial farmer is kept afloat financially by abstract federal policies and commodity markets. By making financial investments, providing a steady market for goods, launching and supporting small enterprises through entrepreneurship, and creating times and places for face-to-face conversation and community-embracing celebrations, we will create stocks of friendship,

neighborliness, and a sense of community membership that are far more valuable than the purported $100 billion accruing in one internet social network.

As consumers, we have an increasingly short amount of time to act on our realization that we are not only primarily benefactors of industrial agriculture but are in many cases its lonely victims. The anonymity and propaganda that supports the fragile industrial system is simultaneously its weakness as well as its strength. We are urged to find satisfaction in ruthless competition and consumption, but we do not—depression and anxiety plague rural and urban Americans at epidemic rates. We are over-stimulated, but obviously, many of us feel something is missing from our lives. Perhaps we sense how fragile our livelihoods have become. While we are urged to enjoy participating in the anonymous consumer economy, we miss the personal connections that have always maintained human communities.

What could a large agribusiness, food processing, or cut-throat retail corporation fear more than for us to begin acting like we don't believe there is much congruence between their sales and quarterly earnings and our security and happiness? Wendell Berry has described such a social shift as nothing less than secession.[14] We would be seceding not from the union, but from anonymity and despair, in order to refashion a democratic economy that reflects the needs of the human and wild communities we depend on.

Gaining access to affordable land for beginning farmers, and providing a financial margin wide enough to allow for the trials and occasional failures of still experimental sustainable agricultural systems is perhaps the crux of problem. But the

[14] Berry, ibid.

middle class so recently had much of its accumulated wealth transformed into debt and negative returns on investment as the housing bubble and financial markets crashed. The home equity and mutual funds that aging baby boomers were dependent upon for economic security in retirement were suddenly shrunk or became a liability in the case of housing values. Recent history is itself the argument we have to make to young people and families to invest a substantial portion of their monthly earnings and accruing wealth in community infrastructure that can yield real, substantial, and resilient wealth and happiness down the line. The human and natural capital that can be built up through stronger producer-consumer relationships is part of a diverse investment portfolio that can complement traditional investment tools.

Among the trade-offs that come with taking personal responsibility for investment in infrastructure and community is that a good portion of the pay-off will come in the long-term rather than in the next quarter or next few years. To engender a long-term outlook and support commitment to sticking together will require cultivating skills for overcoming disagreements between individuals and factions, for facing uncertainty that comes with engaging with an alternative model of community development, for weathering economic hard times, and for practical and joyful skepticism of the intense propaganda that flows from the anonymous economy to its victims. This demands vision, sincerity, and the arts of neighborliness and community engagement.

Nowhere among the frameworks of sustainability have I come across the principle of love for our neighbors and love of land, but indeed love is at the heart of conservation, good farming, and strong communities. We do not know what the future will bring, but it is not likely that resilience to coming shocks can be assured only by better technology,

greater efficiency, better communications infrastructure, or more inclusive certification standards. We need all of these advances, but conservation asks even more of us. Indeed, conservation asks us to give all that we have, and more. In the writing of the most sincere and compelling conservationists, we hear repeated calls to love our neighbors, and the land, as ourselves. Aldo Leopold's words resonated with this call when he summarized his goals for an ecological education: "If the individual has a warm personal understanding of land, he will perceive of his own accord that it is something more than a breadbasket. He will see land as a community of which he is only a member, albeit now the dominant one. He will see the beauty, as well as the utility, of the whole, and know the two cannot be separated. We love (and make intelligent use of) what we have learned to understand."[15] Each of us is an individual, but ecology and ecological economics confirm that you and I exist in the context of the land and our neighbors. By enacting our love for the land and our neighbors—in embracing our context—we assume great risk. We will likely be faced with changes in consumption patterns and the nature of work and exchange that will feel like severe sacrifices. However, many great harvests are indeed possible when we choose to enact our community membership, when we choose to transcend efficiency and strive toward harmony among people and between people and land. Much that might go to waste is brought back into cycles of renewal. As we build the life the community, we tend a field in which many of our hopes and pleasures can bloom.

End of row. Decision time again.

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[15] Leopold, Aldo. "Wherefore Wildlife Ecology?" In *The River of the Mother of God and Other Essays by Aldo Leopold*, edited by Susan L. Flader and J. Baird Callicott. Madison, WI: University of Wisconsin Press, 1991.

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Chapter 2. Dominance by grazing tolerant species limits plant community change in grazed and mowed reconstructed tallgrass prairies

Abstract

Preservation of biological diversity and ecosystem function in the highly-fragmented tallgrass prairie is threatened by the limited breadth of current conservation strategies. Managed grazing of reconstructed prairies offers the potential to increase the scale of restoration through integrating biodiversity conservation into the dominant land use of agricultural production. From an ecological restoration perspective, managed grazing has been proposed as a method for improving biodiversity conservation in tallgrass prairies by reducing dominance of native warm-season (C4) grasses and increasing heterogeneity of plant community composition, but there are persistent concerns about the risk of grazing shifting plant communities to an alternative, degraded state. Under an annual spring prescribed fire regime, two methods of disturbance (mid-summer grazing and mowing) were compared to control plots where the only disturbance applied was fire. Treatments were applied to 10-year-old mesic prairies planted on former cropland. Disturbance treatments showed nonlinear effects on plant community composition, dominance and evenness. After one season of disturbance, grazed and mowed plots differed in composition from control plots, but following two seasons of disturbances, grazed plots remained similar in composition to control plots and mowed plots became increasingly different from control plots. Measures of diversity showed significant

differences only in grazed plots following one year of disturbance. Native and non-native species richness fluctuated slightly over time, and no major differences were observed across disturbance treatments. Within each disturbance treatment, dispersion among experimental units did not change significantly under any treatment. Divergent trends in composition under two levels of disturbance can be attributed to a combination of factors: 1) at low-to-moderate stocking rates, cattle tended to avoid consuming many native forbs, whereas mowing is a height-selective disturbance and tall statured native forbs were repeatedly defoliated during the growing season and reduced in abundance over time; 2) non-native cool-season grass cover increased over time in grazed and mowed plots but declined in burn-only plots; and 3) native C4 grass abundance was not negatively affected by mid-summer defoliation. These results indicate that native C4 grasses and some species of native forbs can persist under managed grazing in the eastern tallgrass prairie.

Introduction

Reclaiming cropland to reconstruct biologically diverse native grasslands is a key strategy for biodiversity conservation in the north central United States, but the scale of public and philanthropic tallgrass prairie restoration is constrained by economic factors (Milton et al., 2007; Rowe, 2010), including conflicting with agriculture in ownership and management of arable and marginal lands. Globally, sustainable agricultural systems that are more resilient to physical and economic disturbances and that result in fewer negative environmental impacts are desirable for meeting food demands and continuing to generate ecosystem services on an increasingly crowded planet (Foley et al., 2011).

Public and private investment in tallgrass prairie reconstruction may increase significantly if diverse plant communities can be valued as natural capital (Aronson et al., 2006) for facilitating joint production of livestock forages at the field-to-landscape scales and accrual of non-crop ecosystem services at broader scales of watersheds and communities (Wossink & Swinton, 2007).

Like many grasslands around the globe, the tallgrass prairie ecosystem has suffered nearly complete conversion to crop production, other human uses, and woody encroachment (Samson & Knopf, 1994), though large areas of botanically diverse remnants persist as ranchland in the central and southern extent (Malin, 1942; Teague et al., 2011). Since the time of European settlement, social and economic factors have consistently influenced farmers to invest in biologically simple cropping systems and pursue management designed to maximize commodity yields to profit in markets for livestock and crops (Leopold, 1934; Smith, 1990; Page & Walker, 1991; Jackson, 2008; Reganold et al., 2011). Consequently, farmers across the region lack cultural traditions for sustaining native grasslands for optimal forage production (Muir et al., 2011), and biodiversity and ecosystem function have declined as native ecosystems have declined in area and connectivity through conversion to agriculture. However, there is broad evidence that some farmers now using management-intensive rotational grazing (managed grazing) for livestock production find value in increasing biodiversity at pasture-to-farm scales. Farmers have expressed that restoring native species to their farms can result in aesthetic and ecological benefits for landowners and society (Doll & Jackson, 2009; Wiltshire et al., 2010), observed that grazing lands dominated by native grass species are more resilient to drought or other extreme weather events linked to

climate change (Sherren et al., 2012), and have articulated that developing and sustaining plant communities suited to the soils and topography of their farms is a central focus of their place-based, knowledge-intensive, and profitable grazing management (Lyon et al., 2011). If prairies can be used to support agricultural production, the area and connectivity of grasslands dominated by native species can greatly increase, particularly in areas where managed grazing is already a common land use or is well-suited to production. Grazed reconstructed prairies could become an important land use for conservation of biodiversity and maintenance of ecosystem function and ecosystem services generated by prairies.

Reconstructing native grasslands on farms to provide summer forage has been proposed as a method for meeting biodiversity conservation goals while maintaining or improving forage production to support farm productivity and (Smart et al., 1995; Jackson, 1999). In the prairie-forest border region, farmers in Iowa and southern Wisconsin have been collaborating with ecologists to investigate methods for restoring tallgrass prairie species to grazing lands currently dominated by non-native species (Jackson, 1999; Woodis & Jackson, 2009; Bouressa et al., 2010; Wiltshire et al., 2010). Experiments have focused on seeding native warm-season grasses and other native prairie species into existing pastures, and collaborators have tested disturbance regimes hypothesized to limit the competitive ability of non-native species, including prescribed fire, mowing, managed grazing, and carbon addition. The success of native species reintroduction has been variable, and published results have been limited to the establishment phase (1-3 years following seeding).

Due to the limitations encountered in these studies, older reconstructed prairies (established from seed additions on previously cropped land) provide a critical living laboratory for determining the effects of rotational stocking on diverse prairies. Reconstructed plant communities are most appropriate for researching management options. Most reconstructions are not as crucial to biodiversity conservation as the few remaining remnants, which often harbor irreplaceable reserves of local genotypes and species across many trophic levels, including microbial organisms, plants, and insects (Howe, 1999).

Degraded plant communities that characterize some historically-grazed remnant prairies do provide a useful caution when exploring the outcomes of managing prairies with grazing (Leach et al., 1999), but relying solely on mensurative studies of historically-grazed prairies to attempt to refine predictions of how grazing impacts prairies (Henderson, 1999) may be counter-productive to understanding the effects of managed grazing. Grazing is a dynamic process, and outcomes depend on environmental variables and initial plant community composition, as well as timing, intensity, and frequency of grazing (Neiland & Curtis, 1956). For mesic prairies in the Upper Midwest, comparison of grazed and ungrazed prairies has been frustrated by the lack of sites available for making adequate comparisons (Dix, 1959).

The degraded state observed in many historically-grazed prairie remnants can be a result of continuous grazing systems, chronic overgrazing, or applications of broadleaf herbicides. Mensurative study of grazed and ungrazed thin-soil prairies in southern Wisconsin has found reduced abundance of native species and high prevalence of non-native unpalatable species in grazed stands (Dix, 1959), but it has also been shown that

continuous grazing can generate similar outcomes even at light stocking rates because intense defoliation combined with inadequate rest between defoliations can kill preferred forage species and create openings that lead to soil erosion and invasion (Teague et al., 2011).

In comparison to continuous stocking, rotational stocking employed in managed grazing in the Upper Midwest subdivides pastures into many small paddocks. In this grazing system, managers can closely manipulate timing and intensity of defoliation. Managers remove livestock from paddocks when goals for grazing intensity have been met (typically determined by residual vegetation height) (Paine et al., 1999). By limiting the intensity of defoliation and providing a period for grazed plants to regrow between grazing bouts, managers can ensure that preferred forage species maintain active photosynthetic tissue to support regrowth. As stocking rate and animal density increases, cattle and other herbivores have fewer opportunities to exercise their plant selection preferences, and consumption of unpalatable species, such as weeds, can increase compared to continuous stocking systems in which animal densities are lower (Augustine & McNaughton, 1998). By improving the competitive ability of preferred forage species, rotational stocking may allow farmers to utilize reconstructed prairies without shifting these plant communities from diverse communities with high ecosystem function to an alternative, degraded state with limited opportunity for recovery (Briske et al., 2005).

Large herbivores such as American bison (*Bison bison* L.) can increase heterogeneity in tallgrass prairies as they create disturbance patches due to selective defoliation, soil disturbance, and patchy redistribution of nutrients as they excrete manure and urine (Steinauer & Collins, 2001). In western tallgrass prairie, moderate grazing by

bison can increase plant community diversity (species richness and evenness) and increase heterogeneity between patches at the 10-m^2 scale (Collins & Smith, 2006). At small spatial scales (0.5 to 3.0 m), selective grazing of C4 grasses by bison increased species richness, diversity and heterogeneity (Veen et al., 2008). Veen et al. (2008) did not find strong correlations between diversity measures and availability of light and soil nitrogen and concluded that grazing directly altered plant-to-plant competition by suppressing dominant C4 grasses. Bison had a similar effect on plant community structure in reconstructed prairies in central Iowa, but positive changes in diversity were moderate due to limited pools of native propagules in the Corn Belt landscape dominated by annual row crops (Martin & Wilsey, 2006). When bison and domestic cattle (*Bos primigenius,* f. *taurus*) were stocked at similar densities (mass per area) in the Flint Hills, Towne et al. (2005) found that native and non-native bovines had similar effects on the tallgrass prairie community at the paddock scale (5 ha).

Large herbivores redistribute nutrients across the landscape by concentrating nitrogen and other nutrients in biomass into relatively small and discrete patches via excretion. Approximately 85 percent of nitrogen consumed by cattle is returned via excreta (Haynes & Williams, 1993). Herbivores also create patches of disturbed soil, creating sites where rudereal species can dominate within systems that are otherwise dominated by perennial species (cite).

Important environmental gradients may limit the fitness and thus dominance of C4 grasses in the prairie-forest border region. Compared to western tallgrass prairies, the prairie-forest border region is located at higher latitude, and the climate is more influenced by cold Arctic air masses as well as humid air masses traveling northward

from the Gulf of Mexico through the Mississippi River corridor (Anderson, 2006). Sunlight intensity is lower, average high temperatures are lower, evapo-transpiration rates are lower, and the mean length of the growing season is shorter. A survey of remnant tallgrass prairie sites ranging from the Gulf of Mexico to Canada showed that the ratio of native C3 grasses:native C4 grasses increased from south to north and was positively correlated to soil organic matter and negatively correlated to annual precipitation and temperature (Diamond & Smeins, 1988). In southeastern Wisconsin, native C4 grasses did not competitively exclude other native plants in a wet mesic prairie remnant when management shifted from semi-annual late summer mowing for hay to spring prescribed fires, and the authors speculated the lack of competitive exclusion by C4 grasses after five decades of frequent fire may be due to relatively higher competitive ability of C3 grass and forb species in this climate regime (Rooney & Leach, 2010). Reconstructed prairies can be similar to remnant prairies in diversity and evenness (Martin et al., 2005; Carter & Blair, 2012), but it is also common for these communities to become dominated by native C4 grasses (Sluis, 2002; Camill et al., 2004), particularly in grasslands reclaimed from cropland for the Conservation Reserve Program (Adler et al., 2009).

My goal in this study was to directly test hypotheses about how rotational grazing with domestic cattle can alter plant community composition in the prairie-forest border region of the Upper Midwest. I measured initial plant community composition prior to conducting defoliation treatments, and I was able observe trends following two seasons of disturbances. In addition to rotational grazing and control treatments, I also compared the effects of defoliation by mowing only. By comparing the community-level effects of

two different defoliation treatments—plant-selective herbivory and height-selective mowing—I was able to explore the importance of selectivity on community composition.

My hypotheses were:

- community composition would diverge between control and defoliated treatments;
- heterogeneity within and among plots (characterized by evenness and dispersion, respectively) in the control treatment would decrease over time;
- heterogeneity within and among grazed plots would increase;
- heterogeneity within and among mowed plots would increase; and
- dominance would be lower among both grazed and mowed plots than control plots.

Methods

Study site and experimental design

This study was located at the University of Wisconsin Arlington Agricultural Research Station in southern Wisconsin (43.30°N, 89.35°W). Soils are Plano silt loam (fine-silty, mixed, superactive, mesic Typic Argiudolls). This soil series covers more than 150,000 hectares in the Midwest (NRCS) and is locally associated with the historic York/Empire Prairie, one of the largest prairie landscapes found in southern Wisconsin at the time of European settlement. The study site is located within the southeast glacial plains ecological landscape classification (WiDNR, in prep.). Soils are strongly influenced by glacial and periglacial action, with calcareous till (material deposited directly by glaciers)

overlain by silts that were redistributed by wind during the period of glacial retreat and prior to re-vegetation of the post-glacial sediments. The southeast glacial plains are characterized by flat to rolling topography, but locally, long, linear ridges (drumlins) are aligned along the northeast-southwest trend of glacial advance out of the Lake Michigan basin. Prior to fragmentation by roads and cultivation, this landscape was very conducive to the spread of fire because ridges are aligned with prevailing winds from the west and south. Elsewhere in southern Wisconsin, moraines, drumlins, dissected uplands, and riparian corridors commonly presented topographic barriers to fire, which facilitated the development of a more heterogeneous landscape with prairie, savanna, forest and wetland plant communities found in close proximity (Curtis, 1959).

Reconstructed prairies were located within a matrix of annual row crops and pastures at the research station, and intensive dairy production utilizing row crops and alfalfa to feed large herds of cows (100 to 1000) kept in confinement is the dominant land use of the Empire Prairie. A large tract of reconstructed prairie (approximately 300 ha) occurs 2 km to the northwest at the Madison Audubon Society's Goose Pond Sanctuary, and a small dry- to dry-mesic prairie remnant (1 ha) occurring on thin, rocky soils is located on the research station approximately 1 km west. The study site is located within the Yahara River watershed, which drains into Lake Mendota in the Madison metropolitan area, and ultimately into the Upper Rock River and Upper Mississippi River watersheds.

The prairies used in this study were planted as part of the Wisconsin Integrated Cropping System Trial (WICST), a long-term study of the agronomic, environmental, and economic performance of cropping systems of varying management and input

intensity (Posner et al., 2008). Prairie restoration began in 1999 (Simonsen et al., 2002). The primary goal was to re-introduce native plants and an associated process (anthropogenic fire) to restore the structure and ecosystem function of the native plant community for comparison with contemporary cropping and forage systems. The 1999 prairie restoration (WICST Prairie) was implemented as a randomized complete block design with three diversity treatments randomly assigned within each of three blocks: 1) a low-diversity (LD) prairie seed mix including six native species, 2) a high-diversity (HD) prairie seed mix including 26 species (the LD complement and an additional 19 species), and 3) a control, continuous corn (CC) planted and harvested annually. The species sown in these treatments are native species found in mesic tallgrass prairie communities, though some are found in greatest abundance in wetter or drier prairie communities (Hoffman, 2002); a list of species planted is included in Appendix 1, Table 1 (adapted from Simonsen et al., 2002).

The prairie seed was hand broadcast and cultipacked in June 1999, and subsequent management included periodic clipping for weed control during the growing seasons of 1999-2002 (Simonsen et al., 2002). The CC treatment concluded in 2006; in June 2007, monocultures of switchgrass (cultivar, Forestburg) (*Panicum virgatum* L.) were established in these plots. Prior to the beginning of this study, the prairies were managed with spring-time prescribed fires and were burned in 2003, 2005, and 2008. During this study, prescribed fires were conducted annually (2009 to 2011) in the spring.

In early spring, prairie vegetation was dominated by two exotic, cool-season sod-forming grasses: Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leyss.). In late spring through early summer, exotic dominance was reduced as

native species emerged, and by mid-summer native, perennial C4 grasses and native forb species in the family Asteraceae formed the matrix of vegetation; the species Indiangrass (*Sorghastrum nutans* [L.] Nash.), saw-tooth sunflower *(Helianthus grossesseratus* M. Martens), and big bluestem (*Andropogon gerardii* Vitmann) each reached mean absolute cover of 20 percent or greater in control plots by fall 2010, and New England aster (*Aster nova-angliae* L.), Canada goldenrod (*Solidago canadensis* L.) yellow coneflower (*Ratibida pinnata* [Vent.] Barnhart), false sunflower (*Heliopsis helianthoides* [L.] Sweet), and rigid goldenrod (*Solidago rigida* [L.] Small) each reached mean absolute cover of 5 percent or greater in control plots by fall 2010); during later parts of the growing season, exotic cool-season grasses remained common in the understory and formed the canopy in local patches (typically < 10-m^2).

Management treatments were applied in a hierarchical, split plot design. Diversity treatments served as whole plots in the nomenclature of the split plot design. Each whole plot was split into three subplots to apply disturbance treatments: grazing, mowing, and control treatments. Due to requirements of the grazing treatment (fencing and supplying water), this split was applied at the block level, with control subplots located in the southern position, and grazing and mowing subplots randomly assigned to the northern or central positions. To account for this spatial arrangement, management blocks was included as a random factor in statistical analyses. This experimental design resulted in 18 experimental units, with 6 experimental units in each block and 3 experimental units in each prairie diversity treatment (Fig. 1). Each experimental unit measured 12.2 ***x*** 35 m, covering approximately 400-m^2 (0.04 ha).

Disturbance treatments

Rotational grazing management methods and tools were comparable to those commonly applied by farmers in the Upper Midwest. A three-strand high tensile electric fence surrounded each WICST Prairie block. Portable electric fences were used to define grazing paddocks within each block. The experimental design included six paddocks (3 blocks ***x*** 2 diversity levels) during each round of grazing management. Due to the limited number of cattle available to conduct the grazing treatment, the experimental units in the grazing treatment could not be treated on the same day. Within each grazing period, treatments were completed across all experimental units within 7 to 9 days (Table 1).

Grazing management included Holstein cattle, the dominant dairy producing breed in Wisconsin. The WICST rotational grazing system uses heifers, which have lower nutritional needs compared to lactating cows or steers being fattened for beef production (Ball et al., 2001). Average animal weight was approximately 230 kg in June and 270 kg in July. Cattle were supplemented with 1 kg of corn per animal on a daily basis.

From May to November, these cattle typically graze on pastures dominated by non-native C3 grasses and forbs planted for forage production. Prairie acclimation plots were established within the WICST prairies, outside of the boundaries of the experimental units, in order to provide the cattle with an opportunity to adjust to new forage species. Cattle grazed stands of restored prairies and switchgrass monocultures for two days prior to grazing on the first experimental unit. Acclimation units also provided researchers the opportunity to observe how the cattle reacted to prairie swards prior to beginning disturbance treatments.

Grazing timing was managed to optimize forage production and stand vigor (Mousel et al., 2005). In 2009 and 2010, the first grazing period began in June, when C4 grasses were 30 to 45 cm in height. Grasses had matured to the 4 to 5 leaf stage and were on the verge of the stem elongation stage. Paddocks were rested approximately 35 days before the second grazing period (Table 1).

Mowing was conducted using a rear-mounted, PTO-driven rotary deck mower, an implement used by a wide range of land managers. The mower deck was adjusted to leave a residual vegetation height of 15 to 20 cm, similar to the residual height of C4 defoliated by cattle in this study's grazing treatment. Mowing coincided closely with grazing events, but this management could not be conducted at simultaneously due to potential disturbance of the cattle in the adjacent grazed plots.

Estimating plant community composition

Crews sampled the plant community in late spring (June) from 2009 through 2011. Sampling was completed prior to application of disturbance treatments. The line-intercept method was used for plant community sampling (Elzinga et al., 1998). Sampling teams identified and recorded each unique species intercepted when a thin rod was lowered vertically through layers of the canopy to the ground. If the rod did not intercept a living plant, observers recorded whether the rod was resting on bare ground or litter. After completing transect observations in each experimental unit, observers carried out a walk through search for plant species that were present in the plot but were not intercepted along any transect. Species observed only on walk throughs were assigned an absolute

cover of 0.5 percent. Taxa nomenclature follows the USDA Plants Database (plants.usda.gov).

Data analysis

Each species was classified according to native or non-native origin. I further classified species into seven growth-form classes (C3 grass, C4 grass, sedge, legume, forb, vine, and tree). By evaluating species under both classifications, I identified 10 unique functional groups for species observed in the prairies (native C3 grass, non-native C3 grass, native C4 grass, non-native C4 grass, native forb, non-native forb, native legume, non-native legume, native sedge, native tree, and native vine).

Multivariate analyses

For multivariate analyses, I used absolute abundance rather than relative abundance data because the coefficient of variation (CV) of total cover across sampling units was relatively low. CV values were relatively low for the grand mean of all plots across all years (10.7%), and the CV of plots within each year was never greater than 14.6% (data not shown). Resemblance among sample units was calculated from absolute cover of each species using the Bray-Curtis semi-metric measure of community dissimilarity. To reduce the effect of shared zeroes in the dataset, I initially selected 49 species that were observed in at least two experimental units.

I used non-parametric permutational multivariate analysis of variance (Anderson, 2001) to test the affects of block, diversity, and management on plant community composition between June 2009, June 2010, and June 2011. PERMANOVA can be used with any ANOVA experimental design and tests the response of multiple variables

without needing to meet the assumptions of traditional parametric multivariate ANOVA (namely, response variables that follow a normal distribution and are not correlated). Ideally, samples within different factors should have homogeneity of dispersion, but this requirement is relatively lax (Anderson et al., 2008). PERMANOVA uses permutational procedures to calculate a pseudo-*F* statistic of the distribution of a large number of random combinations (i.e., 9,999). PERMANOVA tallies the number of times the pseudo-*F* statistic of the random combinations equals or exceeds the pseudo-*F* of the actual data set, and the p-value is calculated from this tally divided by the total number of permutations. A separate test for homogeneity of dispersions is recommended to determine if significant effects found by PERMANOVA are due to location effects, dispersion among experimental units, or both. I also evaluated if disturbance treatments resulted in changes in heterogeneity over time. Within each disturbance treatment, I used PERMDISP to compare heterogeneity in 2009 and 2011.

I used non-metric multi-dimensional scaling (NMDS) to visualize dissimilarity among plots in two dimensions in order to qualitatively evaluate treatment effects on location and dispersion. Discriminant analysis using canonical analyses of principal components (CAP) (Anderson & Willis, 2003) provided a tool for visualizing differences in multivariate space indicated by PERMANOVA. In contrast to unconstrained ordination techniques like NMDS, CAP finds an axis or axes that maximizes separation between a priori groups and can reveal patterns that are otherwise masked by unconstrained ordinations. The CAP routine (Anderson et al., 2008) provides tools to calculate correlations between each variable and the canonical axes. Multivariate

analyses were conducted using PRIMER version 6.0 and PERMANOVA+ software (Clarke & Gorley, 2006; Anderson et al., 2008).

Univariate analyses

The effects of diversity treatment, diversity treatment, and year on native richness, non-native richness, evenness and dominance were also evaluated. Hill's evenness (E) was calculated as exp(H'), where H' is Shannon's diversity index of a sampling unit; Shannon's diversity was calculated as $H' = -\Sigma P_i \log(P_i)$ where P_i is the relative cover of species *i* in sampling unit P. *Sensu* Jost (2006), E improves upon H' because E does not favor common or rare species and weighs all species by their frequency; additionally, E is multiplicably linked to richness, unlike H' (for example, as species richness doubles, E doubles but H' does not).

Simpson's dominance index (D) was calculated as

$$D = \Sigma \frac{n_i(n_i-1)}{N(N-1)}$$

where *n* is the absolute cover of species *i* and *N* is the total cover in a sampling unit.

The effects of diversity treatment, disturbance treatment, and year were evaluated using linear mixed effects models. All mixed effects models were fit with block, management block nested within block, and field as random factors to account for the split plot experimental design as well as variation within blocks caused by lack of complete randomization of management treatments. Models were evaluated using Aikake's Information Criteria (AIC). I used likelihood ratio tests to compare the full model (with diversity ***x*** management ***x*** year interactions), with successively simpler

models, including management + year, management only, and year only. Further model selection followed Crawley (2002)—factor levels were pooled and the simpler model was compared to the more complex model with likelihood ratio tests. The more parsimonious model was chosen unless models were significantly different ($\alpha = 0.05$). Linear mixed effects models were evaluated using the R package lme4 (Bates et al., 2011). To account for the difficulties in calculating *p*-values from linear mixed effects models, upper- and lower-bound *p*-values were calculated using R package LMERConvenienceFunctions (Tremblay, 2011). Tremblay (2011) describes these *p*-values as anti-conservative and conservative, respectively. The df used to calculate upper-bound *p*-values are the number of data points (n) minus the number of df used up by the fixed effects; df for lower-bound *p*-values were calculated n minus the number of df used up by the fixed effects and the number of random effects in the model. Both upper- and lower-bound *p*-values are presented in tables, and conservative *p*-values are referenced in the results. Tukey's Honestly Significant Difference (HSD) was used to evaluate pair-wise comparisons of factor levels in the final model using R package languageR (Baayen, 2011). All mixed effects model analyses used R version 2.13.2 (R Development Core Team, 2011). The R package sciplot (Morales, 2011) was used to graph the means and standard errors of Hill's evenness, Simpson's dominance, and species richness.

Results

Multivariate analyses of community composition

The assumption of homogeneity of dispersions for PERMANOVA was met across all treatments and years (Table 2). PERMANOVA showed no significant differences among high-diversity and low-diversity prairie treatments prior to or following disturbances. Prior to applying disturbance treatments, no significant differences were found among sampling units ($p = 0.12$). Strong differences in composition were apparent among disturbance treatments in June 2010 and June 2011 ($p < 0.01$) (Table 3). In June 2010, pair-wise tests found significant differences between grazed and control plots ($p = 0.02$) and mowed and control plots ($p = 0.03$); in June 2011, mowed and control plots remained significantly different ($p = 0.04$), but evidence for differences between grazed and control plots was no longer strong ($p = 0.12$) (Table 4). Grazed and mowed plots showed weak evidence of diverging by June 2011 ($p = 0.07$).

Comparisons of heterogeneity within disturbance treatments (Table 5) showed that reduced mean dispersion among control plots was not significantly different in 2009 and 2011 ($p = 0.59$). In disturbed plots, reduced mean dispersion of mowed plots was not significant ($p = 0.22$), while reduced mean dispersion of grazed plots was nearly significant for $\alpha = 0.10$ ($p = 0.11$).

NMDS plots for 2009 through 2011 did not illustrate strong separation of treatment groups due to disturbance (Fig. 2). The strong overlap among experimental units in different disturbance treatments suggest that the significant effects of disturbance treatment found by PERMANOVA have not resulted in extreme shifts in plant

community composition. In agreement with PERMANOVA results, CAP was not useful for finding an axis or axes that separated pre-treatment community composition in 2009, and useful axes were found for 2009 and 2010. The CAP plots show separation between grazed, mowed, and control plots in June 2010 (Fig. 3), and for June 2011, the plot (Fig. 4) indicates mowed plots had strongly diverged from control plots in composition, and composition in grazed plots was intermediate. Vector overlays show all species with a Spearman correlation $r > 0.6$ for 2010 and $r > 0.5$ in 2011. Each level was selected because weaker associations included many species that were closely correlated. In 2011, mowed plots and some grazed plots were strongly correlated with the non-native legume red clover (*Trifolium pratense* L.), the non-native forbs greater goat's-beard (*Tragopogon dubius* Scop.) and wild carrot (*Daucus carota* L.), and the non-native C3 grass orchardgrass (*Dactylis glomerata* L.); weaker correlations included the non-native C3 grass Kentucky bluegrass and the native C4 grass Indiangrass (Fig. 4, Tables 6-7). Control plots were strongly correlated with the native forb saw-tooth sunflower and the non-native C3 grass quackgrass (*Elymus repens* [L.] Gould) and less strongly correlated with the native forbs Canada goldenrod and New England aster.

Absolute cover of major functional groups were illustrated by disturbance treatment and year and graphs are provided as ancillary data to aid interpretation of results (Fig. 5).

Evenness and dominance

Plant community evenness was not significantly affected by diversity treatment ($p < 0.40$) (Table 8). Model selection indicated that mow and control plots were similar to

each other but not to grazed plots. The best model indicated that the effect of disturbance was not significant ($p < 0.45$) but that there was a significant year ***x*** disturbance interaction ($p < 0.03$) (Table 9). The response of evenness to disturbance and time was nonlinear, with peak evenness occurring in grazed plots in 2010 disturbance treatments; Tukey's HSD comparisons showed that the evenness in grazed plots in 2010 was similar to mowed and control plots in 2010, but was higher than all disturbance treatments in both 2009 and 2011 (Fig. 6a).

Essentially mirroring the results for evenness, the response of Simpson's dominance was nonlinear, with dominance reduced among grazed plots in 2010 (Fig. 6b), and there was a significant year ***x*** disturbance treatment interaction ($p < 0.024$) (Table 9). Model selection indicated that mow and control plots were similar to each other but not to grazed plots. Tukey's HSD pair-wise tests comparing grazed and ungrazed plots across years indicated that within each year, dominance was similar across disturbance treatments. In grazed plots, mean dominance was lower in 2010 than in 2009 ($p < 0.01$) or 2011 ($p = 0.04$) (data not shown).

Native and non-native species richness

Model selection indicated that diversity treatment had a significant effect on native species richness, and the full model found a significant effect of diversity on native species richness ($p < 0.01$) (Table 10). Mean native species richness was 16.0 in low-diversity prairies and 22.2 in high-diversity prairies (Table 11). Subsequently, the effect of disturbance treatments and sampling year on native species richness was modeled separately for each diversity treatment. In high-diversity prairies, model selection

indicated that disturbance was the only significant factor affecting species richness ($p <$ 0.04) (Table 12). Model selection indicated that grazed plots were different than mowed and control plots. Mean richness of grazed plots was significantly lower than mowed and control plots across all years (Fig. 7a). In low-diversity prairies, model selection found that the best model simplified disturbance treatments into grazed and not grazed treatments. There was weak evidence that a disturbance treatment ***x*** year interaction was significant ($p < 0.09$) (Table 13). Tukey's HSD pair-wise comparisons indicated that mean richness in grazed plots did not change significantly over time and was not significantly different than mowed and control plots (Fig. 7b). There is weak evidence that in control and mow plots, mean richness was greater in 2009 than in 2011 ($p = 0.09$); richness was intermediate in 2010 and did not differ significantly from 2009 or 2011.

Model selection indicated diversity treatment did not have a significant effect on non-native species richness. There was a significant year ***x*** disturbance treatment interaction ($p < 0.02$) (Table 14). Tukey's HSD pair-wise comparisons showed that there were no differences between disturbance treatments in 2009 (Fig 8). Exotic species richness increased across all treatments in 2010, with no difference among treatments. In June 2011, mean non-native richness in control plots was similar to 2009 levels. In grazed plots, exotic richness was lower than in 2010 but higher than 2009; exotic richness was similar across grazed and control plots ($p = 0.65$). In mowed plots, exotic richness was similar in 2011 and 2010; mowed plot exotic richness was similar to grazed plot exotic richness ($p = 0.8$) and higher than control plot exotic richness ($p = 0.02$).

Discussion

Mowing proved to be a more intense disturbance than grazing in these reconstructed tallgrass prairies. Mowed plots diverged in composition from control plots following the first year of disturbance treatments, remained dissimilar to control plots following the second year, and showed weak divergence from grazed plots after two years of disturbance. In contrast, strong differences between community composition in grazed and control plots were transient, and grazed plots remained similar to control plots following two years of disturbance treatments. Predicted changes in dispersion of plots within each of the respective disturbance treatments were not observed, and changes to mean within-plot heterogeneity were only observed as a transient outcome of grazing when dominance was suppressed and evenness increased in 2010.

In contrast to western tallgrass prairies where selective grazing of native C4 grasses has served to increase diversity and heterogeneity through competitive release and other mechanisms (Collins et al., 1998; Veen et al., 2008), the prairies evaluated in this study were subject to several factors that inhibited competitive release and changes in plant community composition and heterogeneity. These characteristics are common to many reconstructed grasslands and some degraded remnant prairies: sod-forming non-native C3 grasses were dominant; initial species diversity was low and richness of native forbs was relatively low; and landscape context (dominated by row crop agriculture) facilitated seed dispersal of non-native rudereal species rather than native species characteristic of tallgrass prairie.

Ten years after initial seeding, the original diversity treatments continued to have a significant effect on native species richness. In both low-diversity and high-diversity prairies, grazed plots had lower species richness prior to the application of disturbance treatments, and this pattern persisted over time. Native seed dispersal to prairie plantings in fragmented agricultural landscapes is strongly limited (Martin & Wilsey, 2006; Foster et al., 2011). Over time, aggressive species included in the high diversity seeding mix (including Indiangrass, saw-tooth sunflower and rigid goldenrod) successfully colonized low diversity plots, contributing to the lack of significant differences in community composition when low- and high-diversity prairies were analyzed with multivariate methods. In contrast to native species richness, mean non-native species richness was not different between low-and high-diversity plantings. Non-native species richness also increased across all disturbance treatments over time. The lack of significant differences between disturbance treatments and control treatments can be attributed to previous invasion by non-native species including C3 grasses, legumes, and forbs, which inherently limited the potential for cattle or mowing equipment to introduce new non-native species. The overall increasing trend for non-native species richness was facilitated in the WICST prairies by small plot size (distance to edge is between 10 and 40 m for all plots) and frequent tillage used to maintain a border between cropping system treatments at WICST, which kept the edges of the reconstructed prairie blocks in a disturbed state.

Overall, dominance in the WICST prairies was lower than reported for western tallgrass prairies. In contrast to the plant community described by Smith et al. (2004), the plant community at WICST was characterized by shallowly-sloping rank-abundance relationships. Biodiversity-ecosystem function (BEF) theory suggests that high species

richness (including redundancy within functional groups) is important for maintaining community stability and ecosystem function under changing conditions (Isbell et al., 2011). The low dominance, high evenness, and redundancy among several native functional groups (two native C4 grass species; multiple native forb species) may help account for resistance to shifting to an alternate, degraded state. For example, the absolute cover of the native C4 grass functional group was relatively stable in grazed and mowed plots, but the effect of defoliation on C4 grasses was species specific. Mean big bluestem cover remained stable in control plots but decreased in both grazed and mowed plots, and mean Indiangrass cover increased across all treatments.

Non-native C3 grasses increased in the grazing treatment, which may have been facilitated by a combination of high initial cover, herbivory avoidance, herbivory tolerance, propagule introductions, and plant-soil interactions. Compared to other values reported in the Upper Midwest, non-native C3 grass cover in these 10-year-old prairie reconstructions was very high. Cool-season pastures in central Iowa restored through herbicide, seed addition, and prescribed fire had less than 5 percent non-native species cover 10 years after restoration began (Carter & Blair, 2012), and non-native C3 grass cover was below 10 percent in 8-year-old reconstructed prairies in southeastern Minnesota (Camill et al., 2004). Non-native C3 grasses flower earlier than the period of grazing in this study, and cows tended to avoid smooth brome and Kentucky bluegrass tillers in flowering or seed development stages, and this phenology-grazing interaction may have allowed expansion by vegetative reproduction or seed production. Cattle were observed consuming these species when tillers remained in the vegetative growth stage.

In a small plot study in western Iowa incorporating a number of similar species, grazed non-native species shifted resources from roots to aboveground growth and recovered aboveground biomass more quickly than native species which maintained belowground root mass (Isbell & Wilsey, 2011). This supports the theory that non-native C3 grasses have evolved stronger compensatory growth in response to grazing pressure than native C4 grasses (Augustine & McNaughton, 1998). Timothy, a non-native C3 bunchgrass, increased in cover over time from very low levels in grazed plots, and grazing may have facilitated introduction of seed into the prairies because this species is common in cool-season pastures grazed immediately prior to the prairies.

Native forb cover increased over time in grazed plots, decreased in control plots from 2009 to 2010 before rebounding to initial levels in 2011, and steadily decreased in mowed plots. Non-native forbs remained a relatively small proportion of the plant community and there was no evidence that grazing facilitated an increase in cover or richness. Non-native forb cover followed a downward trend in control plots, did not vary in grazed plots, and increased in mowed plots. Prior to application of disturbance treatments, the biennial species wild carrot was most abundant in mowed plots and increased under mowing over time, driving the increase in non-native forb cover in this disturbance treatment. Unless mowing occurs when wild carrot when seeds are immature, mowing is relatively ineffective at limiting aboveground biomass and reproduction of this species, particularly on finely-textured soils (Harrison & Dale, 1966).

Native forbs decreased in cover in mowed plots but remained stable or increased under grazing, indicating that many of the dominant native forbs at this site (primarily tall-stature species in the Asteraceae family) can tolerate or benefit from herbivory via

avoidance but are sensitive to defoliation. Mowing removed the majority of photosynthetic tissue in these plants, and belowground reserves were utilized to support regrowth. In some species, regrowth occurred from meristematic tissue at low axils that escaped defoliation, but in other species defoliation stimulated growth from dormant buds in the crowns or rhizomes. Repeated mobilization of belowground reserves and belowground meristems (buds) may account for the trend of decreased native forb cover observed (Dalgleish & Hartnett, 2009).

Plant-soil interactions that operate to increase non-native C3 grass abundance in grazed grasslands may also benefit some species of native forbs—within this functional group, some species exhibit traits similar to non-native C3 grasses, including spreading and shallow root systems (Bingham & Biondini, 2011), as well as thinner leaves, lower root-to-shoot ratios, and lower C:N ratios than native warm-season grasses (Craine et al., 2002). Forb species that exhibit clonal growth forms and establish large patches may be most competitive under grazing. Bison avoid patches of vegetation dominated by forbs (Fahnestock & Knapp, 1993; Vinton et al., 1993), and, in pastures, domestic cattle have been shown to be more selective when palatable and less desirable species are separated into larger patches (Laca, 2009). At higher stocking rates, competitive release of forbs may not be observed because cattle consume a wider variety of species and more forb biomass as grazing pressure increases (Mayer & Huovinen, 2007), and greater canopy removal can facilitate increased herbivory of shorter statured forbs that may escape observation at lower grazing pressures (Hickman & Hartnett, 2002). In European semi-natural permanent grasslands, high stocking rates reduced cattle selectivity and favored small stature forbs, while low stocking rates similarly promoted selectivity and tall

stature forbs were favored (Dumont et al., 2009). In western tallgrass prairie, forbs grew taller in ungrazed patches than in grazed patches due to competition for light, but higher standing biomass, higher reproductive biomass and higher flowering were also observed for various forb species in grazed patches (Fahnestock & Knapp, 1993). These positive results for forbs can cascade down trophic levels and support greater insect biomass and diversity.

Native forbs and non-native C3 grasses increased under grazing, yet native C4 grasses were not effectively excluded by defoliation, plant-plant competition, or plant-soil interactions. The decrease in Indiangrass cover and decrease in big bluestem cover in both the grazed and mowed prairies suggest that local ecotypes of Indiangrass are more resilient to summer defoliation than big bluestem. Both Indiangrass and big bluestem planted in monocultures on sandy soils in central Wisconsin decreased rapidly when grazed by bison in mid- to late-summer at rates of biomass removal (residual vegetation height < 10 cm) (Jackson et al., 2010), reflecting the importance of management on different outcomes for native grasses and grazing. Overall, trends observed in this study suggest that native C4 grasses are highly competitive in the prairie-forest border region, even when defoliation suppresses competitive ability and when herbivore-plant-soil interactions result in higher availability of nitrogen and other resources.

In the long-term, if non-native C3 grasses are slightly more competitive than native C4 grasses under the summer grazing management regime, the better competitor could slowly displace the native species (Inouye & Tilman, 1995) and facilitate a shift to an alternative stable state. After crossing a threshold of higher C3:C4 ratios, maintaining native plant diversity or restoring C4 grass dominance could be difficult because non-

native C3 grass dominance can reduce native species richness (Miles & Knops, 2009) and lead to increased rates of nutrient cycling and increased competitive ability of cool-season gasses (Vinton & Goergen, 2006).

Generally, as the relative abundance of non-native C3 grasses increases, C:N ratios of litter decrease and decomposition rates and soil nitrogen availability increases, which can limit the competitive ability of native species with low C:N ratios and low demand for nitrogen (Vinton & Goergen, 2006). The typical management response to non-native C3 invasion in tallgrass prairie is to increase spring fire frequency to limit nitrogen availability, but the low C:N ratios and high palatability of this functional group also provide an opportunity to implement a different disturbance regime (*sensu* Firn et al., 2010) to limit non-native C3 grass abundance and generate greater heterogeneity in nutrient distribution. In this study, grazing was timed to take advantage of rapid forage production by native C4 grasses and to suppress stem elongation in order to maintain these grasses in a vegetative state to promote high forage quality later in the growing season—however, grazing could be initiated earlier in the season to facilitate selective grazing of non-native C3 grasses. Smooth brome abundance is reduced when prescribed fire is timed to top-kill during the stem elongation phase, but is not effective during the vegetative stages or after inflorescence emergence (Willson & Stubbendieck, 2000) and appropriately-timed grazing may yield similar effects (Salesman & Thomsen, 2011). Late-spring prescribed fire can damage early phenology native forbs (as reviewed by Copeland et al., 2002), but selectivity and preference for grass by large herbivores means many native forbs may avoid herbivory (particularly species in the composite family, which typically emerge and accumulate biomass as a prostrate rosette during spring

before stem elongation begins). Indirect effects of high intensity, short duration spring grazing may benefit native forbs and native C4 grasses because the majority of nutrients present in stems and leaves of C3 grasses will be returned in highly labile form as excreta in small and discrete patches at approximately the same time that native species are initiating rapid growth. Defoliated C3 grasses may suffer from competitive exclusion when attempting to compete for above and belowground resources to support regrowth at the same time that C4 grasses are initiating their rapid period of growth. This effect may be limited due to the capacity of non-native C3 grasses to rapidly mobilize root reserves (Isbell & Wilsey, 2011) but native forbs also demonstrate high root plasticity in response to increased nutrient availability at fine spatial scales (Johnson & Biondini 2001).

Conclusion

In the Upper Midwest, rotational stocking of cattle at low to moderate stocking rates to utilize reconstructed prairies for summer forage can facilitate greater native forb abundance. The stability of C4 grass cover indicates that when timing and intensity of grazing are closely monitored and managed, defoliation and changes in plant-plant competition will not necessarily result in declining survival or abundance of this important functional group. It is important to reiterate that in this study, defoliation by grazing and mowing was managed to limit detrimental effects on C4 grasses, with defoliation height selected to maintain leaf area to support regrowth and to limit removal of apical meristems in order to limit stimulation of meristems in the crown or rhizomes.

To promote native species diversity in grazed reconstructed prairies, managers will need to overcome propagule limitation if initial native species richness is low, as at

the WICST prairies. Combining managed grazing with interseeding of early phenology forbs and native C3 grasses and sedges may help managers pursue adaptive management to reconstruct plant community diversity that more closely resembles remnant prairie communities found in the Upper Midwest (Sivicek & Taft, 2011; Carter & Blair, 2012).

Managed grazing is not a panacea for management challenges facing stewards of tallgrass prairies. The results presented here show equivocal effects of managed grazing by domestic cattle in reconstructed prairies. However, the lack of rapid shift to an alternate, degraded state and the unexpected interactions between plants and method of defoliation suggest that the ongoing development of more sophisticated grazing and mowing management could benefit species diversity in reconstructed prairies in the prairie-forest border region.

Future emphases for research on the processes and outcomes of grazing in prairies in the Upper Midwest could include dry mesic to mesic sites where dominance by native C4 grasses, non-native C3 grasses, or tall stature forbs is limiting the potential to recover the plant community composition and ecological function of highly diverse remnant prairies. Depending on the abundance of functional groups and the goals of the land manager, the type of defoliation treatment (as well as the timing, intensity, and frequency of defoliation) can be manipulated to meet goals for decreasing long-term abundance or providing transient suppression of dominance. A research agenda that includes closely-monitored and adaptive management to apply grazing or mowing to a wide array of reconstructed prairies could bear fruit for land managers and conservation of biodiversity and ecosystem function.

To increase the density of reconstructed prairies in agriculturally-dominated landscapes, it will be necessary to design and fund incentives that recognize the costs to farmers associated with low intensity management of reconstructed prairies (including high planting costs and reduced carrying capacity relative to typical pasture seeding mixes and plant communities), as well as the value of ecosystem services that primarily accrue beyond the farm. Where existing reconstructed grasslands are threatened with conversion to row crops or succession to woody-dominated communities, collaborative grazing research can provide opportunities to forestall threats and organize stakeholders with diverse viewpoints and values around management that can potentially meet the needs of farmers while protecting or enhancing biodiversity and ecosystem function (Miller et al., 2012). Better understanding of how grazing management ramifies to affect ecosystem function and delivery of ecosystem services at farm and watershed scales are needed to inform decision making by land managers and policy makers.

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Tables and Figures

Table 1. Timing of grazing, duration, and instaneous stocking rate across four grazing periods.

Grazing Period	Diversity	Dates	Duration[a]	Rate[b]
June 2009	LD	6/5 – 6/11	22.8	28.5
	HD	6/4 – 6/10	22.0	27.5
July 2009	LD	7/8 – 7/13	10.0	15.0
	HD	7/9 – 7/14	9.8	14.8
June 2010	LD	6/18 – 6/23	12.7	15.8
	HD	6/17 – 6/22	14.8	18.5
July 2010	LD	7/21 – 7/23	8.2	12.3
	HD	7/21 – 7/24	4.5	6.8

[a] Mean hours paddock^{-1}

[b] Mean animal units acre^{-1} day^{-1}

Table 2. Permutational analyses of homogeneity of multivariate dispersions, June 2009 to June 2011.

Year	Factor[a]	F	P
2009	Block	0.247	0.759
	Diversity	2.202	0.132
	Disturbance	1.206	0.233
2010	Block	0.425	0.639
	Diversity	2.986	0.092
	Disturbance	0.091	0.902
2011	Block	1.559	0.23
	Diversity	1.826	0.175
	Disturbance	2.021	0.110

[a] Factor degrees of freedom: block, df1 = 2, df2 = 15; diversity, df1=1, df2 = 16; disturbance, df1= 2, df2 = 15.

Table 3. Results from the PERMANOVA analysis of plant community similarity. Bold numbers indicate significance (α = 0.05). Block is a random effect in the model, and diversity and disturbance treatments are fixed effects.

Year	Source	df	SS	MS	Pseudo-F	P	CoV
2009	Block	2	3237.6	1618.74	1.328	0.38[a]	66.65
	Diversity	1	1348.62	1348.62	1.107	0.419[a]	14.42
	Whole-plot Error	2	2437.74	1218.87	--	--	406.29
	Whole-plot Total[b]	5	7023.9	--	--	--	--
	Disturbance	2	1294.9	647.45	1.524	0.128	37.08
	Sub-plot error	10	4249.9	424.99	--	--	424.99
	Total	17	12569	--	--	--	--
2010	Block	2	3521.1	1760.6	1.910	0.249[a]	139.82
	Diversity	1	1024.44	1024.4	1.112	0.446[a]	11.418
	Whole-plot Error	2	1843.35	921.69	--	--	307.23
	Whole-plot Total[b]	5	6389.1	--	--	--	--
	Disturbance	2	1868.8	934.38	2.818	**0.001**	100.42
	Sub-plot Error	10	3318.5	331.85	--	--	331.85
	Total	17	11576	--	--	--	--
2011	Block	2	2664.96	1332.48	1.604	0.304[a]	83.659
	Diversity	1	1021.74	1021.74	1.230	0.375[a]	21.247
	Whole-plot Error	2	1661.04	830.52	--	--	276.84
	Whole-plot Total[b]	5	5347.8	--	--	--	--
	Disturbance	2	1733.2	866.59	2.521	**0.005**	87.137
	Sub-plot Error	10	3437.7	343.77	--	--	343.77
	Total	17	10519	--	--	--	--

[a] Monte Carlo *p*-values were used because of low number of unique permutations (Perm.); see Anderson and Robinson (2003) for details. All other *p*-values from > 9,000 permutations.

[b] Whole plot total df and SS have been summarized in these rows; the values in these rows should not be double-counted toward total df and SS.

Table 4. Summary of mean Bray-Curtis similarities within and between disturbance treatments. Bold numbers indicate which pair-wise comparisons from within-year PERMANOVA found significant differences among disturbance treatments ($\alpha = 0.05$).

Year	Levels	Similarity	P	Perm.
2009[a]	Control	56.974	--	--
	Graze	65.514	--	--
	Mow	63.556	--	--
	Control-Graze	60.724	--	--
	Control-Mow	62.874	--	--
	Graze-Mow	64.727	--	--
2010	Control	63.834	--	--
	Graze	66.723	--	--
	Mow	64.141	--	--
	Control-Graze	**62.774**	**0.019**	9396
	Control-Mow	**62.536**	**0.033**	9386
	Graze-Mow	65.696	0.133	9406
2011	Control	60.817	--	--
	Graze	71.023	--	--
	Mow	68.838	--	--
	Control-Graze	65.488	0.116	9383
	Control-Mow	**61.651**	**0.037**	9386
	Graze-Mow	69.919	0.072	9384

[a] For 2009, pair-wise comparisons of disturbance treatments were not tested for significance because disturbance was not found to be significant (see Table 3).

Table 5. Summary of permutational tests of dispersion among experimental units within disturbance treatments. Trends in reduced mean deviation from group centroid observed within all disturbance treatments were not significant ($\alpha = 0.05$; permutations = 9999).

Disturbance	Year	n	Similarity	Deviation[a]	SE	F	P
Control	2009	6	56.974	27.549	2.93	0.336	0.592
	2011	6	60.817	25.382	2.32		
Grazed	2009	6	65.514	22.407	1.30	3.765	0.108
	2011	6	71.023	18.721	1.38		
Mow	2009	6	63.556	23.587	1.42	1.542	0.221
	2011	6	68.838	20.086	2.44		

[a] Mean deviation from group centroid (see Anderson et al., 2008)

Table 6. Absolute cover of the most abundant grass and legume species in WICST prairies, June 2009-June 2011. Species are presented within functional groups and are listed by greatest to least change in mean absolute cover between June 2009 and June 2011. Each species included achieved mean percent cover ≥ 1.0 in at least one treatment in at least one year. Italic font indicates non-native species.

	2009			2010			2011			(2009-2011)		
	M	G	C	M	G	C	M	G	C	M	G	C
Graminoids												
Kentucky bluegrass	60.7	44.7	59.7	71.1	64.5	67.7	68.2	64.5	53	7.5	20	-7
Indian grass	24.4	19.5	19	19.1	15.8	17.1	29.5	33.7	25.1	5.1	14	6.1
timothy	3.3	0.1	5	7.1	5.4	4.8	7.8	8.4	0.6	4.4	8.3	-4
smooth brome	24.5	23.5	25.1	18.3	20.1	16.5	25.9	25.9	18	1.4	2.4	-7
quackgrass	8.5	3.8	16	3.2	2.3	9.7	3.8	6.8	13.5	-5	2.9	-3
big bluestem	11.9	12.8	9.9	9.1	9.8	11.9	9.2	9.2	10.1	-3	-3.6	0.2
orchard grass	0.2	0.8	0.3	1	4.2	0.3	2.4	2.5	0.2	2.2	1.6	-0
reed canary grass	0.6	0.3	0	0	1.2	0	0.3	0.3	0	-0	0	0
Legumes												
black medic	0	0	0	7.8	8.7	1.3	2.4	3	1	2.4	3	1
sweetclover	0.4	0.4	2.1	4.2	3.6	1.7	0	1.1	0.3	-0	0.7	-2
red clover	1	0.4	0.4	15	12.5	1.8	2.5	1.4	0.1	1.5	1	-0
white clover	0.8	0.3	0.9	8	9.4	2.3	0.5	0.9	0	-0	0.5	-1
showy tick trefoil	0.6	0.5	1	0.7	0.8	0.4	0.8	1.3	0.6	0.2	0.8	-0
alsike clover	0	0	0	0.8	2.4	0.5	0	0	0	0	0	0

Table 7. Absolute cover of the most abundant forb species in WICST prairies, June 2009-June 2011. Species are presented within functional groups and are listed by greatest to least change in mean absolute cover between June 2009 and June 2011. Each species included achieved mean percent cover ≥ 1.0 in at least one treatment in at least one year. Italic font indicates non-native species.

Species	2009			2010			2011			(2009-2011)		
	M	G	C	M	G	C	M	G	C	M	G	C
wild carrot	1.1	0.1	6	9.4	0.8	4.5	9.5	1.8	1.8	8.3	1.7	-4.2
saw-tooth sunflower	19.6	21.8	26	13.4	19	20.6	13.1	23.1	27.6	-6.5	1.3	1.6
showy sunflower	5.2	3.4	4.4	2.3	5	1.2	0.5	1.8	1.7	-4.6	-1.6	-2.7
yellow coneflower	4.7	5.3	5.2	6	8.3	4.5	7	9.4	5.3	2.4	4.2	0.1
New England aster	3.3	4.3	7.3	3.5	3.8	6.2	2.3	3.6	4.2	-1	-0.6	-3.1
dandelion	8.5	8.3	7.8	5.1	7.2	6.4	5.4	5.4	4.9	-3.1	-3	-2.8
black-eyed Susan	0.2	0.5	0.5	0.9	2.8	1.5	3.1	2.5	1.7	2.9	2	1.2
common milkweed	0.7	0.7	1.2	1.1	1	2	1.3	1.4	3.7	0.6	0.7	2.5
prairie rosinweed	3.3	2	2.1	0.7	1.1	2.2	2.5	1.5	4	-0.8	-0.5	1.9
false sunflower	5.7	6.4	4.6	4.4	4.7	2.9	7.3	5.7	4.9	1.6	-0.7	0.3
rigid goldenrod	3.2	3	1.7	3.2	5.7	2.6	2.3	4.5	2.5	-0.9	1.5	0.8
Canada goldenrod	2.3	5.5	6	0.9	5.3	7.3	1.1	4.1	6.7	-1.1	-1.3	0.7
Canada thistle	3.5	0.6	3.3	2.5	0.7	2.8	2.5	0.6	2.8	-1.1	0	-0.5
bee balm	2.5	1	2.4	1.6	0.4	3	1.4	0.7	1.4	-1	-0.3	-1
northern bedstraw	0.9	0.2	1.8	0.8	0.5	1.9	1.3	1.1	1.5	0.4	0.9	-0.3
field sow-thistle	0	0	1.1	0.4	0	0.3	0.6	0	1	0.6	0	-0.1

Table 8. Results of repeated measures ANOVA for Hill's Evenness across 2009-2011.

Factor	Df	SS	MS	F	P[a]
Diversity	1	0.693	0.693	0.729	$0.399 < p < 0.404$
Disturbance	2	0.559	0.279	0.294	$0.747 < p < 0.749$
Year	2	33.373	16.686	17.557	$0.000 < p < 0.001$
Dist. ***x*** Div.	2	2.713	1.357	1.427	$0.253 < p < 0.266$
Year ***x*** Div.	2	2.116	1.058	1.113	$0.340 < p < 0.350$
Dist. ***x*** Year	4	9.147	2.287	2.406	$0.067 < p < 0.088$
Dist. ***x*** Div. ***x*** Year	4	3.542	0.885	0.932	$0.457 < p < 0.468$

[a] Bounded *p*-values calculated using bounded denominator degrees of freedom; less conservative upper-bound denominator Df = 36, more conservative lower-bound denominator Df = 18.

Table 9. Results of analyses of best models of the effects of disturbance and year on Hill's Evenness and Simpson's Dominance.

Response	Factor	Df	SS	MS	F	P[a]
Hill's evenness	Disturbance[b]	1	0.678	0.678	0.588	$0.447 < p < 0.449$
	Year	2	33.373	16.686	14.490	$0.000 < p < 0.001$
	Dist. ***x*** Year	2	9.071	4.535	3.939	$0.026 < p < 0.03$
Simpson's Dominance	Disturbance[b]	1	0.001	0.001	1.467	$0.232 < p < 0.235$
	Year	2	0.001	0.003	1.392	$0.259 < p < 0.264$
	Dist. ***x*** Year	2	0.002	0.005	4.230	$0.02 < p < 0.024$

[a] Bounded *p*-values calculated using bounded denominator degrees of freedom. Less conservative upper-bound denominator df = 48, more conservative lower-bound denominator df =30.

[b] The simplest model to explain the deviance combined mowed and control plots for comparison to grazed plots.

Table 10. Results of repeated measures ANOVA for native species richness across 2009-2011.

Factor	Df	SS	MS	F	P[a]
Disturbance	2	24.111	12.056	2.908	$0.068 < p < 0.080$
Year	2	21.778	10.889	2.627	$0.086 < p < 0.100$
Diversity	1	91.868	91.868	22.163	$0.000 < p < 0.001$
Dist. ***x*** Year	4	19.111	4.778	1.153	$0.348 < p < 0.364$
Dist. ***x*** Div.	2	7.148	3.574	0.862	$0.431 < p < 0.439$
Year ***x*** Div.	2	4.148	2.074	0.5	$0.611 < p < 0.615$
Dist. ***x*** Year ***x*** Div.	4	33.63	8.407	2.028	$0.111 < p < 0.133$

[a] Bounded *p*-values calculated using bounded denominator degrees of freedom; less conservative upper-bound denominator Df = 36, more conservative lower-bound denominator Df = 18.

Table 11. Native species richness in high-diversity planted prairies across disturbance treatments and years.

		HD[a]		LD[a]	
Disturbance	Year	Richness	SE	Richness	SE
Control	2009	23.0	7.8	17.3	4.2
	2010	21.3	1.0	16.0	6.5
	2011	23.3	1.8	13.0	2.9
Graze	2009	20.7	18.1	14.0	11.4
	2010	20.0	2.9	15.3	0.5
	2011	20.0	4.9	15.3	1.0
Mow	2009	22.7	0.5	18.0	2.9
	2010	23.3	3.4	15.0	5.3
	2011	20.3	6.7	14.3	5.0

[a] 2009 mean richness across disturbance treatments: high-diversity = 22.2; low-diversity = 16.0.

Table 12. Results of analyses of best models of the effects of disturbance and year on native species richness in high diversity prairies.

Factor	Df	SS	MS	F	P[a]
Disturbance[b]	1	26.741	26.741	5.601	$0.026 < p < 0.034$

[a] Bounded *p*-values calculated using bounded denominator degrees of freedom; less conservative upper-bound denominator Df = 25, more conservative lower-bound denominator Df = 13.

[b] The simplest model to explain the deviance combines mowed and control plots for comparison to grazed plots.

Table 13. Results of analyses of best models of the effects of disturbance and year on native species richness in low diversity prairies.

	Df	SS	MS	F	P[a]
Disturbance[b]	1	3.13	3.13	0.667	$0.424 < p < 0.436$
Year	2	22.296	11.148	2.373	$0.112 < p < 0.149$
Dist. ***x*** Year	2	29.370	14.685	3.126	$0.065 < p < 0.093$

[a] Bounded *p*-values calculated using bounded denominator degrees of freedom; less conservative upper-bound denominator Df = 21, more conservative lower-bound denominator Df = 9.

[b] The simplest model to explain the deviance combines mowed and control plots for comparison to grazed plots.

Table 14. Results of analysis of best model of the effects of disturbance and year on exotic species richness. Exotic species richness was similar between diversity levels.

Factor	Df	SS	MS	F	P
Disturbance	2	7.055	3.528	2.696	$0.078 < p < 0.121$
Year	2	169	84.5	64.571	$0.000 < p < 0.001$
Dist. ***x*** Year	4	23.222	5.806	4.436	$0.004 < p < 0.03$

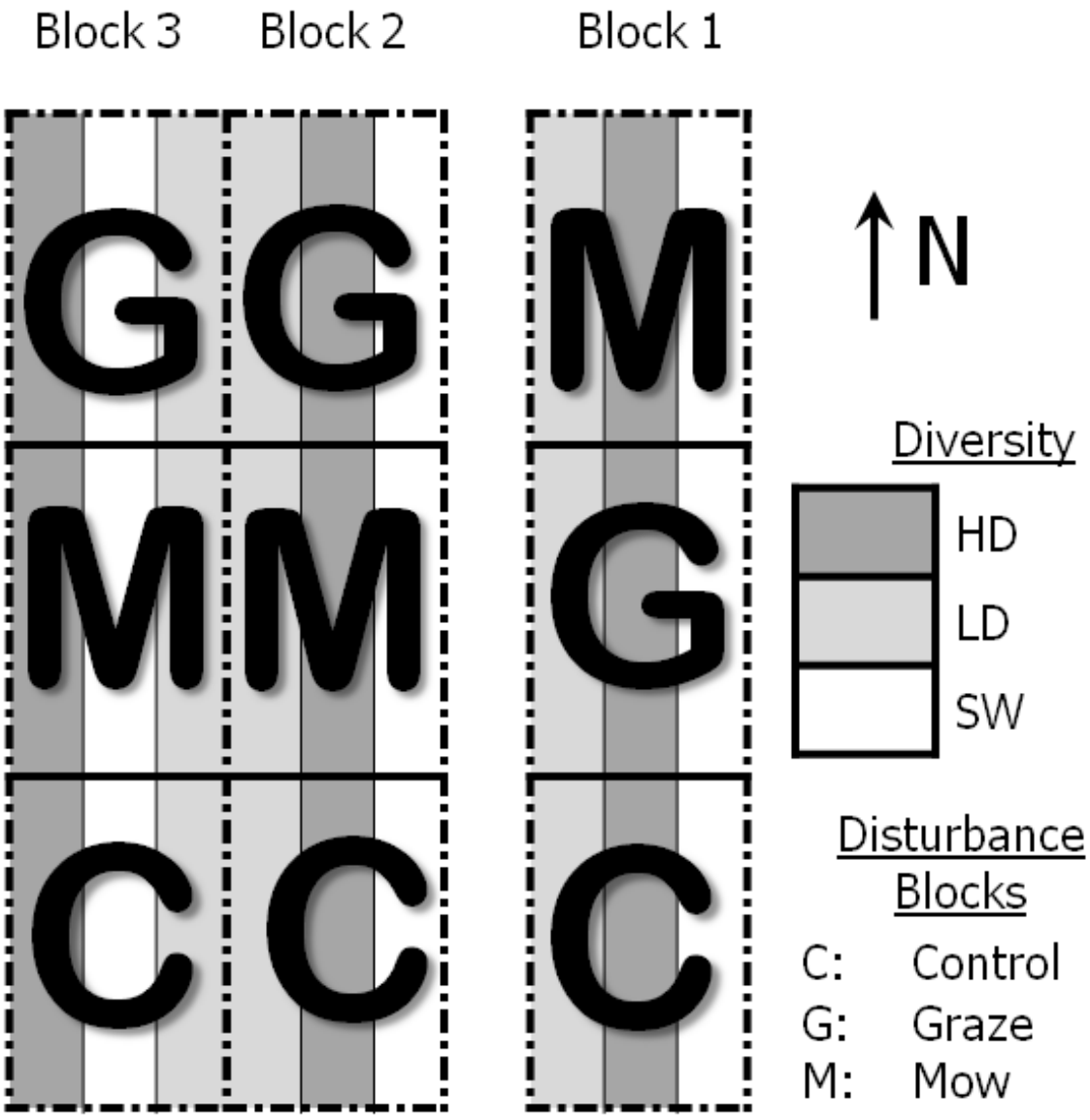


Figure 1. Experimental design of WICST Prairies diversity treatments and disturbance treatments at University of Wisconsin Arlington Agricultural Research Station. Block 1 and Block 2 were separated by cropped fields and were 70 m apart. Block 3 was separated from Block 2 by a fence. Diversity treatment SW indicates planted switchgrass monocultures not discussed in this paper.

1

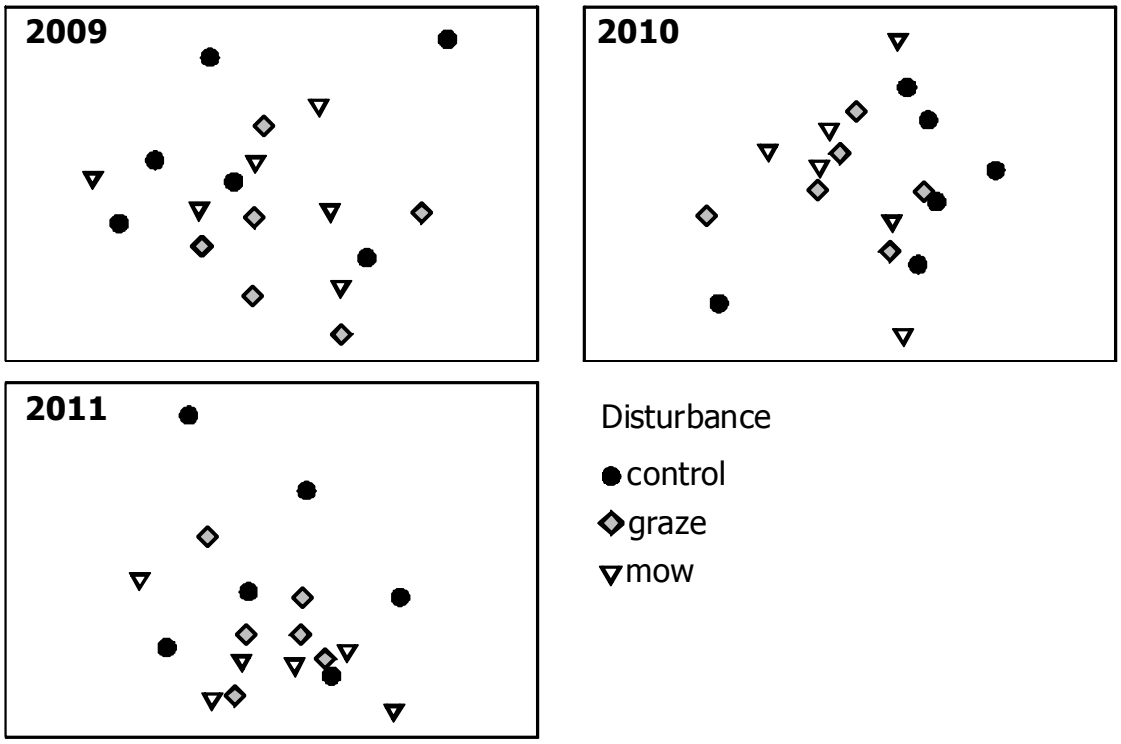


Figure 2. Non-metric multi-dimensional scaling (NMDS) plots of community similarity across three years. Substantial overlap among experimental plots within treatment groups persists over time, suggesting that disturbance by mowing and grazing has not caused extreme shifts in community composition following two years of mid-summer disturbance. Sampling occurred in June of each year, prior to application of disturbance treatments. For each treatment, n = 6. Stress levels are suitable for two-dimensional visualization (2009 = 0.16; 2010 = 0.16; 2011 = 0.14).

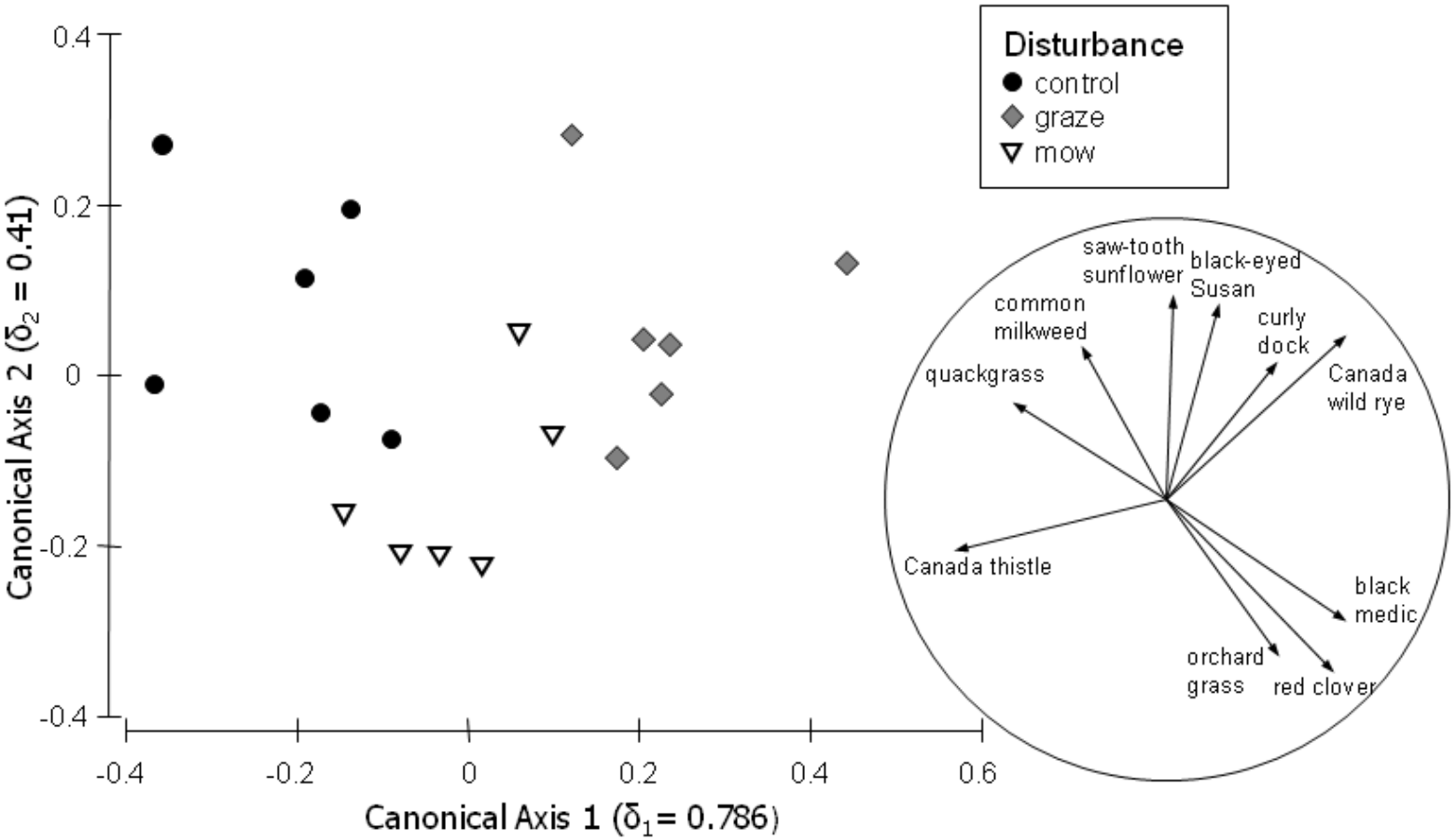


Figure 3. Discriminant analyses of disturbance treatment effects in June 2010 illustrated by canonical ordination of principal coordinates. Axis 1 was selected as the best principal coordinates axis for discriminating between management groups in multivariate space. The second canonical axis shows separation of graze and mow treatments but has a much lower squared canonical correlation than Axis 1.Vectors (inset) indicate the relative direction and strength of individual species' Spearman correlations to axes ($r \geq 0.6$ for species shown).

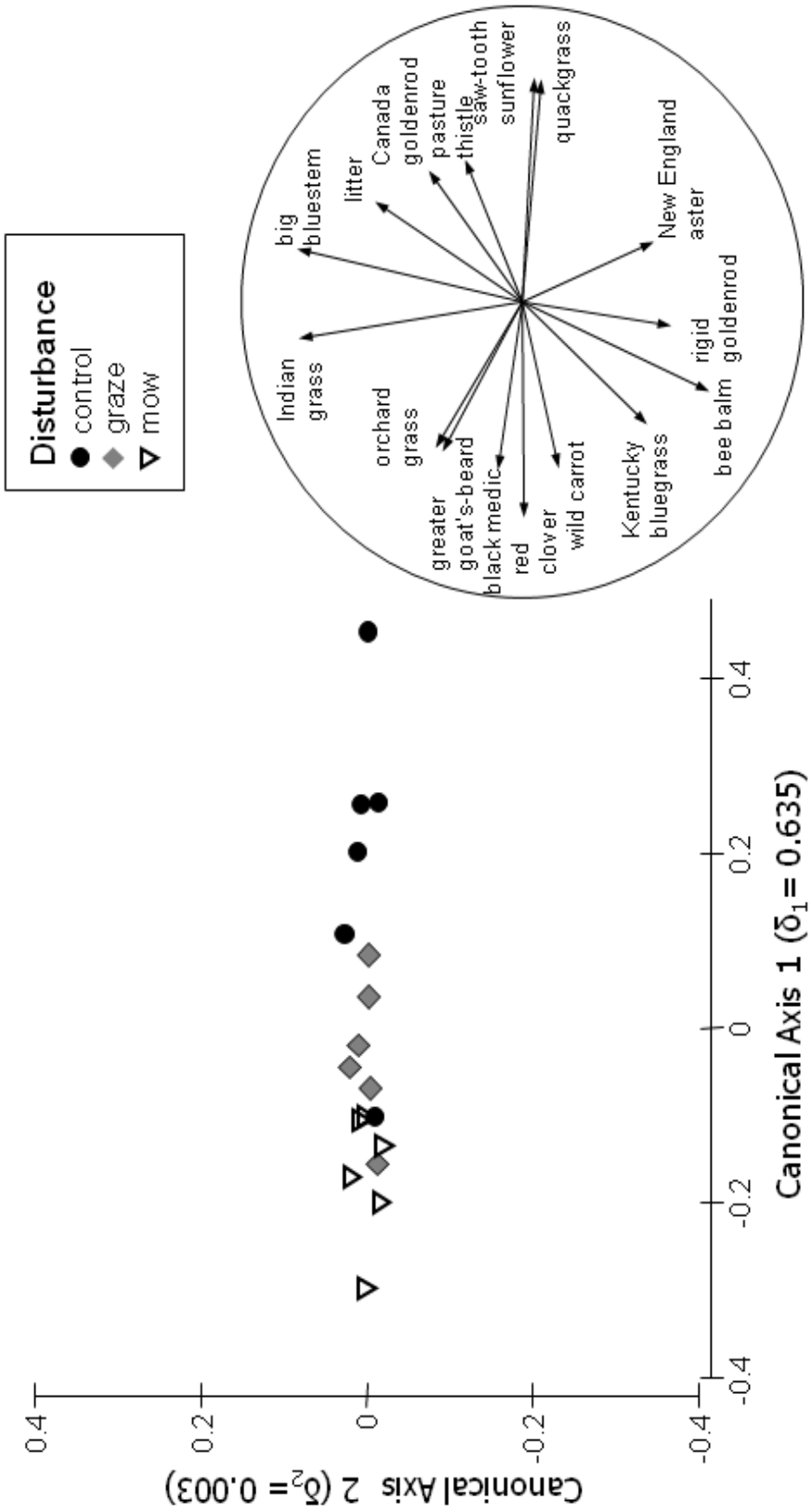


Figure 4. Discriminant analysis of disturbance treatment effects in June 2011 illustrated by canonical ordination of principal coordinates. Axis 1 was selected as the best principal coordinates axis for discriminating between management groups in multivariate space. Axis 2 was not useful for discriminating between groups. Vectors (inset) indicate the relative direction and strength of individual species' Spearman correlations with CAP axes ($r \geq 0.5$ for species shown).

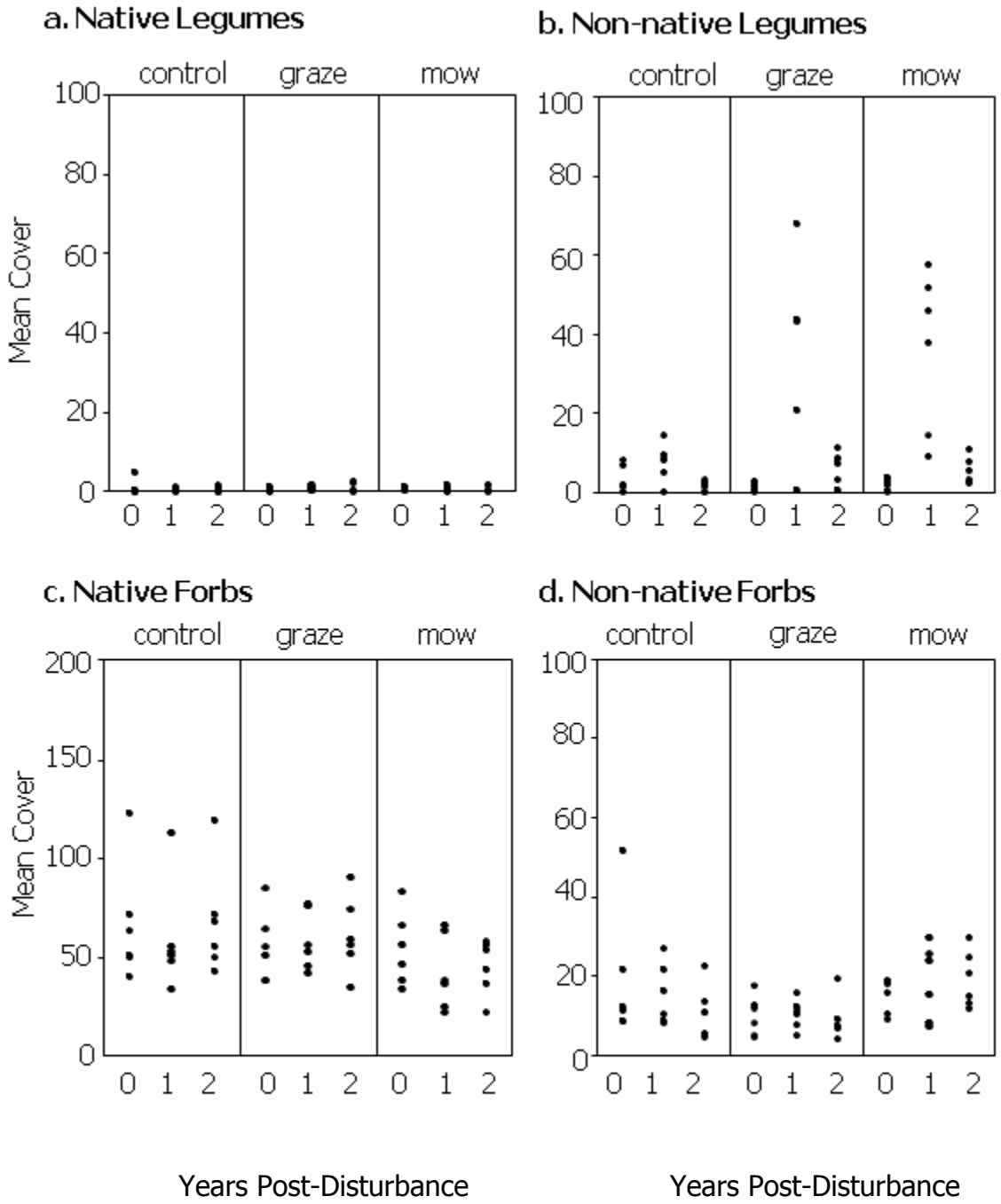


Figure 5. Absolute cover of functional groups across disturbance treatments and years. Points illustrate absolute cover of functional groups estimated within each experimental unit. Note change in y-axis label for native forb absolute cover.

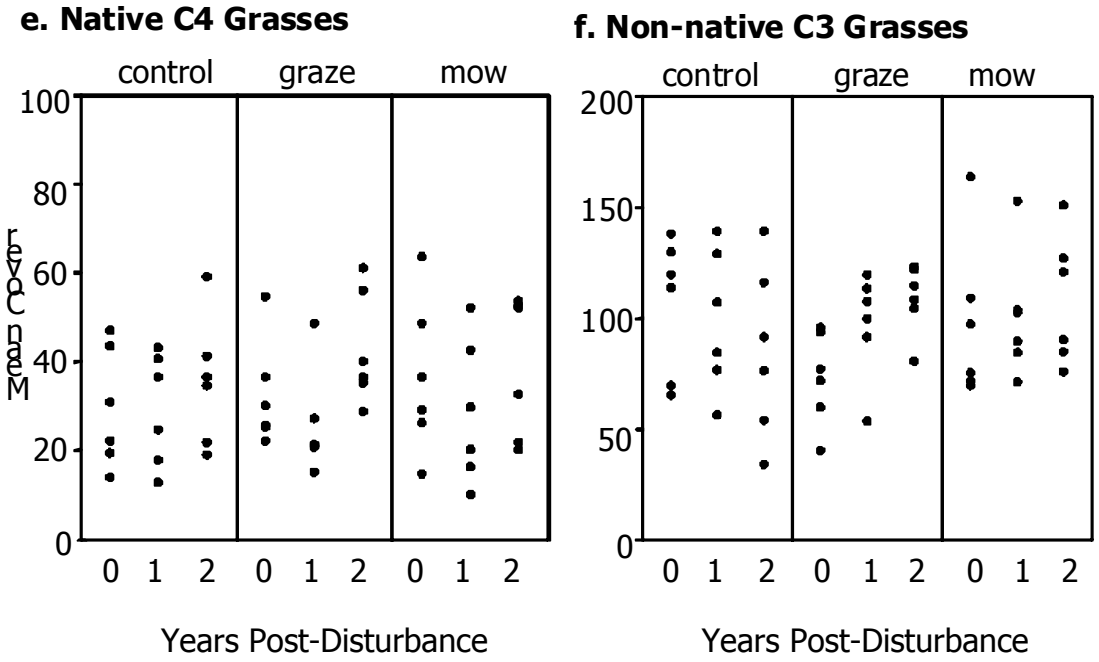
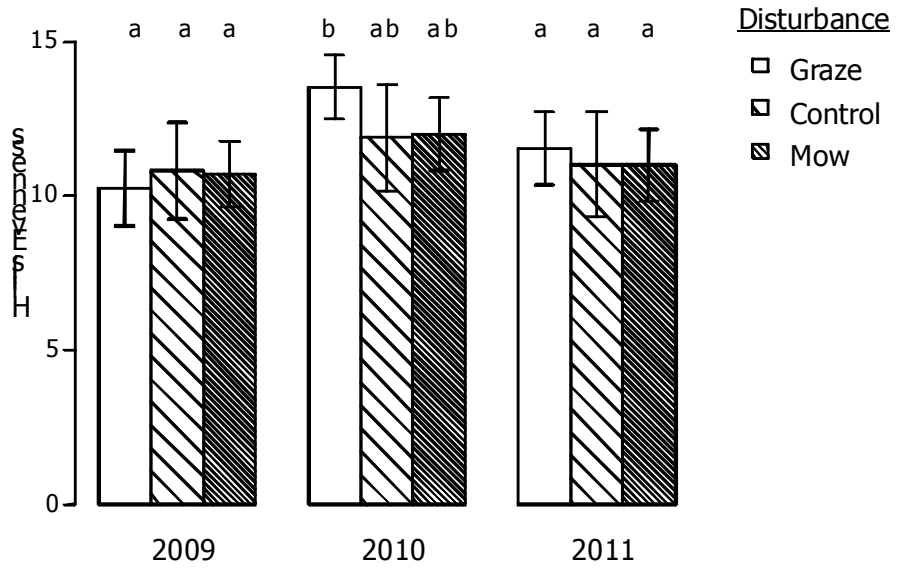


Figure 5 (continued). Note different y-axis labels for absolute cover of native C4 grasse3s and non-native C3 grasses.

1

2

a. Hill's Evenness



b. Simpson's Dominance

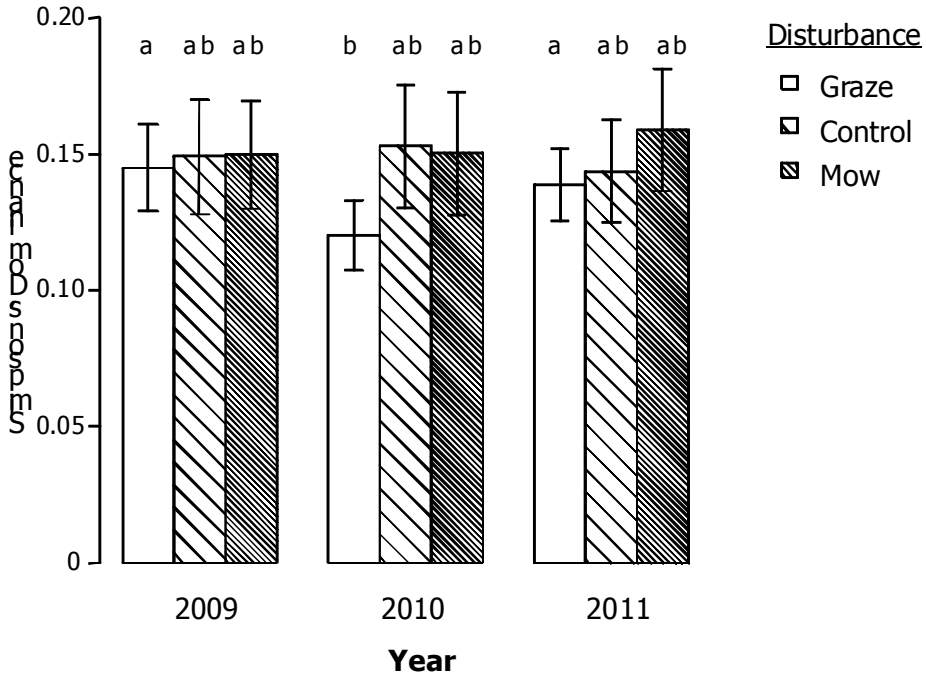


Figure 6. Effects of year and disturbance on Hill's evenness and Simpson's dominance. The effect of diversity treatment was not significant. Bars represent means ±1 standard error. Different letters on bars represent significant differences (Tukey's HSD for pair-wise comparisons of grazed and non-grazed disturbance treatments across all 3 years; $\alpha = 0.05$).

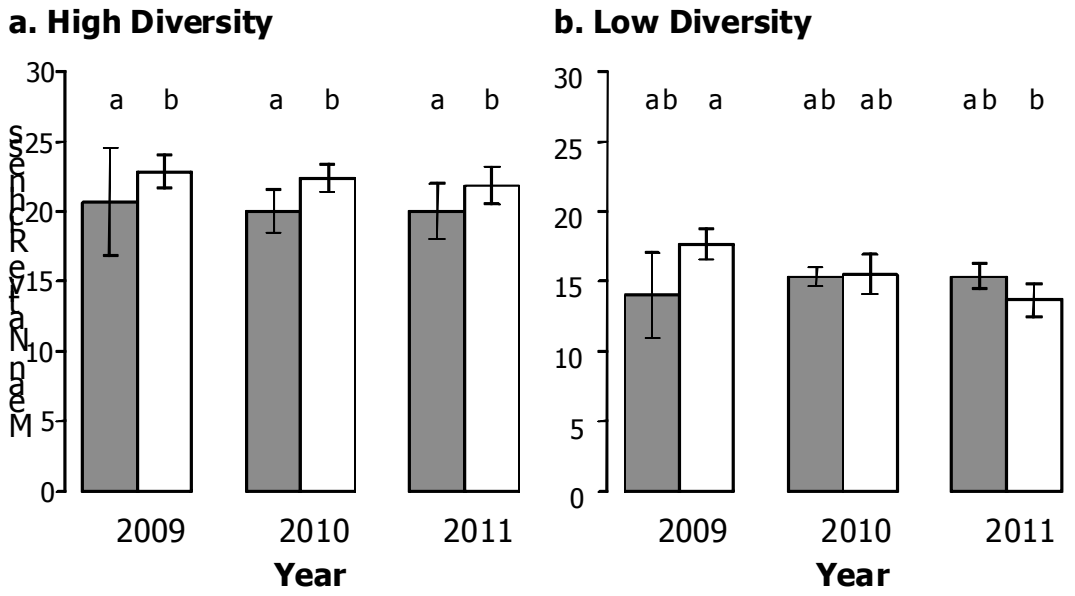


Figure 7. Effects of diversity treatment, disturbance, and year on native species richness. Native species richness was significantly lower in low-diversity plantings ($p < 0.001$). Bars represent means ± 1 standard error. Grey bars indicate mean richness across the mow and control levels of the disturbance treatment. Within each diversity treatment, different letters over bars represent significant differences across all three years ($\alpha = 0.05$) (Tukey's HSD for pair-wise comparisons for low-diversity native richness; for high-diversity native richness, differences between disturbances were evident from simplifying the linear mixed effects model).

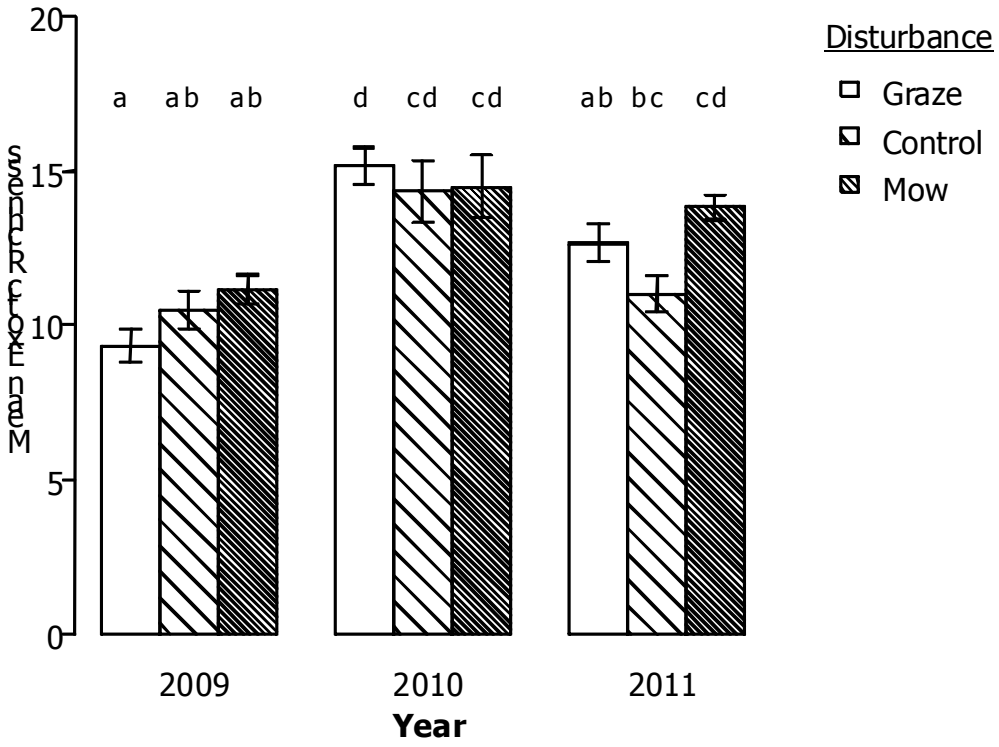


Figure 8. Effects of year and disturbance on non-native species richness. The effect of diversity treatment was not significant. Bars represent means ±1 standard error. Different letters over bars represent significant differences across all three years ($\alpha = 0.05$) (Tukey's HSD for pair-wise comparisons).

Chapter 3. Tradeoffs between functional group diversity, forage availability, and resistance to compositional change in reconstructed tallgrass prairies

Abstract

Non-native cool-season (C3) grasses and legumes are the preferred forage system for grass-based livestock systems in the north central United States, but these pastures can suffer from a slump in productivity and quality during warm, dry summers. Incorporating pastures dominated by native, warm-season (C4) grasses has been proposed as an insurance policy to ameliorate the short-term and long-term effects of summer slumps, but basic research and farmer adoption remains limited. This study compared switchgrass monocultures and prairies planted with native C4 grasses, native legumes, and native forbs to investigate relationships between plant functional group diversity and forage quality and availability. Overall, forage quality in reconstructed native grasslands was suitable to meet the dietary needs of non-lactating cattle across the diversity treatments. Cattle tended to avoid consuming native forbs and avoided foraging for palatable species interspersed within dense patches of native forbs, which significantly reduced forage availability in diverse prairies relative to switchgrass stands. A new method based on the concept of feeding stations was developed to improve estimates of forage availability in herbaceous plant communities with high dispersion of unpalatable species, patchy distribution of palatable grasses, and high cattle selectivity. Feeding station frequency was significantly higher in switchgrass stands than in diverse prairies, and forage yield at

feeding stations was higher in switchgrass stands than in diverse prairies; consequently, mean forage yield at the paddock scale was twice as high for switchgrass than for diverse prairies. Across diversity levels, mowed and undefoliated control plots differed significantly in plant community composition during both years, but grazed and control plots did not differ. Native grasslands with high abundance of tall-statured native forbs may be less suitable for adoption in production systems due to impacts on forage availability, but vulnerability of C4 grass monocultures to weed invasion following defoliation suggests that functional group diversity may be useful for limiting shifts in community composition to support high forage yields over longer time periods.

Introduction

The potential benefits and tradeoffs of high plant diversity in grazing lands have been explored for cool-season pastures of the temperate United States (Sanderson et al., 2004), but it is unknown if positive biodiversity-productivity relationships found for ungrazed tallgrass prairies in the north central U.S. (Biondini, 2007; Fargione et al., 2007) are maintained when reconstructed (planted) native grasslands are managed to support domestic cattle production.

Grazing lands in the north central to northeastern U.S. are typically composed of a low diversity of cool-season (C3) grasses and legumes, and additional plant diversity is contributed by native and non-native forbs that colonize disturbed soils and are adapted to escape grazing through prostrate growth form or chemical and physical defenses (Paine et al., 1999; Sanderson et al., 2004; Sanderson et al., 2007). In sub-humid

environments, these novel plant communities are very productive, but season-long carrying capacity can be reduced when peak growth occurs during early summer (Casler et al., 1998; Riesterer et al., 2000). Incorporating grasslands dominated by native, warm-season (C4) grasses through mixed C3-C4 stands or via sequential grazing has been explored as a means for farmers in southern Wisconsin and nearby regions of the north central U.S. to alleviate the consequences of poor summer performance by cool-season pastures (Smart et al., 1995; Jackson, 1999; ; Jackson et al., 2008; Bouressa et al., 2010).

Historically, the tallgrass prairie ecosystem was common and widespread across southern Wisconsin, Minnesota, Iowa, northern Missouri, and Illinois, but less than 1 percent of this ecosystem remains north and west of the Missouri River (Anderson, 2006). The most abundant and productive species in the tallgrass prairies are warm-season (C4) grasses that emerge in late spring and flower in mid-summer, including *Andropogon gerardii* Vitman (big bluestem), *Panicum virgatum* L. (switchgrass), and *Sorghastrum nutans* (L.) Nash (Indiangrass). The C4 photosynthetic pathway utilized by these grasses is an adaptation to warm, dry growing conditions and has evolved in at least 19 plant families (Sage, 2004). From a production perspective, this adaptation to more challenging environmental conditions includes a tradeoff because C4 grasses typically have lower leaf digestibility and reduced levels of nitrogen-rich photosynthetic enzymes compared to non-native C3 grasses selected for use in improved pastures (Barbahenn et al., 2004).

With sequential grazing, managers leverage the advantages of separate C3- and C4-dominated grasslands by grazing in sequence: at the beginning of the grazing season, animals are stocked on C3 pastures; then, in early summer, animals are stocked on

pastures dominated by C4 grasses to utilize rapid vegetative growth (allowing C3 pastures longer rest periods); and animals remain on C3 pastures from late summer through fall after C4 grass productivity and quality have declined. In tallgrass and mixed-grass prairies, native herbivores (*Bison bison* L. [American bison]) have demonstrated grazing behavior that includes selecting patches of C3 grasses in autumn and winter and increasing C4 grass consumption during summer (Plumb & Dodd, 1993; Vinton et al., 1993).

Sequential grazing trials in the north central U.S. have been limited. When steer weight gains in cool-season-only and sequential grazing systems were compared in central Wisconsin, researchers found no difference in animals that grazed throughout the season on a monoculture of non-native C3 grass *Poa pratensis* L. (Kentucky bluegrass) and those that utilized a switchgrass monoculture during mid-summer (Smart et al., 1995). In southern Iowa, cattle that remained on cool-season pastures throughout the season gained more than those in sequential monocultures (Moore et al., 2004). In a southwestern Michigan trial, animal performance data has not been published, but research from grazing trials showed native C4 grasses matured early in the growing season and had to be grazed while cool-season grasslands were still producing high quality forage (Hudson et al., 2010), and the overlap between C3 and C4 grass production potentially compromises adoption of sequential grazing in the north central U.S. In the Wisconsin study, relatively cool and wet summer weather conditions favored C3 grass growth during the length of the trial. In the Iowa study, C4 grass grazing was initiated fairly late in the growing season (early July) when forage mass was high but crude

protein concentrations (CP) were low (6 percent), which may have negatively impacted animal performance in the sequential grazing system.

Previous sequential grazing studies have used reconstructed grasslands dominated by C4 grasses, or simple C4 grass-legume mixtures, but remnant tallgrass prairies have high functional group diversity, even when compared to many reconstructed prairies (Sivicek & Taft, 2011). Increasing plant functional group diversity can better mimic natural communities and may result in better productivity and forage quality. In reconstructed prairies, productivity and C4 grass tissue quality can increase with plant diversity due to niche complementarity and increased soil fertility (Fargione et al., 2007; Dybzinski et al., 2008).

Native legumes may be the most important group to facilitate increased forage productivity and quality in C4-dominated grasslands. Legumes can improve forage quality in C4-dominated grasslands through direct and indirect pathways. In ungrazed mixed prairie plantings, the presence of native legumes in mixtures has been correlated to increased leaf nitrogen status and overall nitrogen pool in co-occuring species (Lee et al., 2003). Reanalysis of the positive correlation between diversity and productivity found in tallgrass prairie mixtures (Tilman 2006) highlighted C4 grass-legume mixtures as being as productive as the most diverse mixtures (DeHaan et al., 2010). Several native legume species of the tallgrass prairie have been evaluated for forage quality, productivity, and palatability (McGraw et al., 2004; Fishbach et al., 2006), and combinations of C4 grasses and native legumes in small plot studies have demonstrated improved forage quality and production for some pairings (Posler et al., 1993; Springer et al., 2001).

High productivity in mesic tallgrass prairies may limit competitiveness of interseeded legumes, requiring disturbances such as grazing or mowing to make light and nutrients available to new plants. Either grazing or mowing can remove aboveground biomass and limit competition for light, but trampling in grazed plots may limit seedling germination and survival, and timing grazing to best suit establishment of seedlings is difficult (Jackson, 1999). In an Iowa prairie restoration dominated by C4 grasses, Williams et al. (2007), documented that interseeding followed by frequent mowing increased the abundance of seedlings that flowered during the second growing season, and, after five years, seedlings taller than 3.0 cm were twice as abundant in mowed treatments compared to control plots.

Research into palatability, forage quality and production of native forbs remains relatively limited, perhaps due to many historical observations of decreased native forb richness and abundance under conditions of overgrazing (Drew, 1947; Dix, 1959). For tallgrass prairie forbs, research has shown that CP and fiber concentration of *Rudbeckia hirta* L. (black-eyed Susan) and *Heliopsis helianthoides* (L.) Sweet (false sunflower) was intermediate between C4 grasses and native legumes, and concentrations of some micronutrients were higher in forbs than in grasses (Bonin, 2011). When native forbs were planted in monocultures on sandy soils at Cedar Creek LTER in central Minnesota, there were wide variations in plant tissue quality (C:N ratio) and productivity across species and a strong correlation between high C:N ratios and high productivity (Craine et al., 2002). These results suggest that shorter-statured prairie forbs typically have lower C:N ratios than taller forbs and may complement C4 grasses and legumes in a prairie pasture system due to relatively low fiber concentrations and relatively high CP.

In native grasslands in Kansas, dominance by C4 grasses was found to be important for resisting invasion by an exotic legume (Smith et al., 2004), but grazing has also been shown to reduce C4 dominance in this system (Veen et al., 2008). In reconstructed grasslands, species richness was found to be important for reducing disease outbreak and resisting weed invasion (Knops et al., 1999). Increasing plant functional diversity by incorporating native forbs may add value for farmers by providing increased resistance to weed invasion in grazed, reconstructed native grasslands and reducing or eliminating the cost of applying herbicides to manage undesirable species.

Ecosystem functions in diverse plant communities, such as increasing concentrations of soil carbon and nitrogen or facilitating development of soil aggregrates (Jastrow, 1987), are considered ecosystem services when they provide benefits to humans. Increased soil fertility and stability are ecosystem services that operate primarily at the field-to-farm scales and may have clear economic benefits by enhancing plant vigor, reducing disease outbreaks or insect attacks, and supporting high animal performance without relying on inputs of artificial fertilizers (Culman et al., 2009). Other ecosystem services supported by diverse tallgrass prairie communities, such as flood control, nitrogen sequestration, and climate regulation, primarily benefit people at watershed to global scales; policies that facilitate the flow of financial capital to landowners who manage for biological diversity and contribute to these large-scale services are lacking, but farmers now incorporating diverse tallgrass prairies into their land use may stand to be early beneficiaries of payments for ecosystem services if national or international markets for these services mature.

Due to strong climatic gradients across the north central states, an ecological tension zone (Curtis, 1959) occurs across Minnesota, Wisconsin, and Michigan, with forests historically dominating north of this zone and prairies limited to south of this line. In Wisconsin, many northern plant communities were kept open by fire, such as oak and pine barrens, but these communities were dominated by fire-tolerant shrubs and C3 grasses rather than C4 grasses (Curtis, 1959). The productivity, persistence and utility of C4 grass stands established north and east of the historic tension zone may remain highly constrained over the next few decades, as climate-induced northward shifts in the tension zone have been minimal over the last 60 years (Kucharik et al., 2010).

To explore the relationships between plant functional diversity, forage production, and forage quality, managed grazing was employed across a diversity gradient in reconstructed tallgrass prairie communities. A well-established switchgrass monoculture was compared to prairies that had been planted with varying levels of native plant functional diversity (and which had been invaded by non-native C3 grasses and non-native legumes prior to the beginning of this experiment). Native legumes were interseeded across all diversity levels to determine if increased legume cover would significantly increase forage productivity and quality, and managed grazing and mowing were tested as management treatments to promote legume establishment in highly-productive native grasslands.

I hypothesized that:

- forage quality and productivity would be higher in diverse prairies than in C4 monocultures;

- legume interseeding would result in a significant diversity ***x*** legume interaction, with greater increases in forage quality and production in C4 monocultures than in diverse reconstructions; and
- diverse prairie communities would be more resistant to plant community change than C4 monocultures.

Methods

Study site and experimental design

The study was located at the Arlington Agricultural Research Station in southern Wisconsin (43.30°N, 89.35°W). Soils were Plano silt loam (fine-silty, mixed, superactive, mesic Typic Argiudolls). The reconstructed native grasslands used in this study were part of the Wisconsin Integrated Cropping System Trial (WICST), a long-term study of the agronomic, environmental, and economic performance of cropping systems of varying intensity (Posner et al., 2008).

Diversity, management, and legume interseeding treatments were applied in a hierarchical, split-split plot design. Diversity treatments served as whole plots in the nomenclature of the split-split plot design. Each whole plot was split into three subplots to apply disturbance treatments: grazing, mowing, and control treatments. Due to requirements of the grazing treatment (fencing and supplying water), this split was applied at the block level, resulting in management blocks. Control subplots were located in the southern position, and grazing and mowing subplots were randomly assigned to the

northern or central positions. To account for this spatial arrangement, these management blocks were included as a random factor in statistical analyses. To test the effect of native legumes, each subplot was split into interseeded (IS) and non-interseeded (NIS) sub-subplots, with interseeding treatment randomly assigned. This experimental design resulted in 54 experimental units, with 18 experimental units in each block and six experimental units in each diversity treatment (Fig. 1). Each experimental unit measured 12.2 m by 17.5 m, covering approximately 200 m^2 (0.02 ha).

Diversity treatments

Native grasslands reconstructions began at WICST in 1999 (Simonsen et al., 2002). The primary goals were to re-introduce native plants and an associated process (anthropogenic fire) to reconstruct a native plant community for education and outreach, restore ecosystem function (sequestering carbon and nitrogen in soils), and provide baseline conditions for comparisons of crop and forage systems to a natural system. The 1999 prairie restoration (WICST Prairie) was implemented as a randomized complete block design. Three diversity treatments were randomly assigned to each block and replicated across three blocks. Treatments included: 1) a low diversity (LD) prairie seed mix including six native species, 2) a high diversity (HD) prairie seed mix including 26 species (the LD complement and an additional 19 species), and 3) a control, continuous corn (CC) planted and harvested annually. The species sown in these treatments are native species found in mesic tallgrass prairie communities, though some are found in greatest abundance in wetter or drier prairie communities (Hoffman, 2002); a list of species planted is included in Appendix 1, Table 1 (adapted from Simonsen et al., 2002).

According to Simonsen et al. (2002), the prairies were established in June 1999: prairie seed was broadcast by hand and the plots were cultipacked to improve seed-soil contact; during the growing seasons of 1999-2002, the prairies were clipped periodically to control weeds. The CC treatment concluded in 2006, and in June 2007 the CC plots were planted with switchgrass (cultivar Forestburg; original collections from eastern South Dakota). Prior to the beginning of this study, the prairies were managed with prescribed fire and were burned in 2003, 2005, and 2008. During this study, an annual fire regime was established with fires conducted in April 2009 and April 2010.

In early spring, vegetation in LD and HD prairies was dominated by two non-native, C3, sod-forming grasses: Kentucky bluegrass and *Bromus inermis* Leyss. (smooth brome). In late spring through early summer, non-native dominance was reduced as native species emerged, and by mid-summer native, perennial C4 grasses and native forb species in the family Asteraceae formed the matrix of vegetation. Indiangrass*, Helianthus grosseratus* M. Martens (saw-tooth sunflower), and big bluestem each reached a mean absolute cover of 20 percent or greater in control plots by fall 2010, and *Aster novae-angliae* L. (New England aster), *Solidago canadensis* L. (Canada goldenrod)*,* black-eyed Susan, false sunflower, and *Solidago rigida* (L.) Small (rigid goldenrod) each reached mean absolute cover of 5 percent or greater in control plots by fall 2010); during later parts of the growing season, exotic C3 grasses remained common in the understory and formed the canopy in local patches (typically 3 m by 3 m or smaller).

Management treatments

Rotational stocking was employed using methods and tools commonly applied by farmers in the north-central U.S. A three-strand high tensile electric fence surrounded

each WICST Prairie block. Portable electric fencing was used to define grazing paddocks within each block. Logistics prohibited grazing all experimental units on the same day. In order to reduce spatial and temporal variability within grazed treatments, paddocks allowed cattle to simultaneously graze both of the sub-subplots (IS and NIS) within each diversity plot. Water and salt were made available at the boundary between IS and NIS sub-subplots to reduce potential effects of these resources on the spatial distribution of cattle. This design yielded 9 paddocks during each round of grazing management. Grazing was completed across all plots within 7-9 days (Table 1).

The grazing treatment used 6 Holstein heifers, the typical breed and age class utilized in the WICST rotational grazing system. This livestock class has lower nutritional needs compared to lactating cows or steers being fattened for beef production (Ball et al., 2001). Average animal weight was approximately 230 kg in June and 270 kg in July. Cattle diets were supplemented with 1 kg of corn per animal on a daily basis.

In the WICST rotational grazing system, these cattle grazed on pastures dominated by C3 grasses and legumes planted for forage production. When herbivores encounter a new plant community, behavioral and physiological adjustments may be necessary. Acclimation areas were created within the WICST Prairie blocks to provide time for adjustments to begin prior introduction to the experimental units. Acclimation areas were located adjacent to experimental units. In June 2009 and 2010, cattle were allowed to graze across all diversity treatments for two days prior to grazing on the first experimental unit.

Timing and intensity of grazing followed recommendations for optimizing forage production and stand vigor in rotationally-stocked C4 grasslands (Mousel et al. 2005).

Grazing was initiated in early June, when C4 grasses were 30-45 cm in height; surveys of the plants prior to grazing indicated that the majority were in the 4-5 leaf stage and few had begun stem elongation. Cattle were removed when residual height of grazed C4 grasses was approximately 15-20 cm. Rest periods prior to the second round of grazing were approximately 35 days long. Throughout the course of the study, the length of time cattle spent on each experimental unit was adjusted according to forage availability.

Mowing was completed using a rear-mounted, PTO-driven, rotary deck mower, an implement used by a wide range of land managers. The mower deck was adjusted to leave a residual vegetation height of 15-20 cm, which was similar to the residual height of grazed C4 grasses observed in this study's grazing treatment and the typical height selected for weed control in establishing prairies. Mowing could not be completed at the same time as grazing due to possible disturbance to the cattle and was carried out following the completion of grazing treatments.

Legume interseeding treatment

Literature review provided data for screening potential native legumes for forage quality, productivity, and palatability (Posler et al., 1993; McGraw et al., 2004; Fischbach et al., 2005). Five legumes were selected for their potential utility to grazing farmers in the Upper Midwest: *Amorpha canescens* Pursh. (lead-plant), *Desmanthus illinoensis* Michx.) MacMill. ex B.L.Rob. & Fernald (Illinois bundle-flower), *Desmodium canadense* (L.) DC. (showy tick trefoil), *Lespedeza capitata* Michx. (round-headed bush-clover), and *Dalea purpurea* Vent. (purple prairie-clover).

Native legume species differ in maturity rate (number of years between establishment and seed production) and lifespan (R. Henderson, Wisconsin Department

of Natural Resources, personal communication), and the five legume mixture included species that can establish quickly and provide significant biomass within one or two growing seasons (e.g. Illinois bundleflower) as well as species that can persist over time even without subsequent seed production and establishment (e.g. lead-plant and round-headed bush-clover). Local genotype seed was purchased (Shooting Star Native Seed, Spring Grove, Minnesota), with the exception of Illinois bundle-flower. The natural range of Illinois bundle-flower did not extend into southern Wisconsin, but parent plants at the seed nursery demonstrated the ability to survive and reproduce at similar latitude to WICST.

Germination rates for native legumes interseeded into existing prairie were not available from review of scientific literature. An establishment trial using former cropland in Minnesota showed a positive linear relationship between seeding rate and plant population when five native legume species were paired with *Schizachyrium scoparium* (Michx.) Nash (little bluestem) and seeded into tilled ground in June (Fischbach et al., 2005). Species were planted in mixtures including 20 pure live seeds (PLS) m^{-2} for each species, or 100 PLS m^{-2} for the mixture. The seed supplier used in this study provided estimates of PLS $gram^{-1}$ and these values were used to calculate the weight of seed needed to plant 20 PLS m^{-2} for each species; the resulting seeding rate was 3.8 kg ha^{-1} for the five species mixture.

Interseeding occurred on June 26, 2009, following completion of the June grazing and mowing treatments. Prior to planting, each species was inoculated with appropriate *Rhizobium* bacteria to promote healthy growth of legume seedlings. Interseeding was

accomplished using a Great Plains no-till drill, an implement designed for interseeding in grasslands with minimal soil disturbance

Legume recruitment sampling

Native legume recruitment was estimated in August-September 2009, June 2010, and August 2010 using seedling counts. Five 0.5 m^2 quadrats were located in each IS experimental unit. The 1 m by 0.5 m frame was wider than five rows of the no-till interseeding implement. In each quadrat, native legume seedlings rooted inside the quadrat were identified to species and species counts were recorded. In June 2010, quadrats were again randomly located, and the northwest corner of each quadrat was marked with a large plastic stake. The same quadrat locations were revisited in August 2010.

The Central Region Seedling Identification Guide for Native Prairie Plants (NRCS, 2005) provided adequate information to identify native legume seedlings used in this study to species.

Standing biomass and forage sampling

Within the grazing treatment, vegetation was harvested to estimate standing biomass and available forage quantity and quality. In June 2009, standing biomass and available forage was estimated using five 0.1 m^2 quadrats randomly located in each experimental unit. Within each quadrat, biomass was clipped to ground level. Spring prescribed fire removed standing stems and litter remaining from the previous growing season. Biomass was sorted into palatable and unpalatable fractions, based on observations of which species cattle were selecting while grazing in switchgrass and prairie stands in the acclimation paddocks. Forage yield and quality were estimated using palatable fraction

subsamples. Mass of the palatable and unpalatable fractions from each quadrat were combined to estimate standing biomass for each subsample.

For 2010, biomass and forage sampling methods were altered to reflect cattle behavior. Patches of tall-stature unpalatable species (such as saw-tooth sunflower, rigid goldenrod, and Canada goldenrod) repelled foraging by cattle, and sparse, short-statured palatable plants (such as Kentucky bluegrass, smooth brome, and legumes) that grew within these patches were not grazed by cattle. Consequently, random sampling with a number of subsamples typical of pasture research (3-5) may have led to estimates of forage yield that were actually lower than the forage yield in patches where cattle were foraging.

To reflect cattle behavior, a sampling technique was developed to estimate the frequency of feeding stations (FS). *Sensu* Bailey et al. (1998), a FS is the "array of plants available to a herbivore without moving its feet," and Steinauer and Collins (1995; 2001) found that American bison grazing in tallgrass prairies are able to select food patches at scales as small as 0.25-m^2. Mean FS frequency in each experimental unit was estimated with stratified random sampling. Five parallel transects were spaced 3 m apart, and five subsamples located approximately 2 m apart were taken along each transect (25 subsamples per experimental unit). At each subsample location, a 0.25-m^2 quadrat was placed at canopy level and the cover of palatable species was visually-estimated. Each subsample with greater than 50 percent cover of palatable species was counted as a FS.

Forage yield at the FS scale was estimated by clipping palatable species within a 0.25-m^2 quadrat to 10 cm residual height. Available forage was estimated using three subsamples located by stratified random sampling. A random point was defined along

three transects per experimental unit. If a feeding station was located at the identified point, palatable species were harvested. If the point was not a feeding station due to dominance of unpalatable species, the researcher moved 1 m down the transect, repeating the random location process until arriving at a feeding station. Forage yield at the paddock-level scale (PS) was estimated for each experimental unit by multiplying the mean forage yield at the FS scale by the mean frequency of feeding stations.

Standing biomass (SB) was estimated by clipping stem and leaf biomass within a 0.25-m^2 quadrat to ground level. Three subsamples were located per experimental unit using stratified random sampling.

All biomass was dried at 60°C to constant weight. Forage samples were ground in a mill until dry matter passed through a 2 mm screen. Samples were analyzed for forage quality by near infrared reflectance spectroscopy (NIRS). CP, neutral detergent fiber (NDF), and relative forage quality (RFQ) were estimated using the mixed grass equation from the NIRS Forage and Feed Testing Consortium and WinISI II Version 1.50 software (Infrasoft International, LLC, Port Matilda, PA).

Plant community composition sampling

Absolute cover of plant species was estimated using the line-intercept method along transects (Elzinga et al., 1998). Sampling teams consisted of 1-2 observers and one recorder in each experimental unit. Observers identified each unique species that was intercepted when a thin rod was lowered vertically through layers of the canopy to the ground. If the rod did not intercept any living plant, observers noted whether the rod rested on bare ground or litter. After completing transect observations in each experimental unit, observers carried out a search for plant species that were present in the

plot but had not been recorded on any transect; when a species was observed in an experimental unit only on walk through, the species was assigned an absolute cover of 0.5 percent. Plant communities were sampled in 2009 and 2010. Sampling was conducted near peak standing biomass and following completion of management treatments (mid-August to early-September). Taxa nomenclature follows the USDA Plants Database (plants.usda.gov). Each taxa was assigned to a plant functional group based on origin (native or non-native) and life form (C3 grass, C4 grass, sedge, legume, forb, tree, or vine) (Appendix 1, Table 2).

Univariate statistical analyses

Within the grazing treatment, standing biomass, available forage yield, forage quality, and frequency of feeding stations was analyzed using linear mixed effects models. For summer 2010 data, several response variables were transformed to meet the assumptions of normal distribution and homogenous variance of residuals: square root transformation was used for CP, FS forage availability, PS forage availability, and SB; mean FS frequency was log transformed. All mixed effects models were fit with block as a random factor, with diversity level as the fixed effect in 2009 and diversity level and month as fixed effects in 2010. Models were evaluated using Aikake's Information Criteria (AIC), and model selection followed Crawley (2002). For 2009, likelihood ratio testing was used to compare the full model (with all levels of diversity) with the simpler models comparing switchgrass and prairies. The more parsimonious model was chosen unless models were significantly different ($p \leq 0.05$). The model with the lower AIC was chosen when $p \leq 0.05$. In 2010, a sampling error occurred during June data collection, resulting in no data being collected for one of the low diversity experimental unit;

subsequently, all experimental units from diverse prairies were included as one diversity level (June 2010, n = 5; July 2010, n = 6). Model selection was used to determine if there were significant differences between the two diversity levels and if month should be included in the model as an additive effect or interaction. Linear mixed effects models were evaluated using the R package lme4 (Bates et al., 2011). To account for the difficulties in calculating *p*-values from linear mixed effects models, upper- and lower-bound *p*-values were calculated using the R package LMERConvenienceFunctions (Tremblay, 2011). Tremblay (2011) describes the upper- and lower-bound *p*-values as anti-conservative and conservative, respectively. The df used to calculate upper-bound *p*-values are the number of data points (n) minus the number of df used up by the fixed effects; df for lower-bound p-values were calculated as n minus the number of df used up by the fixed effects and the number of random effects in the model. Both upper- and lower-bound *p*-values are presented in tables, and conservative, lower-bound *p*-values are referenced in the results (expressed as $p <$ lower-bound *p*-value). When the best model included an interaction term, Tukey's Honestly Significant Difference (HSD) test was used to understand the interaction; HSD tests were conducted using the R package languageR (Baayen, 2011). The R package sciplot (Morales, 2011) was used to graph means and standard errors. All mixed effects model analyses and graphing used R version 2.13.2 (R Development Core Team, 2011).

Multivariate statistical analyses

Switchgrass and diverse prairies were analyzed separately for trends in plant community composition due to very dissimilar composition. To model random effects and the split

plot design for the switchgrass treatment, management treatments were whole plots and the legume interseeding treatments were subplots.

A species was included in multivariate analyses if absolute cover in any plot in any year was greater than 2 percent. Absolute cover values were not converted to relative abundance because the coefficient of variation (CV) of total cover across sampling units was relatively low (CV < 0.15) (McCune & Grace, 2002). Resemblance among sample units was calculated from absolute cover of each species using the Bray-Curtis semi-metric measure of community dissimilarity.

Changes in plant community composition were assessed using non-parametric permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). Plant community composition was analyzed separately on fall 2009 and fall 2010 data. PERMANOVA can be used with any ANOVA experimental design and tests the response of multiple variables without needing to meet the assumptions of traditional parametric multivariate ANOVA (namely, response variables that follow a normal distribution and are not correlated). Ideally, samples within different factors should have homogeneity of dispersion, but this requirement is relatively lax (Anderson et al., 2008). PERMANOVA uses permutational procedures to calculate a pseudo-*F* statistic of the distribution of a large number of random combinations (i.e., 9,999); the permutated *p*-value derived from comparing how many values from the randomly-shuffled experimental units were more extreme than the value observed from the actual data. A separate permutational test of the homogeneity of ecological distance among plots within treatment groups (PERMDISP) is recommended to determine if significant effects found by PERMANOVA are due to location effects, dispersion effects, or both. For diverse

prairies, the model included block as a random effect and diversity, management, and interseeding as fixed effects; for switchgrass, block was included as a random effect and management and interseeding were fixed effects.

Initial analyses of diverse prairies and switchgrass with PERMANOVA and PERMDISP revealed no effect of legume interseeding on community composition or dispersion in any year (data not shown). To avoid pseudo-replication in further analyses, absolute cover values in sub-subplots within the diversity-management sub-plots were averaged. All further statistical analyses were calculating using the averaged data (n = 18 for prairies, n = 9 for switchgrass).

For switchgrass, principal coordinates ordination (PCO) was effective for visualizing differences when PERMANOVA found significant differences in similarity among treatment groups. PCO is a more general form of principal components analysis (PCA) that can be used with any distance measure (Anderson et al., 2008), including the Bray-Curtis measure used by ecologists. The PCO routine provides tools to evaluate which species are most strongly correlated to an axis or axes that separate different management groups in multivariate space.

For diverse prairies, the first two PCO axes were not effective for projecting the data in two dimensions, and discriminant analysis using canonical analyses of principal components (CAP) (Anderson & Willis, 2003) was used to visualize differences in similarity between groups found by PERMANOVA. In contrast to unconstrained ordination techniques like PCO, CAP finds an axis or axes that maximizes separation between a priori groups and can reveal patterns that are otherwise masked by unconstrained ordinations. Like PCO, the CAP routine provides tools to evaluate which

species are most strongly correlated to an axis or axes that separate different management groups in multivariate space.

Multivariate analyses were conducted using PRIMER version 6.0 and PERMANOVA+ software (Clarke & Gorley, 2006; Anderson et al., 2008).

Results

Forage quality and quantity

In June 2009, CP concentrations in switchgrass were significantly higher than in diverse prairies ($p < 0.019$), likely due to slower maturity of switchgrass than big bluestem and Indiangrass in 2009; less rapid biomass accumulation is reflected in lower SB in switchgrass than diverse prairies ($p < 0.049$) (Table 7; Fig. 2 and 3). Diversity level did not have a significant effect on NDF ($p < 0.126$) or RFQ ($p < 0.308$), or available forage yields (0.299 (Table 7; Fig. 2 and 3).

In 2010, CP levels were lower for switchgrass than diverse prairies in both June and July ($p < 0.053$) and NDF was higher in switchgrass than prairies across both months ($p < 0.002$) (Table 8), reflecting more advanced development in switchgrass in 2010. The higher fiber concentrations may explain the low consumption of switchgrass in both June and July. RFQ was significantly different across diversity levels ($p < 0.007$) and month ($p < 0.001$), and there was a weak diversity ***x*** month interaction ($p < 0.081$) (Table 8). Pairwise comparisons found that RFQ was similar across diversity treatments in June ($p = 0.664$) and dropped for both prairies and switchgrass in July. RFQ was significantly

lower in switchgrass than prairies in July ($p < 0.001$), reflecting minimal switchgrass defoliation by June grazing and advanced developmental stage in mid-summer.

Because different methods were used to sample forages in 2009 and 2010, no statistical comparison of forage response variables between years was possible. Qualitative comparison of means suggests that RFQ and CP were higher in 2009 than 2010, reflecting earlier grazing dates in 2009. Switchgrass forage yield measured in 2010 was higher than in 2009, but low palatability resulted in poor utilization, and measurements from June and July 2010 overestimate forage availability. In June 2009, forage quality across diversity levels was adequate to meet the needs of lactating beef cows (Ball et al., 2001).

In 2010, mean frequency of FS was significantly higher in switchgrass than in prairies ($p < 0.001$). Mean FS-scale available forage yield was significantly higher in switchgrass than diverse prairies ($p < 0.001$), and there was a significant diversity $\boldsymbol{x}$ month interaction ($p < 0.045$) (Table 8). FS-scale forage yield was similar between June and July in switchgrass ($p < 0.666$), but within prairies there was a weakly significant decrease from June to July ($p < 0.0923$) (Table 8; Fig. 5a). Results were similar for paddock-scale available forage; available forage yield was significantly higher in switchgrass than diverse prairies ($p < 0.001$), and there was a significant month $\boldsymbol{x}$ diversity interaction ($p < 0.05$) (Table 8), but the more conservative Tukey pairwise comparisons did not find significant differences within diversity levels between June and July. Mean standing biomass was not significantly different across diversity levels, and increased across all levels from June to July ($p < 0.001$).

Legume recruitment

Native legumes failed to reach one percent mean absolute cover across all diversity and disturbance treatments. Differences in recruitment to seedling stage were not ecologically significant because few seedlings were observed surviving to maturity. Mean recruitment to the seedling stage varied among species (Table 2). There were no significant effects of interseeding or interactions between other factors and interseeding.

Plant community composition

In the switchgrass diversity treatment, management had a weakly significant effect on composition in 2009 ($p = 0.056$) and a significant effect in 2010 ($p = 0.026$) (Table 3). Pair-wise tests found that control and mowed plots were the only treatments that differed significantly, with weak significance found in 2009 ($p = 0.050$) and 2010 ($p = 0.062$) (Table 4). A vector overlay of all functional groups showing a Spearman correlation $r > 0.8$ was added to the principle coordinates ordinations. Across both years, native C4 grasses (switchgrass) were highly correlated with control plots, and non-native C3 grasses and native and non-native forbs were correlated with mowed and grazed plots; correlations were slightly stronger in 2010 (Figure 8). Absolute cover of switchgrass was nearly 100 percent in control plots, and mean absolute cover of species in other functional groups was approximately 30 percent in control plots but was between 50 to 90 percent in mowed and grazed plots (Table 9).

In the diverse prairie reconstructions, diversity treatments did not significantly affect plant community composition in the diverse prairie reconstructions ($p = 0.399$) (Table 5). In 2009, management treatments resulted in significantly different composition ($p = 0.021$), and pair-wise comparisons found that differences between control and

mowed plots were significant ($p = 0.05$), and differences between grazed and mowed plots were weakly significant ($p = 0.088$); grazed and control plots were not significantly different ($p = 0.259$). In fall 2010, patterns were similar but differences found in 2009 had strengthened. The effect of management was highly significant ($p = 0.002$). Pair-wise comparisons found significant differences between control and mowed plots ($p = 0.03$), and grazed and mowed plots ($p = 0.023$); evidence that grazed and control plots were not significantly different had weakened ($p = 0.16$). Discriminant analysis using CAP found principal coordinate axes through multivariate space that can illustrate significant separation among groups in 2009 ($p = 0.05$) and 2010 ($p = 0.045$). A vector overlay of all functional groups showing a Spearman correlation $r > 0.5$ was added to the constrained ordinations. In fall 2009, the CAP plot shows separation between grazed, mowed, and control plots in fall 2009, with native forbs and native C3 grasses correlated with control and grazed plots, and non-native forbs correlated with mowed and control plots. (Figure 6). In fall 2010, the CAP plot shows strong separation between mowed and control plots with grazed plots in an intermediate position (Fig. 7). Native C4 grasses were not significantly correlated to the axis separating management groups, reflecting similar abundance of C4 grasses across management treatments (Table 9). Native forbs and native C3 grasses were strongly correlated with the control treatment, and non-native legumes were strongly correlated with the mow treatment. *Trifolium repens* L. (white clover) likely experienced competitive release in mowed plots due to its low stature.

Discussion

Plant functional group diversity did not have a strong effect on forage quality, and functional diversity resulted in an unexpected and strong negative relationship to forage availability in reconstructed prairies.

Overall, plant functional group diversity did not affect forage quality, contrary to my hypothesis. However, the strong diversity ***x*** month interaction in 2010 reflects the consequences of missing the optimum initial grazing period for switchgrass in early June of that year: the result of low palatability was limited consumption in June, continued rapid biomass accumulation and plant maturity, and poor quality and limited consumption in July. In diverse prairies, higher functional group diversity, combined with slower maturity of big bluestem and Indiangrass, led to a less severe decline in prairie forage quality between June and July, and mean RFQ remained higher than 100. In this case, higher diversity conferred greater flexibility in management and prevented major losses in productivity and quality when grazing timing was misaligned with one dominant species. Planting one highly productive or high quality species or cultivar of C4 grass may maximize animal performance when management is optimal, but higher diversity of forage species may provide insurance against greater losses when weather or other variables challenge optimal management.

Forage quality was similar to mixed C4 grasses grazed under a similar schedule during the same time period in southern Wisconsin (Chamberlain, 2011), but available forage was much greater in the mixed C4 grasses in July than in the switchgrass monocultures and diverse prairies evaluated here. NDF and crude protein concentrations

reported from switchgrass monocultures by Smart et al. (1995) were intermediate between 2009 and 2010 levels reported here. Mean available forage yield of the diverse prairie was low in comparison to the switchgrass monoculture and in comparison to mixed C4 grasses evaluated at a nearby study location (Chamberlain, 2011). Diverse prairie mean forage mass was higher than yields reported for switchgrass grown on sandier soils further north in Wisconsin (Smart et al., 1995) and was comparable to productivity of cool-season-only mixtures in southern Wisconsin managed with rotational stocking of beef cow-calf pairs (Oates et al., 2011). Because functional group diversity reduced forage availability rather than quality, the decreased forage availability found with increased functional diversity would primarily impact the amount of land producers must use for pasture to support animal productivity, rather than leading to reduced animal performance by reducing diet quality. In European semi-natural grasslands, when forage availability was low animals were able to maintain a high quality diet and animal performance was not affected (Isselstein et al., 2007)

In 2010, forage yield at feeding stations was greater in switchgrass stands and prairies, but because forage yields were sampled at feeding stations where the biomass of unpalatable vegetation was potentially half of the total standing biomass, this result alone does not provide strong evidence that switchgrass plants were more productive than Indiangrass or big bluestem plants in the diverse prairies. Lower forage yield in prairie feeding stations may also be due to high dispersion of unpalatable species, such as native forbs (reflected in the low ratio of palatable:unpalatable species standing biomass found by the sampling method in 2009), as well as high dispersion of exotic palatable species such as Kentucky bluegrass, smooth brome and white clover which invaded the prairies

prior to the beginning of this study. Plant-plant competition mediated by herbivory may have reduced C4 grass productivity in diverse prairies. When palatable species are dispersed among unpalatable species, as in the WICST prairies, selective grazing can negatively impact grass regrowth; in productive, sub-humid Flooding Pampa grasslands in Argentina, Semmartin and Oesterheld (2001) showed that when grazed patches were small (approximately 0.25-m^2), neighboring plants continued to shade the grazed plants and increased nitrogen availability benefited ungrazed neighbors.

The productivity of individual functional groups was not assessed, but non-native C3 grasses occurring in the prairies did not appear to be as vigorous or productive as in conventionally-managed cool-season grasslands in the region. Plant-plant competition in the prairies may have stressed non-native cool season grasses and legumes (Scherling et al., 2010) and it has long been documented that prescribed fire can reduce productivity of cool-season grasses depending on timing of the fire relative to plant maturity and weather conditions (Curtis & Partch, 1948), and prescribed fire has been observed to reduce productivity of cool-season pastures in southern Wisconsin (Doll et al., 2009). The timing of grazing in this experiment coincided with the late-spring to mid-summer flush of C4 growth because the primary goal was to evaluate native grasslands for sequential grazing. Adaptive management of native grasslands that are highly-invaded by cool-season forage species may include an earlier grazing period timed to increase harvest non-native C3 biomass. Just as some farmers clip paddocks following grazing to defoliate unpalatable species and create a more homogenous sward, early grazing in native grasslands may be an important cultural practice to increase forage productivity and quality later in the season by increasing nitrogen mineralization and light availability

when C4 grasses begin their initial flush of growth, and to improve competitive ability of C4 grasses.

Temporal forage availability may also be improved for sequential grazing by using later-maturing cultivars or ecotypes of C4 grasses from lower latitudes, which are adapted to longer growing seasons, just as Hudson et al. (2010) suggested in light of sequential grazing results in Michigan. Compared to native ecotypes adapted to relatively short growing seasons, some cultivars exhibit delayed onset of stem elongation and flowering of C4 grasses. This postpones the decline in forage quality and could allow farmers using sequential grazing to use C3 grasses later into the grazing season, to forestall use of C4 grasses until the period when higher temperatures, higher evapo-transpiration rates, and longer drought periods are more likely to occur, and to benefit from greater forage biomass.

The forage quality of native forbs was not evaluated due to limited consumption by cattle. A question that was brought to light by this research but remains unanswered is how native forb palatability, quality and productivity is influenced by defoliation during the growing season (either by grazing or post-graze mowing). Mowing greatly reduced the stature of tall species with stiff stems (e.g., the family *Asteraceae*, which dominated the native forb functional group), and vegetative regrowth of defoliated plants may exhibit higher leaf:stem ratios and thus lower C:N ratios than undefoliated plants. In a grazing plus clipping management regime, changes in structure and quality could alter the palatability of similar species and lead to greater consumption by cattle. Following grazing with clipping would defoliate tall stature forbs and ameliorate shading and N uptake that may be suppressing productivity and quality of defoliated C4 grasses in

grasslands with high forb abundance. Clipping could greatly increase FS frequency and available forage yield at the FS and paddock scales through these two mechanisms.

In central Iowa, reconstructed prairies managed with bison grazing had higher water, light availability and seedling germination compared to ungrazed prairies (Martin & Wilsey, 2006). In the diverse prairies at WICST, high absolute cover of Kentucky bluegrass and smooth brome was very high, and these species are able to shift belowground reserves toward rapid aboveground growth (Isbell & Wilsey, 2011) and these species may have quickly responded to and captured resources needed by legumes to germinate and survive. In the switchgrass monocultures, legume seedlings were in competition with diverse propragules, including non-native grasses and forbs in the seedbank of formerly-cropped soils as well as aggressive native species introduced by seed rain from the adjacent prairies, and species from these functional groups successfully colonized grazed and mowed plots. Due to the late emergence of switchgrass and native legume seedlings relative to many undesirable species, appropriately timed herbicide applications in switchgrass stands may have increased legume recruitment. However, many broad-leaf specific herbicides labeled for use in pastures have grazing restrictions or can suppress emergence of legume seedlings, conflicting with the goals of sequential grazing.

Plant community composition in C4 grass monocultures was not significantly different between graze and control treatments. Undisturbed monocultures remained highly dominated by C4 grasses, but growing season defoliation by grazing and mowing created canopy gaps colonized by non-native C3 grasses, non-native annual C4 grasses (*Setaria spp.* L. [yellow, green and giant foxtails]), and both native and non-native forbs.

These may be nascent trends leading toward a severe decline in C4 cover over time, as was observed in C4 monocultures grazed by bison in central Wisconsin (Jackson et al., 2008). Over longer time scales, higher plant diversity in reconstructed grasslands may provide greater stability of C4 grass abundance and productivity by reducing invasion by unpalatable species or by species that can outcompete stressed C4 grasses. Grazed and undisturbed prairies remained similar in composition over time, suggesting that the combination of burning and low intensity grazing has not yet significantly altered competitiveness of C4 grasses, native forbs, and non-native C3 grasses. However, long-term grazing management could result in a shift in composition. In a study of native and non-native grasses in the north central U.S., Inouye and Tilman (1995) concluded that when competitive abilities are similar, displacement is delayed, yet more competitive species can ultimately displace the less competitive species.

Mid-summer mowing, suggested earlier as a potential management to increase forage availability, could lead to long-term decline of tall-stature native forbs, which typically flower during mid- to late-summer. Mid-summer clipping may also lead to changes in soil moisture and fertility due to changes in the sub-canopy microenvironment, as noted by Dornbush (2004). When Kaslow Prairie in Iowa was resurveyed following cessation of mid-summer haying, increases in cover of tall-stature native forbs (including saw-tooth sunflower and rigid goldenrod) were observed, along with decreases in cover for species adapted to dry soil conditions and high levels of light availability, including little bluestem or other mid-height C4 grasses, low-stature native forbs, native legumes, and Kentucky bluegrass (Dornbush, 2004). Similar trends were

observed at Faville Prairie in southern Wisconsin after the management regime shifted from mid-summer haying to frequent prescribed fires (Rooney & Leach, 2010).

The plant species composition of tallgrass prairies under former haying regimes has been described as degraded (Rooney & Leach, 2010), but it is apparent that haymeadows in Iowa and Wisconsin remained resilient in that these plant communities were able to recover favorable characteristics when the management regime changed. From a biodiversity conservation perspective, low stature species adapted to dry soils and more open canopies are also considered species of conservation concern in the north central U.S., and are in need of management to ensure their long-term survival (Kraszewski & Waller, 2008). At the farm-to-landscape scales, various long-term management regimes including prescribed-fire only, managed grazing, and haying may be useful for providing a wide range of niches to meet the habitat needs of a broad array of native plant species and the insect species that depend on them, similar to the heterogeneity-diversity relationship demonstrated by differing levels of disturbances due to fire and grazing in tallgrass prairies in the Flint Hills and Iowa (Fuhlendorf & Engle, 2004; Brudvig et al., 2007; Vogel et al., 2007). Further research comparing the outcomes of post-graze clipping and biomass removal for hay production in reconstructed native grasslands is necessary to address questions surrounding these potential gains for biodiversity through increasing management intensity.

Whereas research had shown that reconstructed prairies often fail to resemble remnant prairies in species richness and other diversity measures (Sluis, 2002; Camill et al., 2004; Martin et al., 2005), research has recently high-lighted that reconstructed prairies may be similar to remnants in richness and abundance of C4 grasses and late-

phenology native forbs but do not resemble remnants in the diversity of species found in the cool-season sedges and early phenology forb functional groups (Carter & Blair, 2012; Sivicek & Taft, 2011).To reduce the potential for grazed reconstructions to be invaded by non-native C3 grasses and non-native forbs, it may be useful to increase the complement of native C3 sedges and grasses, early phenology forbs, and annual/biennial species represented in seed mixes. Given the life history, phenology, relative growth rates, root:shoot ratios, and root architecture of some species in these functional groups (Levang-Brilz & Biondini, 2003), it is plausible that these species can decrease non-native species invasion through direct competition for light and other resources at similar times and at similar soil depths. Given that American bison select C3-dominated patches in spring, autumn, and winter, tallgrass prairies have historically included a niche for native species that could thrive under conditions created by grazing, such as increased light, increased nitrogen availability, and treading. Selecting species such as these to confer desired function in grazing systems (Sanderson et al., 2007) may depress floristic quality rankings because rudereal species may be more abundant, yet if these species provide mechanisms to resist invasion by non-native cool season grasses, the long-term result could be higher native plant diversity and ecosystem function in reconstructed grasslands.

Incorporating C4 grasses or diverse prairie restorations into grazing operations may provide ecosystem services at the farm scale by allowing farmers to reduce demands on C3 grasses during periods of water- and temperature-stress during mid-summer. Having a small proportion of pasture land devoted to C4 grasses (10-25 percent) could make it easier to manage the rapid growth of cool-season pastures following spring

emergence from dormancy. Reducing the proportion of cool-season pasture used by a grazing operation could facilitate increased utilization of rapid early growth rates and reduce the need for mechanical forage management such as haying or post-graze clipping. Overall animal performance and farm profitability may be also be improved by providing opportunities to decrease the intensity of summer defoliation on cool-season stands, increase rest periods, and ultimately support higher vigor of the cool-season stands, which graziers typically rely upon to provide high-quality forage in the spring for lactating animals as well as in the fall for finishing grass-fed beef. In areas where native grasslands are already established, farmers may be able to expand pasture acreage at low financial risk or investment through converting existing warm-season grasslands in the Conservation Reserve Program to summer pasture as federal leases expire, or by renting land from community members who seek to offset the costs of restoration or who have conservation goals that could be met through managed grazing (such as increasing diversity and abundance of native forbs). Farmers in the Grand River Grasslands in southern Iowa are participating in grazing of unplowed grasslands and other conservation lands at reduced leasing rates (Miller et al., 2012), and the Wisconsin Department of Natural Resources and partners plan to facilitate similar opportunities in southwestern Wisconsin (M. Rowe, WiDNR, personal communication).

Farmers may also benefit from markets for products derived from diverse grasslands. A sustainability program that requires growers to restore and manage native plant communities to qualify for certification is already in use in the north-central U.S. (Zedler et al., 2009). Direct marketing and values-based value chains (Diamond & Barham, 2011) may also provide opportunities for farmers who utilize diverse native

grasslands to differentiate their products based on positive ecological attributes associated with their products.

Conclusion

This research provided two benchmarks for sequential grazing of diverse tallgrass prairie reconstructions in the north central U.S.: 1) forage quality of diverse prairie reconstructions can be similar to, or higher than, C4 grass monocultures, and 2) diverse prairies and C4 grass monocultures managed with rotational stocking can resist significant plant community change over short time scales.

Worldwide, optimizing forage availability, animal performance, biodiversity, and ecosystem function in permanent grasslands remains a frontier in ecological restoration and sustainable agriculture. For ecologists and agroecologists in the north-central U.S., the research tracks being pursued in tallgrass prairie rangeland science and in biodiversity conservation in European semi-natural grasslands provide models for future transdisciplinary research (Wrage et al., 2011). Further collaborations between farmers and researchers through on-farm research (Wiltshire et al., 2010) can help identify niches where sequential grazing fits best in the physical and economic terrain of this region. Research to explore diversity-productivity trade-offs and synergies among varying levels of functional group diversity and management intensity will likely require research to be conducted on new and established reconstructions at research institutions or on conservation lands.

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Tables and Figures

Table 1. Timing of Grazing, Duration and Instantaneous Stocking Rate.

Grazing	Diversity	Dates	Duration[a]	Rate[b]
June 2009	SW	6/5 – 6/10	5.0	6.3
	LD	6/5 – 6/11	22.8	28.5
	HD	6/4 – 6/10	22.0	27.5
July 2009	SW	7/10 – 7/13	14.4	21.6
	LD	7/8 – 7/13	10.0	15.0
	HD	7/9 – 7/14	9.8	14.8
June 2010	SW	6/17 – 6/21	24.3	30.4
	LD	6/18 – 6/23	12.7	15.8
	HD	6/17 – 6/22	14.8	18.5
July 2010	SW	7/20 – 7/23	18.8	28.3
	LD	7/21 – 7/23	8.2	12.3
	HD	7/21 – 7/24	4.5	6.8

[a] mean hours paddock^{-1}

[b] instantaneous stocking rate: mean animal units acre^{-1} day^{-1}

Table 2. Proportion of native legume seed recruited to seedling stage for five species of native legumes measured at three sampling periods.

a. *Desmodium canadense*

	Fall 2009			June 2010			Fall 2010		
Diversity	Cont.	Graze	Mow	Cont.	Graze	Mow	Cont.	Graze	Mow
SW	0.04	0.19	0.08	0.00	0.08	0.12	0.05	0.02	0.02
LD	0.07	0.08	0.14	0.07	0.24	0.13	0.02	0.01	0.02
HD	0.04	0.12	0.13	0.28	0.26	0.07	0.02	0.07	0.05

b. *Desmanthus illinoiensis*

	Fall 2009			June 2010			Fall 2010		
Diversity	Cont.	Graze	Mow	Cont.	Graze	Mow	Cont.	Graze	Mow
SW	0.02	0.04	0.03	0.07	0.07	0.07	0.00	0.01	0.01
LD	0.04	0.04	0.04	0.03	0.13	0.07	0.01	0.00	0.00
HD	0.02	0.08	0.11	0.03	0.10	0.15	0.00	0.01	0.01

c. *Dalea purpurea*

	Fall 2009			June 2010			Fall 2010		
Diversity	Cont.	Graze	Mow	Cont.	Graze	Mow	Cont.	Graze	Mow
SW	0.01	0.06	0.02	0.00	0.03	0.03	0.00	0.00	0.00
LD	0.00	0.03	0.05	0.00	0.00	0.00	0.00	0.00	0.00
HD	0.01	0.06	0.04	0.00	0.00	0.00	0.00	0.00	0.00

d. *Lespedeza capitata*

	Fall 2009			June 2010			Fall 2010		
Diversity	Cont.	Graze	Mow	Cont.	Graze	Mow	Cont.	Graze	Mow
SW	0.01	0.12	0.05	0.00	0.03	0.00	0.00	0.00	0.00
LD	0.04	0.09	0.05	0.00	0.00	0.00	0.00	0.00	0.00
HD	0.01	0.14	0.08	0.00	0.00	0.00	0.00	0.00	0.00

e. *Amorpha canescens*

	Fall 2009			June 2010			Fall 2010		
Diversity	Cont.	Graze	Mow	Cont.	Graze	Mow	Cont.	Graze	Mow
SW	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
LD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HD	0.00	0.01	0.00	0.00	0.03	0.00	0.00	0.00	0.00

Table 3. Results from PERMANOVA analyses of within-year plant community similarity in switchgrass plots.

Year	Source	df	SS	MS	Pseudo-F	P	CoV
2009	Block	2	1152.3	576.17	4.707	0.023	151.25
	Management	2	976.58	488.29	3.989	0.056	121.96
	Residual	4	489.64	122.41			122.41
	Total	8	2618.6				
2010	Block	2	657.43	328.72	2.262	0.071	61.127
	Management	2	1088.7	544.36	3.746	0.026	133.01
	Residual	4	581.34	145.34			145.34
	Total	8	2327.5				

Table 4. Summary of mean Bray-Curtis similarities in switchgrass plots. P-values calculated from pair-wise comparisons of management treatments using PERMANOVA.

Year	Levels	Similarity	P
2009	Control	86.219	--
	Graze	78.79	--
	Mow	69.361	--
	Control-Graze	80.904	0.139
	Control-Mow	70.096	0.05
	Graze-Mow	73.577	0.287
2010	Control	82.807	--
	Graze	81.169	--
	Mow	77.005	--
	Control-Graze	78.477	0.188
	Control-Mow	71.137	0.062
	Graze-Mow	77.573	0.223

Table 5. Results from PERMANOVA analyses of within-year plant community similarity in diverse prairie plots.

Year	Source	df	SS	MS	Pseudo-F	P	CoV
2009	Block	2	3234.3	1617.18	1.602	0.289	101.27
	Diversity	1	1091.49	1091.49	1.081	0.399	9.103
	Whole-plot error	2	2019.12	1009.56			336.52
	Whole-plot total	5	6345				
	Management	2	1482.5	741.27	2.091	0.021	64.453
	Sub-plot error	10	3545.5	354.55			354.55
	Total	17	11373				
2010	Block	2	2986.95	1493.46	1.532	0.337	86.457
	Diversity	1	889.53	889.53	0.913	0.479	-9.467
	Whole-plot error	2	1949.46	974.73			324.91
	Whole-plot total	5	5826				
	Management	2	1747.4	873.72	3.018	0.002	97.376
	Sub-plot error	10	2894.6	289.46			289.46
	Total	17	10468				

Table 6. Summary of mean Bray-Curtis similarities in diverse prairie plots—within management treatments and pair-wise comparisons of management treatments.

Year	Levels	Similarity	P
2009	Control	61.531	
	Graze	66.332	
	Mow	65.798	
	Control-Graze	64.354	0.259
	Control-Mow	62.387	0.05
	Graze-Mow	65.953	0.088
2010	Control	63.198	
	Graze	66.956	
	Mow	70.837	
	Control-Graze	65.706	0.16
	Control-Mow	64.189	0.03
	Graze-Mow	67.592	0.023

Table 7. Analyses of best models for grazing treatments, June 2009: forage availability response variables.

Response	Factor	Df	SS	MS	F	P	
CP	Div[a]	1	28.467	28.467	21.056	0.004	$\leq p \leq$ 0.019
NDF	Div	2	12.791	6.395	2.825	0.151	$\leq p \leq$ 0.262
RFQ	Div	2	42.803	21.402	2.247	0.201	$\leq p \leq$ 0.308
Forage Yield	Div	2	3291.306	1645.653	1.854	0.236	$\leq p \leq$ 0.299
SB	Div[a]	1	16551.89	16551.89	7.872	0.026	$\leq p \leq$ 0.049

[a] High and low diversity prairies pooled into one prairie diversity level.

Table 8. Analyses of best models for summer 2010 grazing treatments: forage quality and availability response variables.

Response	Factor	Df	SS	MS	F	P
CP	Div	1	0.6673	0.667	4.626	$0.048 \leq p \leq 0.053$
NDF	Div	1	269.911	269.911	16.571	$0.001 \leq p \leq 0.002$
	Month	1	51.127	51.127	3.139	$0.098 \leq p \leq 0.104$
RFQ	Div	1	664.258	664.258	11.446	$0.005 \leq p \leq 0.007$
	Month	1	2094.139	2094.139	36.084	$0.000 \leq p \leq 0.001$
	Div *x* Month	1	218.851	218.851	3.771	$0.074 \leq p \leq 0.081$
FS Frequency	Div	1	1.0	1.0	26.904	$0.000 \leq p \leq 0.001$
FS Forage Yield	Div	1	92.284	92.284	51.04	$0.000 \leq p \leq 0.001$
	Month	1	2.545	2.545	1.408	$0.257 \leq p \leq 0.263$
	Div *x* Month	1	9.493	9.493	5.250	$0.039 \leq p \leq 0.045$
Paddock Forage Yield	Div	1	188.506	188.506	74.700	$0.000 \leq p \leq 0.001$
	Month	1	1.0512	1.0512	0.417	$0.530 \leq p \leq 0.533$
	Div *x* Month	1	12.581	12.581	4.986	$0.044 \leq p \leq 0.050$
SB	Month	1	46.245	46.245	30.005	$0.000 \leq p \leq 0.001$

Table 9. Mean absolute coverof the most abundant functional groups across years, management treatments, and diversity treatments.

	2009						2010					
	control		graze		mow		control		graze		mow	
Functional Group	PR	SW	PR	SW	PR	SW	PR	SW	PR	SW	PR	SW
Native C4 grass	46.8	99.5	44.4	91.8	48.1	81.1	54.8	97.3	52.2	90.2	59.1	89.6
Non-native C3 grass	109.7	10.8	94.6	12.8	98.0	22.8	94.5	17.8	91.1	28.1	107.0	48.6
Native forb	84.0	2.8	72.1	9.1	46.1	10.3	87.0	3.9	68.1	7.8	46.1	12.3
Non-native forb	11.8	14.9	6.5	28.9	14.2	26.8	10.5	6.4	6.3	10.8	16.5	14.7
Non-native legume	3.6	0.2	11.5	0.6	10.6	1.3	2.8	0.2	10.1	0.3	8.3	0.3
Non-native C4 grass	0.8	3.4	1.9	4.3	0.6	9.7	0.0	3.3	0.8	4.8	0.7	13.8
Native legume	3.9	0.4	6.5	0.3	3.0	0.1	1.4	0.0	2.4	0.6	0.9	0.2
Native C3 grass	2.7	0.1	1.4	0.6	0.2	0.0	1.8	0.1	1.4	1.5	0.1	0.5

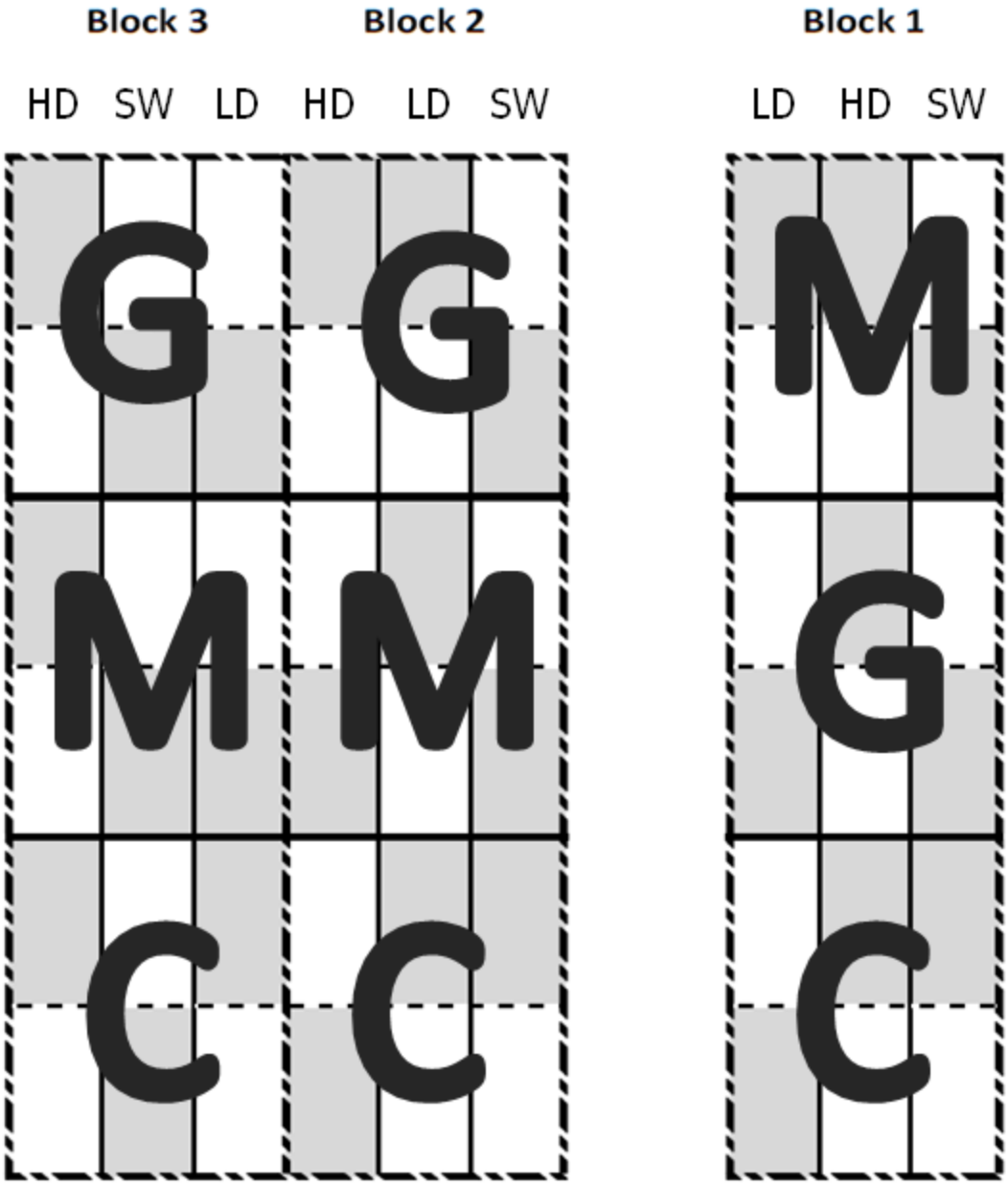
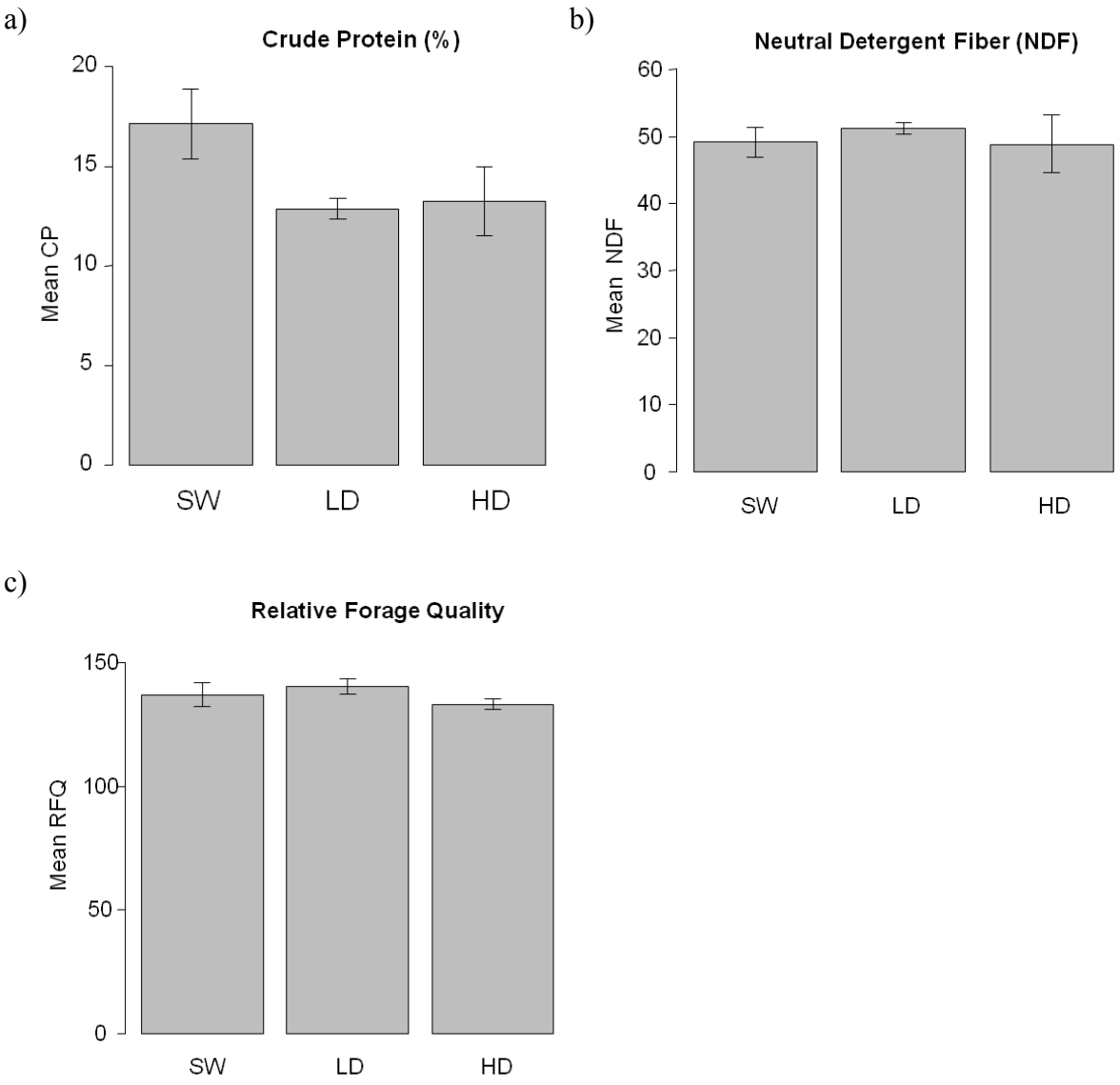


Figure 1. Experimental design at University of Wisconsin Arlington Agricultural Research Station. Original diversity treatments (HD – high diversity prairie; LD – low diversity prairie; MC – switchgrass monoculture) are 105 m by 13 m and were established in a randomized complete block design. Management treatments (C – control; M – mow; G – graze) and legume interseeding (shaded) are applied in a heirarchical split-split plot design. Block 1 and Block 2 are separated by cropped fields and are 70 m apart. Block 2 and Block 3 are separated by a fence.

1

1



2

3 **Figure 2.** Comparison of several forage quality parameters across diversity treatments
4 sampled in June 2009. Values are means +/- 1 SE of the mean. Crude protein in
5 switchgrass was significantly higher than prairies ($p < 0.019$). Means were not
6 significantly different for neutral detergent fiber ($p < 0.262$) or relative forage quality (p
7 < 0.308).

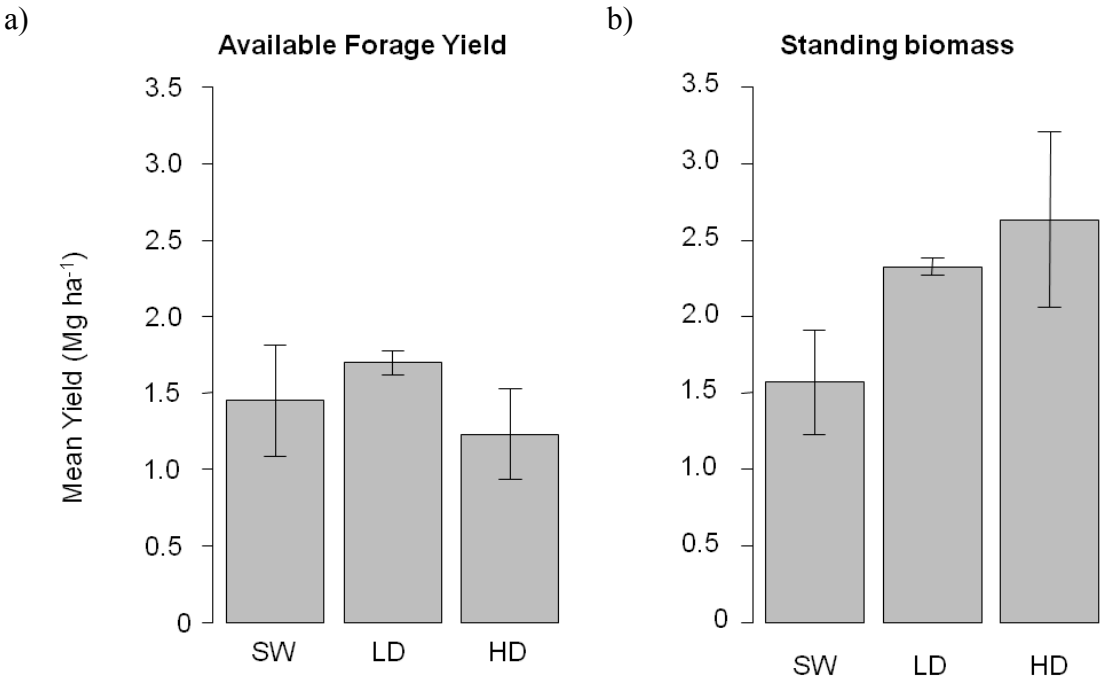


Figure 3. Comparison of available forage and standing biomass across diversity treatments in June 2009. Values are means +/- 1 SE of the mean. Mean yields of available forage means are not significantly different ($p < 0.229$); mean switchgrass standing biomass is significantly lower than diverse prairies ($p < 0.049$), but model simplification indicated that the difference observed between diversity levels in prairies was not significant.

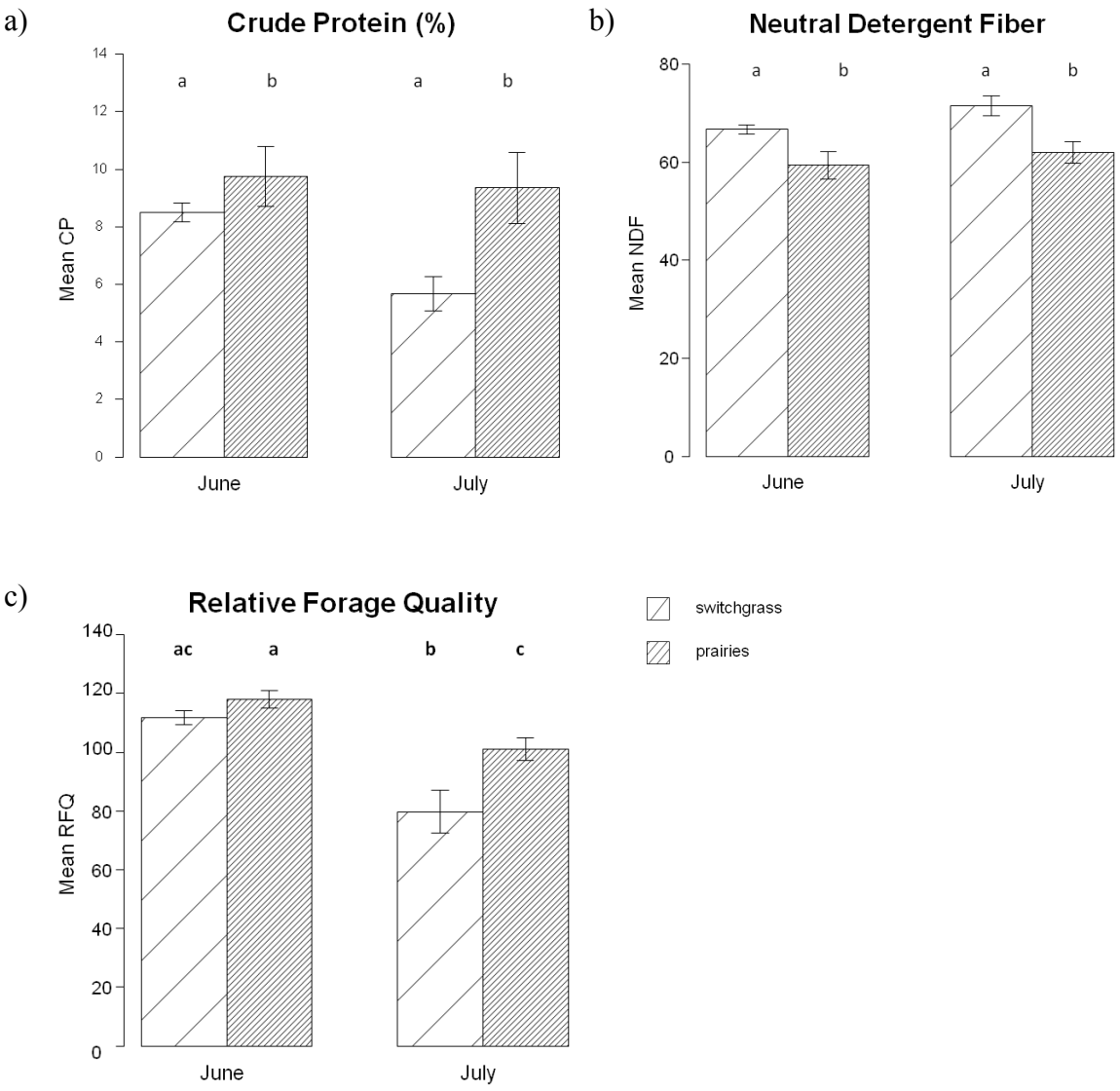


Figure 4. Comparisons of several forage quality parameters across diversity treatments sampled in June and July 2010. Bars show means; bars show +/- 1 SE of the mean. Letters indicate which means are significantly different ($\alpha = 0.05$) across diversity treatments and month.

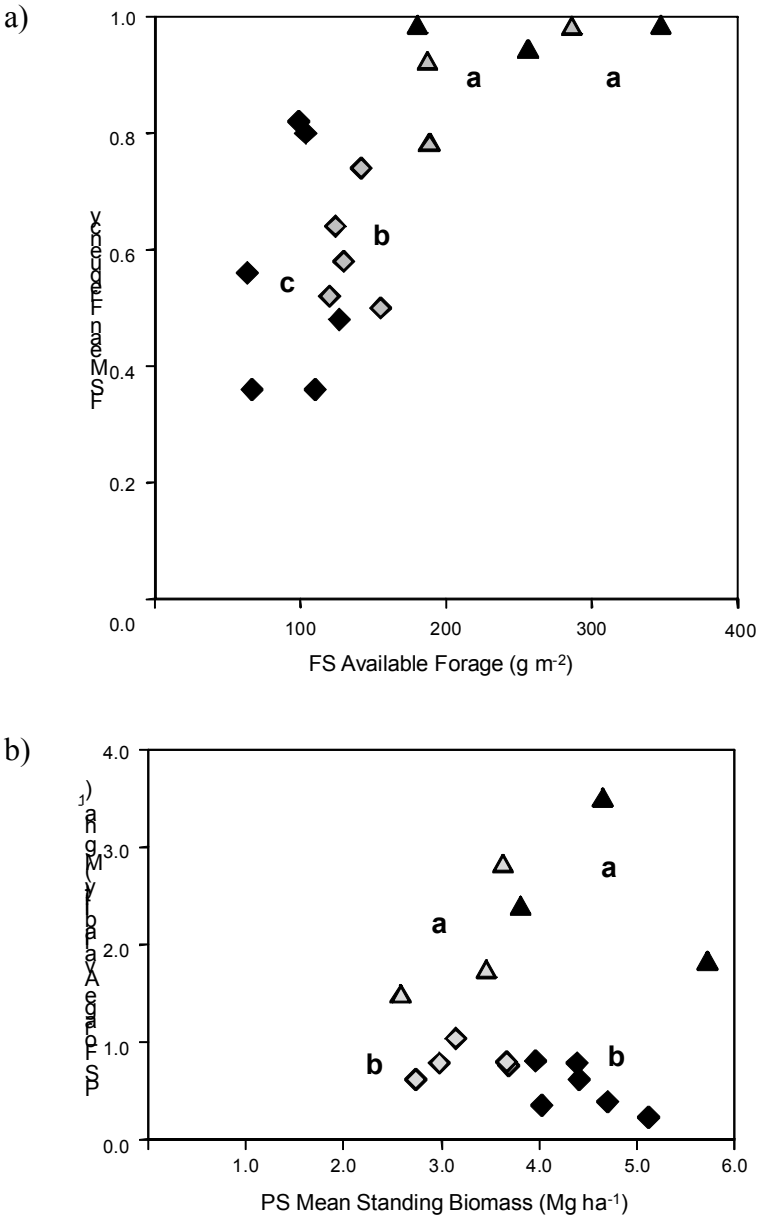


Figure 5. Comparisons of forage availability in switchgrass and prairies, summer 2010. Triangles indicated switchgrass experimental units; diamonds indicate prairie experimental units; June samples are gray and July samples are black. a) Feeding stations (FS) were much more frequent in switchgrass stands than in diverse prairies, and forage availability at the FS scale was higher in switchgrass than in diverse prairies; groups that share letters have similar mean forage yield at the FS scale. b) Mean standing biomass was similar across diversity treatments and increased from June to July. However, forage yield at the paddock scale was significantly higher in switchgrass stands than diverse prairies; groups that share letters have similar mean yield at the paddock scale.

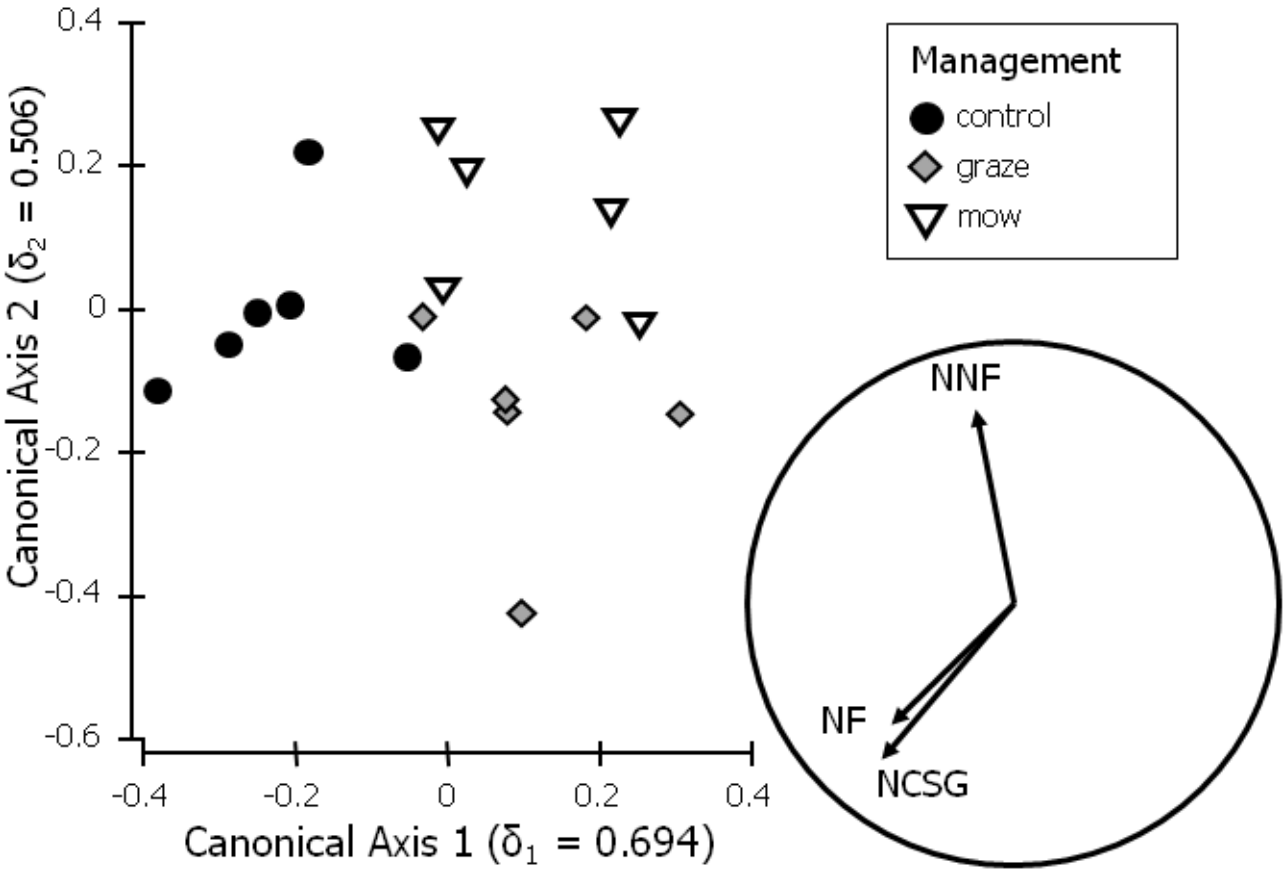


Figure 6. Effect of management treatments on diverse prairie composition illustrated by canonical ordination, fall 2009. Axis 1 was selected as the best principal coordinates axis for discriminating between management groups in multivariate space. The second axis has a slightly lower squared canonical correlation and primarily separates separation grazed and mowed plots. Vectors (inset circles) indicate the relative direction and strength of functional groups' Spearman correlations with canonical axes (for $r \geq 0.5$). Functional groups included are: NCSG –native cool-season grasses; NF – native forbs; and NNF – non-native forbs.

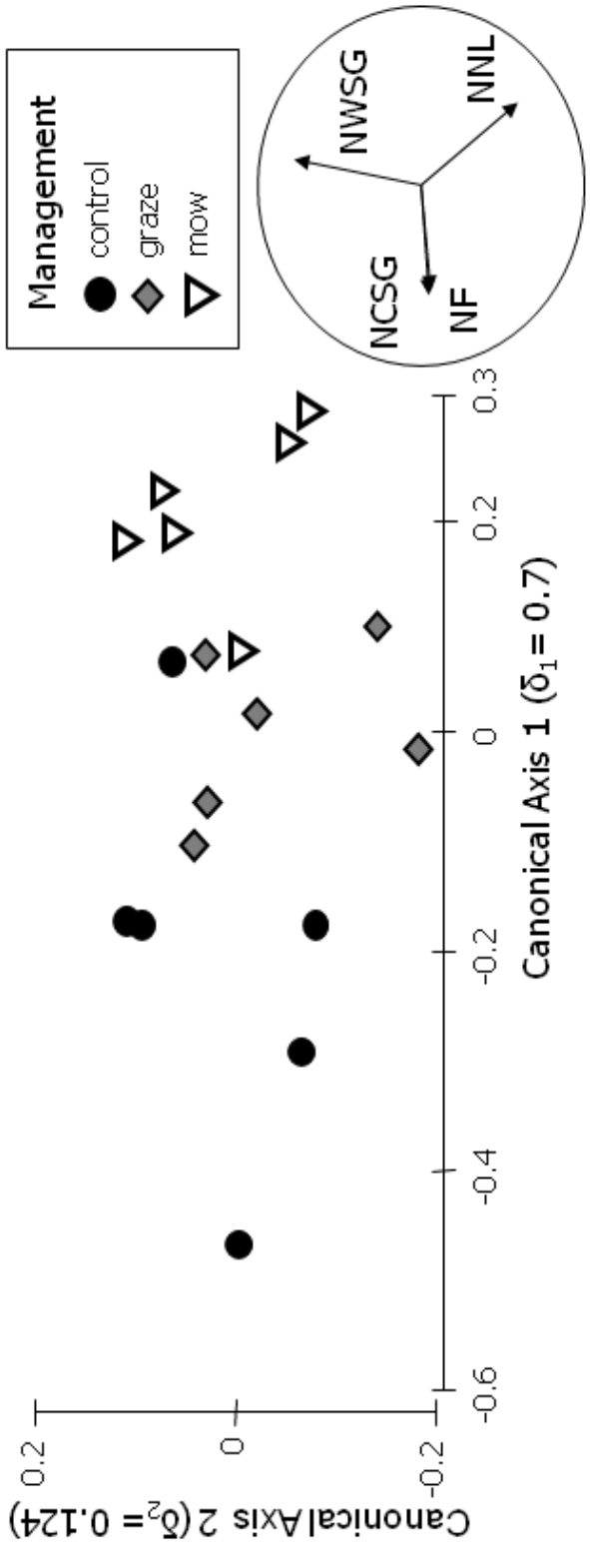


Figure 7. Effects of management treatments on diverse prairie composition illustrated by canonical ordination, fall 2010. Axis 1 was selected as the best axis for discriminating between management groups in multivariate space. Axis 2 was not useful for discriminating between groups. Vectors (inset circles) indicate the relative direction and strength of functional groups' Spearman correlations with canonical axes (for $r \geq 0.5$). Functional groups included are: NCSG –native cool-season grasses; NF – native forbs; NWSG – native warm-season grasses; and NNL – non-native legumes.

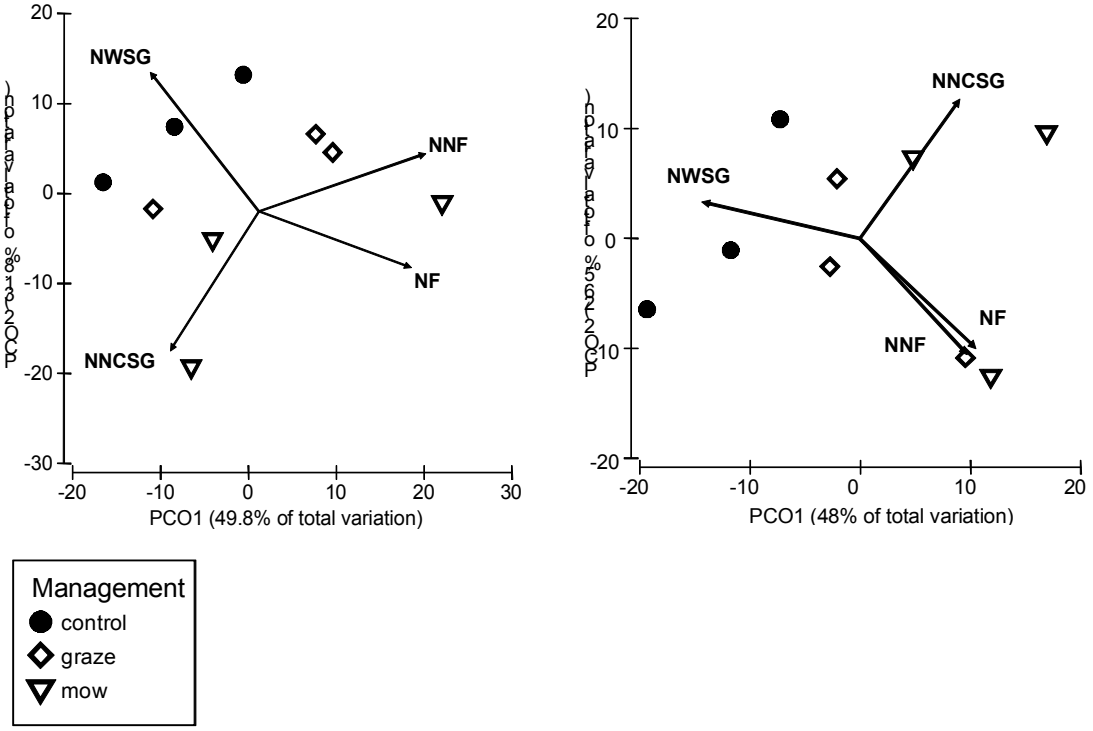


Figure 8. Principal coordinates ordination of management treatments in the switchgrass diversity treatment. Similar relationships were observed across years. Arrows illustrate Spearman correlations of functional groups to PCO axes (for $r \geq 0.8$). Functional groups included are: NF – native forbs; NWSG – native warm-season grasses; NNCSG – non-native cool-season grasses.

Overall conclusion

The interaction of varying types of disturbance and plant diversity levels resulted in a number of tradeoffs in reconstructed tallgrass prairies. Higher species and functional group diversity conferred greater resistance to invasion by undesirable species under grazing and mowing, but high abundance of native forbs in diverse prairies greatly reduced forage availability and yield compared to native C4 grass monocultures. The low-to- moderate stocking rates that foster selective grazing and benefit forbs in wildflower-rich prairies means that fewer head of cattle can be supported on a diverse prairie than on equal acreage of grassland dominated by native C4 grasses. However, the nutritive quality of forage was similar across diversity levels, and animal performance should not be reduced by increased diversity if sufficiently large pastures can be provided. In diverse prairies, mowing resulted in lower native forb cover and significant differences in plant community composition compared to control plots, but these patterns were not observed in grazed plots; these outcomes indicate that many of the native forb species present at our study can thrive under low to moderate stocking rates but are adapted to avoid, rather than tolerate, defoliation by large herbivores.

These results highlight a key difference between the typical objectives for farm production and conservation lands. In non-native grasslands in the Upper Midwest, farmers use rotational stocking typically create small paddocks within their pastures to increase animal density. This tactic can successfully alter cattle behavior and result in more homogenous defoliation of the plant community because high animal density influences cattle to reduce selection of preferred forage species and increase consumption

of species or plant parts that the animals find less desirable. This has important ramifications for plant-plant interactions—increased uniformity of residual vegetation height across all species can favor grasses, because this functional group can typically regrow faster than weedy forbs that invest in physical or chemical defenses to avoid herbivory. Both the intensity and frequency of defoliation are limited so plants support aboveground growth without significant withdrawal of belowground reserves.

In tallgrass prairies, land managers using grazing have generally stocked cattle and bison at relatively low animal densities to encourage these herbivores to exercise their selection preferences for grasses. In addition, continuous stocking is generally employed, and herbivores defoliate grasses at high rates of intensity and frequency, limiting aboveground biomass and dominance of highly-competitive species. With this type of management, grazing confers a competitive advantage to subdominant forbs that contribute the most to species richness and diversity in tallgrass prairies.

Integrating biodiversity conservation and agricultural production in grasslands in the Upper Midwest requires tackling the fact that farmers and conservationists both describe their strategies as managed grazing, yet each can have in mind very dissimilar plant communities, objectives and tactics. Managed grazing in reconstructed prairies can encompass a range of objectives, and tactics, and I propose that at least three terms are needed to clarify objectives and tactics:

- *management-intensive rotational stocking:* on farms, reconstructed prairies are managed at high stocking densities to encourage uniform defoliation; plant species include in these reconstructions are selected for herbivory tolerance, and plant species represent multiple functional groups and functional group

redundancy (including multiple species of C4 grasses, C3 grasses, legumes, and forbs) to encourage high productivity via niche complementarity, reduce response of forage yield to interannual weather variability (increase stability of forage mass), and to confer resistance to weed invasion.

- *low density rotational or continuous stocking:* on farms or conservation lands, reconstructed prairies with high functional group diversity are managed with moderate-to-low animal densities to promote selective grazing—yielding high quality forage to support animal performance as well as promoting forb diversity to support a broad array of ecosystem services; and
- *prescribed grazing:* on conservation lands where prairie reconstructions have become dominated by C3 or C4 grasses, timing, stocking rate, and stocking system are managed specifically to reduce grass dominance and increase the competitiveness, abundance, distribution, and reproduction of rarer species (particularly species of high conservation value).

Any of these strategies could also be combined with haying, mowing, patch-burn grazing, multi-species grazing or seeding introductions to meet goals in an adaptive-management framework.

In the short term, research that proposes to integrate ecological restoration and sustainable agriculture in the prairie-forest border region must compete for funding from public agencies with different outlooks and funding priorities. With respect to this limitation, I have identified three tracks of research that are relevant to traditional disciplines of agronomy, restoration ecology, and landscape ecology. These tracks could be pursued separately or in some combinations:

1. Explore relationships between different levels (and combinations) of plant functional group diversity and utility for farmers to determine how many species and functional groups are needed, and at what levels of abundance, to support high yields, high quality forage, and resistance to invasion. Over 200 species of forbs occur in prairie and savanna habitats in Wisconsin, but there has been little to no research to screen species for forage quality and productivity, anti-quality secondary chemicals, and herbivory tolerance. Our knowledge of herbivory tolerance is primarily inferred from observations of the frequency and abundance of forbs in historically-grazed prairies).
2. Explore impacts of prescribed grazing to plant community composition, plant-organism interactions across trophic levels, nutrient cycling, and other ecosystem functions.
3. Model potential landscape configurations of reconstructed prairie pastures and predict outcomes for biodiversity, ecosystem functions, and ecosystem services at various spatial scales relevant to socio-ecological systems.

The trends in plant community composition observed in this study suggest that some combination of native prairie and savanna species can be deeply integrated into locally-adapted agriculture. The cow is not simply an agent of prairie degradation, and prairie restoration need not be limited to reclaiming agricultural lands to fulfill a vision of pristine nature untouched by humans. Integrating ecological restoration and low-input, diversified agricultural systems could meet broad goals for biodiversity conservation, food security and food sovereignty, and climate change adaptation. These objectives

reflect the intrinsic value of every unique species and complex ecosystem, as well as the immense instrumental value of biodiversity and ecosystem function as the foundation of human well-being.

Integrating agriculture and conservation via grazing in diverse tallgrass prairie communities may be ecologically feasible, yet this form of management remains highly constrained by social and economic factors. The sustainable agriculture community is actively addressing how changes in public policy can sustain or improve production of food, fiber, timber, and energy while increasing biodiversity, ecosystem function, and ecosystem services (Jordan & Warner, 2010; Reganold et al., 2011). However, technologically-advanced and energy-intensive agricultural systems in much of the developed world are extremely resistant to social and environmental stressors due to continued investment of financial capital, social capital, and energy (Allison & Hobbs, 2004; Jackson, 2008). Pursuing restoration ecology's overarching goal of restoring "sustainable relationships between nature and culture" (Jackson et al., 1995) in the Upper Midwest will require better understanding of the social factors that limit adoption of grassland restoration in complex socio-ecological systems. While the over-arching goals for prairie restoration remain the same whether or not production is involved—restoring biodiversity, ecosystem processes, and ecological function at landscape scales—strategies, tactics and objectives need to evolve in order to propel restoration beyond the limited cultural relevance, social commitment, and spatial scale of current efforts. The scope and scale of prairie restoration in the Upper Midwest can greatly expand through improved coordination of grazing research and through the restoration community's

continued engagement with farmers and other stakeholders in local and regional food systems.

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Appendix

Table 1. Native species seeded in low-diversity and high-diversity WICST prairie plantings in 1999.[1]

Species	Common name	Guild	LD	HD
Andropogon gerardii	big bluestem	C4 grass	X	X
Elymus canadensis	Canada wild rye	C3 grass	X	X
Sorgastrum nutans	Indiangrass	C4 grass		X
Allium cernuum	nodding wild onion	summer/fall forb		X
Asclepias tuberosa	butterfly milkweed	spring forb		X
Aster novae-angliae	New England aster	summer/fall forb		X
Astragalus canadensis	Canada milk-vetch	legume		X
Baptisia leucantha	white wild indigo	legume		X
Coreopsis palmata	prairie coreopsis	summer/fall forb		X
Desmodium canadense	showy tick trefoil	legume	X	X
Eryngium yuccifolium	rattlesnake master	summer/fall forb		X
Galium boreale	northern bedstraw	spring forb		X
Geum triflorum	prairie smoke	early spring forb		X
Helianthus	saw-tooth sunflower	summer/fall forb		X
Helianthus pauciflorous	showy sunflower	summer/fall forb		X
Lespedeza capitata	round-headed bush	legume	X	X
Monarda fistulosa	wild bergamot	summer/fall forb		X
Potentilla arguta	prairie cinquefoil	spring forb		X
Ratibida pinnata	yellow coneflower	summer/fall forb	X	X
Rosa carolina	pasture rose	woody shrub		X
Rudbeckia hirta	black-eyed Susan	summer/fall forb	X	X
Silphium integrifolium	prairie rosinweed	summer/fall forb		X
Solidago rigida	stiff goldenrod	summer/fall forb		X
Tradescantia ohioensis	common spiderwort	spring forb		X
Viola pedatifida	prairie violet	early spring forb		X

1. adapted from: Simonsen, K., E. Howell, and J. Posner 2002. Prairie Establishment in Agricultural Soils. Pages 136-144. Wisconsin Integrated Cropping System Trial 9th Technical Report. University of Wisconsin-Madison, Madison, WI.

Table 2. Plant taxa observed from 2009-2011 across all planted native grasslands at WICST. Several taxa were identified to genus only and may represent two or more closely-related species. One hundred nine taxa were recorded during five sampling campaigns, representing 61 native species, 48 non-native species, and 29 families. Asterisks (*) denote non-native taxa. Alphas (α) denote planted species.

Species	Common name	Family	Functional Group
*Abutilon theophrasti**	velvet leaf	Malvaceae	non-native forb
Allium cernuum$^{\alpha}$	nodding wild onion	Liliaceae	native forb
*Amaranthus spp.**	pigweed	Amaranthaceae	non-native forb
Ambrosia artemisiifolia	common ragweed	Asteraceae	native forb
Ambrosia trifida	giant ragweed	Asteraceae	native forb
Amorpha canescens$^{\alpha}$	lead-plant	Fabaceae	native legume
Andropogon gerardii$^{\alpha}$	big bluestem	Poaceae	native C4 grass
*Arctium minus**	common burdock	Asteraceae	non-native forb
Arnoglossum atriplicifolium	pale Indian-plantain	Asteraceae	native forb
Asclepias syriaca	common milkweed	Asclepiadaceae	native forb
Asclepias tuberosa$^{\alpha}$	butterfly milkweed	Asclepiadaceae	native forb
Aster lateriflorus	calico aster	Asteraceae	native forb
Aster novae-angliae$^{\alpha}$	New England aster	Asteraceae	native forb
Aster pilosus	frost aster	Asteraceae	native forb
Aster simplex	aster hybrid	Asteraceae	native forb
Astragalus canadensis$^{\alpha}$	Canada milk-vetch	Fabaceae	native legume
Baptisia alba$^{\alpha}$	white wild indigo	Fabaceae	native legume
*Bromus inermis**	smooth brome	Poaceae	non-native C3 grass
*Capsella bursa-pastoris**	shepherd's-purse	Brassicaceae	non-native forb
*Carduus acanthoides**	plumeless thistle	Asteraceae	non-native forb
*Carduus nutans**	musk thistle	Asteraceae	non-native forb
Carex bicknelli	Bicknell's sedge	Cyperaceae	native sedge
*Cerastium fontanum**	mouse-ear chickweed	Carophyllaceae	non-native forb
*Chenopodium album**	lamb's-quarters	Chenopodiaceae	non-native forb
*Cirsium arvense**	Canada thistle	Asteraceae	non-native forb
Cirsium discolor	pasture thistle	Asteraceae	native forb
*Cirsium vulgare**	bull thistle	Asteraceae	non-native forb
Conyza canadensis	Canada horseweed	Asteraceae	native forb

Species	Common name	Family	Functional Group
Coreopsis palmata[α]	prairie coreopsis	Asteraceae	native forb
*Crepis tectorum**	narrow-leaved hawk's-beard	Asteraceae	non-native forb
*Dactylis glomerata**	orchard grass	Poaceae	non-native C3 grass
Dalea purpurea[α]	purple prairie-clover	Fabaceae	native legume
*Daucus carota**	wild carrot	Apiaceae	non-native forb
Desmanthus illinoensis[α]	Illinois bundle-flower	Mimosaceae	native legume
Desmodium canadense[α]	showy tick trefoil	Fabaceae	native legume
*Digitaria spp.**	crabgrass	Poaceae	non-native C4 grass
*Echinochloa crus-galli**	barnyard grass	Poaceae	non-native c4 grass
Elymus canadensis[α]	Canada wild rye	Poaceae	native C3 grass
*Elymus repens**	quackgrass	Poaceae	non-native C3 grass
Erigeron strigosus	daisy fleabane	Asteraceae	native forb
*Eriochloa villosa**	woolly cup grass	Poaceae	non-native C4 grass
Eryngium yuccifolium[α]	rattlesnake-master	Apiaceae	native forb
Galium boreale[α]	northern bedstraw	Rubiaceae	native forb
Gaura biennis	biennial gaura	Onagraceae	native forb
Geum triflorum[α]	prairie smoke	Rosaceae	native forb
Helianthus grosseserratus[α]	saw-tooth sunflower	Asteraceae	native forb
Helianthus pauciflorus[α]	showy sunflower	Asteraceae	native forb
Heliopsis helianthoides	false sunflower	Asteraceae	native forb
Heuchera richardsonii	prairie alumroot	Saxifragaceae	native forb
*Hieracium spp.**	hawkweed	Asteraceae	non-native forb
*Hordeum jubatum**	foxtail barley	Poaceae	non-native C3 grass
*Lactuca serriola**	prickly lettuce	Asteraceae	non-native forb
Lespedeza capitata[α]	round-headed bush-clover	Fabaceae	native legume
*Malus spp.**	apple	Rosaceae	non-native tree
*Malva neglecta**	common mallow	Malvaceae	non-native forb
*Matricaria discoidea**	pineapple weed	Asteraceae	non-native forb
*Medicago lupulina**	black medic	Fabaceae	non-native legume
*Medicago sativa**	alfalfa	Fabaceae	non-native legume
*Melilotus spp.**	sweetclover	Fabaceae	non-native legume
Monarda fistulosa[α]	bee balm	Lamiaceae	native forb
*Morus spp.**	mulberry	Moraceae	non-native tree
Muhlenbergia frondosa	wirestem muhly	Poaceae	native C4 grass
Oenothera biennis	evening primrose	Onagraceae	native forb
Oxalis stricta	tall wood-sorrel	Oxalidaceae	native forb
Panicum	fall panic grass	Poaceae	native C4 grass

Species	Common name	Family	Functional Group
dichotomiflorum			
Panicum virgatum[α]	switchgrass	Poaceae	native C4 grass
*Phalaris arundinacea**	reed canary grass	Poaceae	non-native C3 grass
*Phleum pratense**	timothy	Poaceae	non-native C3 grass
Physalis spp.	ground-cherry	Solanaceae	native forb
*Plantago spp.**	Plantago spp.	Plantaginaceae	non-native forb
*Poa pratensis**	Kentucky bluegrass	Poaceae	non-native C3 grass
*Polygonum aviculare**	prostrate knotweed	Polygonaceae	non-native forb
*Polygonum convolvulus**	wild buckwheat	Polygonaceae	non-native forb
Polygonum pennsylvanicum	smartweed	Polygonaceae	native forb
Populus spp.	Populus spp.	Salicaceae	native tree
Potentilla arguta[α]	prairie cinquefoil	Rosaceae	native forb
Prunus spp.	cherry	Rosaceae	native tree
Ratibida pinnata[α]	yellow coneflower	Asteraceae	native forb
Rosa carolina[α]	pasture rose	Rosaceae	native forb
Rudbeckia hirta[α]	black-eyed Susan	Asteraceae	native forb
Rudbeckia subtomentosa	sweet black-eyed Susan	Asteraceae	native forb
*Rumex crispus**	curly dock	Polygonaceae	non-native forb
*Schedonorus phoenix**	tall fescue	Poaceae	non-native C3 grass
*Senecio vulgaris**	common groundsel	Asteraceae	non-native forb
*Setaria faberi**	giant foxtail	Poaceae	non-native C4 grass
*Setaria pumila**	yellow foxtail	Poaceae	non-native C4 grass
*Setaria spp.**	foxtail	Poaceae	non-native C4 grass
*Silene latifolia**	white campion	Carophyllaceae	non-native forb
Silphium integrifolium[α]	prairie rosinweed	Asteraceae	native forb
Silphium perfoliatum var. perfoliatum	cup-plant	Asteraceae	native forb
Solanum ptycanthum	black nightshade	Solanaceae	native forb
Solidago canadensis	Canada goldenrod	Asteraceae	native forb
Solidago rigida[α]	rigid goldenrod	Asteraceae	native forb
*Sonchus arvensis**	field sow-thistle	Asteraceae	non-native forb
Sorghastrum nutans[α]	Indiangrass	Poaceae	native C4 grass
*Taraxacum officinale**	dandelion	Asteraceae	non-native forb
Tradescantia ohioensis[α]	common spiderwort	Commelinaceae	native forb
*Tragopogon dubius**	greater goat's-beard	Asteraceae	non-native forb
*Trifolium hybridum**	alsike clover	Fabaceae	non-native legume
*Trifolium pratense**	red clover	Fabaceae	non-native legume
*Trifolium repens**	white clover	Fabaceae	non-native legume

Species	Common name	Family	Functional Group
*Triticum aestivum**	wheat	Poaceae	non-native C3 grass
Ulmus spp.	elm	Ulmaceae	native tree
Verbena stricta	hoary vervain	Verbenaceae	native forb
Verbena urticifolia	white vervain	Verbenaceae	native forb
Veronica peregrina	purslane speedwell	Scrophulariaceae	native forb
Viola pedatifida[α]	prairie violet	Violaceae	native forb
Viola spp.	violet	Violaceae	native forb
Vitis spp.	grape	Vitaceae	native vine

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