SOIL ECOSYSTEM SERVICE TRADEOFFS AND SOCIAL-ECOLOGICAL RESILIENCE IN THE NORTH CENTRAL GREAT PLAINS

By

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SOIL ECOSYSTEM SERVICE TRADEOFFS AND SOCIAL-ECOLOGICAL

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University of Nebraska, 2017

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ABSTRACT: Humans seek to improve their wellbeing by altering ecological processes

to maximize the output of specific ecosystem services, which often leave the system

vulnerable to unintended and undesirable side effects. Ecosystem services emerge from

complex interactions among ecological structures and processes occurring at multiple

scales. The degree to which an ecosystem maintains a predictable range of structures and

processes in the face of disturbance can be described as its resilience. The 1930s Dust

Bowl of the North American Great Plains is an example of a system reconfiguration and

loss of resilience that was ultimately driven by human optimization for a single

ecosystem service, and proximately triggered by an environmental disturbance. In part to

avoid another social-ecological catastrophe, in 1985 Congress approved a 12 million ha

set aside program known as The Conservation Reserve Program. In 2017, The

Conservation Reserve Program (CRP) remains the largest soil conservation initiative in

U.S. history in terms of acres enrolled, and provides a myriad of ecosystem services.

However, the reliable production of these services is uncertain in the face of enrollment

variability, potentially conflicting management objectives, and global change.

Additionally, since its inception CRP objectives have expanded beyond soil conservation

to include pollinator conservation and game habitat -the establishment of which often

makes use of soil destructive practices like disk tillage. The goal of this work was to

uncover whether management intended to achieve multiple, simultaneously objectives for the CRP may ultimately lead to non-linear, unwanted outcomes for CRP grassland ecosystems in the North Central Great Plains.

DEDICATION

For B

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1 THE POLITICAL, SOCIAL, AND ECOLOGICAL CONTEXT OF THE CONSERVATION RESERVE PROGRAM

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ABSTRACT: Humans seek to improve their wellbeing by altering ecological processes to maximize the output of specific ecosystem services, which often leave the system vulnerable to unintended and undesirable side effects. Ecosystem services emerge from complex interactions among ecological structures and processes occurring at multiple scales. The degree to which an ecosystem maintains a predictable range of structures and processes in the face of disturbance can be described as its resilience. The 1930s Dust Bowl of the North American Great Plains is an example of a system reconfiguration and loss of resilience that was ultimately driven by human optimization for a single ecosystem service, and proximately triggered by an environmental disturbance. In part to avoid another social-ecological catastrophe, in 1985 Congress approved a 12 million ha set aside program known as The Conservation Reserve Program. In 2017, The Conservation Reserve Program (CRP) remains the largest soil conservation initiative in U.S. history in terms of acres enrolled, and provides a myriad of ecosystem services. However, the reliable production of these services is uncertain in the face of enrollment variability, conflicting management objectives, and global change. Additionally, since its inception the CRP objectives have expanded beyond soil conservation to include pollinator conservation and game habitat –the attempted creation of which often includes soil destructive practices like disking. Here I explore the complex social, ecological, and

economic components that underpin the Conservation Reserve Program and the ecosystem services it provides.

1.1 INTRODUCTION: The political, social, and ecological context of the Conservation Reserve Program

Humans seek to improve their wellbeing by altering ecological processes to maximize the output of specific ecosystem services, which often leave the system vulnerable to unintended and undesirable side effects. Grassland ecosystems, including those in the United States Great Plains, provide many ecosystem services such as water purification, food and fiber production, erosion control, waste recycling, and disease and pest mitigation (Hönigová et al., 2012). These ecosystem services emerge from complex interactions among ecological structures and processes occurring at multiple scales. The objective of this work is to understand how human management of ecosystems elicits unintended ecological feedbacks, especially from the soil system, and how these feedbacks might ultimately undermine original management objectives.

The degree to which an ecosystem maintains a predictable range of structures and processes in the face of disturbance can be described as its resilience. First termed by Holling in 1973, resilience theory invigorated the decade's old debate surrounding stability in ecology. Holling distinguished two alternate models of ecological response to disturbance: near-equilibrium stabilizing behavior and adaptive behavior that allowed the system to persist in its current state over the long-term. The former, so-called "equilibrium" understanding of ecosystems relies on the eventual return to steady state following variability ranging from small fluctuations to catastrophic shifts.

An ecosystem assumed to reliably return to equilibrium could be managed with intensive practices to generate desired ecosystem services (e.g., food or fiber production) and then

abandoned to eventually restore itself through successional processes, the rate of return perhaps amplified with human intervention (restoration). The latter, or non-equilibrium view of ecosystems rejects that the ecosystem inevitably returns to a determined equilibrium following the removal of disturbance even with intensive intervention. Instead, it understands systems as having multiple possible stable states. In the non-equilibrium view, the persistence of any one state is promoted by one or a set of key ecological structures and processes that can be eroded and eventually eliminated through repeated disturbances, with a proximate disturbance triggering reconfiguration into an alternative state. Once it occupies this alternative stable state, the non-equilibrium view understands that the system cannot return to a state resembling the initial state without considerable management intervention, and even then such pseudo-reversibility may be unachievable because old feedbacks and thresholds have been supplanted by new, dominant processes.

1.1.1 European Settlement of the Great Plains: Social-Ecological Transformations

The 1930s Dust Bowl of the North American Great Plains is an example of a system reconfiguration and loss of ecosystem services that was ultimately driven by human optimization for a single ecosystem service and proximately triggered by an environmental disturbance. The Great Plains, for this context, is defined as extending across all or a portion of ten mid-continental United States (Colorado, Kansas, Montana, New Mexico, Nebraska, North Dakota, Oklahoma, South Dakota, Texas, and Wyoming) and the southern most parts of two Canadian prairie provinces (Saskatchewan and Manitoba), and the very northeastern part of Mexico (Figure 1.1).

As European settlers immigrated to the Great Plains in the early 19th century, they cultivated the land using knowledge from more mesic eastern United States (U.S.) and European farming traditions. A relatively wet period extending from the early 19th to early 20th centuries (Miao et al., 2007), the 1837 invention of the steel plow, and innovations in irrigation facilitated the temporary success of European and eastern U.S.' farming traditions poorly suited to the Great Plains (McDonald, 2010). Yet transforming native grasslands to wheat croplands was an arduous undertaking, requiring heavy, oxen-pulled plows, cutting multiple furrows through the densely rooted grassland soil (i.e., "sodbusting") before it was arable (Schob, 1973).

The conversion of Great Plains grasslands to cropland drove a loss of multiple ecosystem components, including soil organic matter. Soil organic matter is the decomposing plant and microbial fraction of the soil, and is central to soil functioning (Schmidt et al., 2011). Soil organic matter (SOM) is the central supply of energy and nutrients to belowground biota (including plant roots), retains moisture, contributes to complex soil structure, and provides belowground habitat. As a result, declines in SOM correspond to loss of soil fertility and biodiversity that supports a variety of ecosystem services (Wall et al., 2004; Schmidt et al., 2011). Sodbusting and tillage disrupt soil aggregates that protect SOM from microbial attack, and accelerate decomposition of recent and labile carbon (C) inputs by increasing contact between decomposing organisms and substrates (Burke et al., 1995; Dungait et al., 2012). Cropping also leads to reduced SOM through residue removal, shallow rootedness of crop species, and perhaps through declines in plant productivity associated with lower species diversity (Doran, 1980; Burke et al., 1995; DuPont et al., 2014; Steinauer et al., 2015). The exact amount of recently fixed C (i.e.,

productivity) transferred belowground and incorporated into SOM is difficult to experimentally assess, but a metaanalysis of 271 studies puts the estimate at $5\% \pm 1\%$ (with the rest sequestered into living root tissue or lost to microbial and root respiration) (Jones et al., 2009).

This reduction of SOM and rhizosphere, or zone of high soil biological activity influenced by plant roots (Lynch and Whipps, 1990; Hinsinger et al., 2011), had profound implications for the resistance of soil to wind erosion in the post-European settlement Great Plains. The rhizosphere typically extends about 2 mm from root surface, after which there is a sharp decline in activity (i.e., "bulk soil") (Jensen et al., 2005; Raynaud, 2010). Due to the dense root systems of native grasslands, the entire volume of the top meters of soil can be considered rhizosphere (Hinsinger et al., 2011). In the rhizosphere, complex interactions among soil physical and biological components contribute to the production of multiple ecosystem services. Uptake of nutrients, water, and ions; exudation of carbon substrates; and gas exchange create heterogeneous resource gradients throughout the rhizosphere. Diverse microbiota abound in these microhabitats, transforming nutrients and organic matter, serving as prey for higher trophic levels, and contributing to soil aggregate formation (de Deyn and van der Putten, 2005). Bacterial residues, arbuscular mycorrhizal (AM) fungi, fine roots, and larger plant roots contribute to aggregate formation and increased soil pore network complexity (Hinsinger et al., 2009; 2011). Destruction of deep-rooted perennial vegetation reduced these rhizosphere processes, including soil-stabilization, leaving the system vulnerable to wind erosion during periods of low precipitation. In tilled soils with sufficient moisture, a crust of consolidated soil and microorganisms can temporarily protect the soil surface from wind

erosion (Chepil and Woodruff, 1963), but they are readily degraded by tillage (Zobeck, 1991), especially in low-clay soils and under low precipitation and drought conditions (Fryrear, 2011).

In the 1890s, European settlers of the Great Plains experienced their first major drought, bringing to fruition the consequences of sod busting and intensive agriculture. The now little-known 1890s drought lasted nearly the entire decade, and extended across almost the entire North American Great Plains (Warrick, 1980). The drought nearly collapsed the burgeoning agricultural industry and elicited a significant decline of European settlers, with conservative estimates putting population declines at ~45-75\% of the population – a much greater relative population loss than at any other point in European settlement of the Great Plains, including the later Dust Bowl (Warrick, 1980). While the majority of population loss was the result of emigration, starvation was not uncommon. Many recent immigrants to the region arrived with few resources, and the drought depleted what meager reserves they had (Warrick, 1980). Scarcity of locally available assistance and the desire by government and business leaders in the region to maintain an image of Great Plains as destination to make an easy fortune (Baltensperger, 1974; Bowden, 1977) likely exacerbated population loss and obscured crucial social-ecological leaning for future settlers.

Another wave of settlers attracted by promises of wealth concurrent with a wet climatic period during the early 20th century set the stage for another drought-triggered, social-ecological disaster, this time during the 1930s. During the first two decades of the 20th century, population levels rebounded and then surpassed that of pre-1890s Great Plains.

In addition to the sustained above-average precipitation, settlers were drawn by cheap land promoted by Homestead and Kincaid Acts, high grain prices driven by the First World War, rapid farming technological advances, and government manifest destiny campaigns (Warrick, 1980).

In the 1920s, suddenly plummeting grain prices and expensive technological improvements led settlers to acquire and convert more farmland to meet the debtors' demands. This drove rapid conversion of grasslands for agriculture, including that of land once considered too marginal for production (Warrick 1980). Fewer people began farming more land with diminishing returns but greater profits than ever before in the post-European settlement Great Plains. Yet costs were hidden both belowground, with the depleted rhizosphere leaving the soil increasingly vulnerable to drought, and a growing agricultural commodity price bubble.

In the early 1930s, as wheat prices continued to drop, an anomalously cool eastern Pacific and simultaneously anomalously warm northern Atlantic sea surface temperatures caused a persistent high-pressure system over the Great Plains that was likely exacerbated locally by lack of soil moisture feedbacks above the central U.S., triggering the extreme droughts of the 1930s (Schubert et al., 2004; Miao et al., 2007; Cook et al., 2009). The droughts lasted the entire decade, and the top meter of soil weakly held by the depleted rhizosphere and soil crust was desiccated and eroded by the persistent Great Plains winds. Over more than 40 million ha of topsoil and tens of thousands of families were displaced from the Great Plains by the end of the decade (Hakim, 1995).

The social-ecological destruction of the 1930s dust storms remains firmly entrenched in U.S. cultural and political memory. Songs, photographs, and books on the subject are core works of Americana. For the first time in U.S. history, federal emergency relief was dispatched in response to a social-ecological agricultural disaster, and aid to the Great Plains region reached 1 billion 1930s USD by the end of the decade, with destitute farm families receiving the bulk of the aid (Warrick et al., 1975).

The Dust Bowl reveals both the cost of not understanding hidden feedbacks in the pursuit of maximizing a single ecosystem service, and the relatively small frame of reference within which management operates. The vulnerability to drought driven by lost soil resilience was masked by periods of high returns and lack of a mechanism to incorporate knowledge from past failures into the management of the system. Importantly, the effect of intensive agriculture on soil was far from unknown in the course of human history. In the 4th century B.C.E., Plato lamented the loss of "formerly rich land" transformed "like the skeleton of a sick man", attributing the destruction to intensive agriculture (in Hillel, 1991:104). Lessons from the 1890s U.S. did not prevent the Dust Bowl, and the world famous Dust Bowl did not prevent a similar series of events in the Soviet Union fewer than 40 years later. In the Soviet episode, state directed tillage of 40 million hectares of virgin prairie within the brief span of 1954-65, followed by a severe drought, led to the wind erosion of more than 2.8 million ha and plummeted millions of peasant farmers into destitution and starvation (Worster, 2004).

Perhaps more surprising was the effect of drought in the United States only twenty years on from the Dust Bowl. The 1950s drought was slightly smaller in both intensity and

spatial extent, and farmers experienced less absolute loss in crop than in the Dust Bowl. However, when crop losses during the 1950s drought are normalized according to decline per division month of drought (an index combining drought length and intensity for normalizing the comparison of different droughts), the impacts of the 1950s drought on non-irrigated wheat yield losses were indistinguishable from that of the 1930s (Warrick, 1980), 1970s (Warrick, 1980), and late 1980s (Riebsame et al., 1991) droughts. The social impacts of each drought in the Great Plains were successively less due to shifting attitudes and government programs and increased technological advances that buffer the social system from this specific type of ecological variability.

Whether technology such as center pivot irrigation buffer society against drought have hidden tradeoffs that leave the system inadvertently vulnerable to other social or ecological stressors is unknown. "Trading" social resilience for ecological resilience through technological advances is not a new concept, and there is thought that such behaviors actually leave society more vulnerable to extreme climatic variability (e.g., engineering rivers with storage projects to buffer against moderate to high droughts and floods can enhance vulnerability to mega-droughts and mega-floods [Birge et al., 2015a]). Indeed, exploring tradeoffs among food, energy, and water production in these complex social-ecological systems is a current research priority for both the U.S. National Science Foundation and United States Department of Agricultural.

1.2 THE CONSERVATION RESERVE PROGRAM

The Conservation Reserve Program (CRP) was established as part of the 1985 Farm Bill, and its social, scientific, and political lineage can be traced back to Dust Bowl response.

Like most conservation policy, the program is inextricably a product of past efforts (and failures), and its primary objective is to solve ecological problems from a top-down, command-and-control perspective – the reasoning of which has been largely abandoned by ecologists and scholars of environmental policy (Craig, 2010). However, there is some flexibility built into the CRP, specifically through the incorporation of new ecological knowledge in successive Farm Bills and local flexibility, like the Conservation Reserve Enhancement Program (CREP), which is implemented at the state level. As a result, a holistic assessment of the CRP's potential and limitations to influence complex ecosystem service tradeoffs requires an understanding of its historical and social-ecological contexts as well as its measurable ecological impacts.

In March 1935, two dust storms originating from the Great Plains' darkened the midday sky in Washington, D.C. as Congress met to pass the Soil Conservation Act (PL 74-46), the first of its kind in U.S. history. President Roosevelt signed the Act in April of that year to establish the Soil Conservation Service (the precursor to the modern Natural Resources Conservation Service) under the United States Department of Agriculture (USDA). The Soil Conservation Service quickly established "soil conservation districts", a unit still in use today, with over 3,000 unique districts across the United States. The Soil Conservation Service (SCS) implemented conservation districts as their primary unit of management partly based on the notion that local rather than federal agencies would be most efficacious for soil conservation and landowner engagement (Malone, 1986). Less than a decade later, during the Second World War, Congress increased their appropriations to the SCS to support farmers as they met rising agricultural commodity demands.

The 1950s-70s elicited even more federal funding for soil erosion prevention including aid programs to landowners for the protection of marginal lands, research to improve scientific understanding, and sweeping conservation policies spurred by 1960s and 70s environmental movement. The 1950s marked the first major drought in the Great Plains following that of the 1930s, and farmers found measurable relief in the set aside programs offered by the SCS (Warrick, 1980). The Environmental Movement of the 1960s and 1970 saw the creation of the Environmental Protection Agency (P.L. 91-190) and Clean Air Act and Amendments of 1977 (P.L. 95-95; 91 Stat. 685), which joined the 1948 Water Pollution Control Act (Ch. 758; P.L. 845), more commonly referred to as the Clean Water Act. During this period, Congress also authorized the National Resources Inventory in the Rural Development Act of 1972 (P.L 42-419) and The Water Resources Conservation of 1977 (P.L. 95-192), which tasked the Soil Conservation Service with regularly monitoring and reporting to Congress on the status of soil resources on private lands to better inform conservation policy.

However, this improved scientific understanding, political awareness, and social support for conservation did not trigger the formation of the Conservation Reserve Program; an economic crisis did. After two decades of rising farm incomes, low interest rates, rapid cropland expansion, and rising farm debt (to keep pace with technological improvements in the 1960s and 70s), a U.S. agricultural bubble was formed and was eventually burst in the early 1980s by a trade embargo imposed on the Soviet Union causing commodity prices to plummet. Farm indebtedness in the 1980s was fifteen times that incurred by the 1950s drought, and the U.S. lost 3% of its two million farmers during each year of the

1980s crisis (Barnett, 2000). Rural communities were hit especially hard during this period, with three non-farming jobs lost for every one farming job lost from the community (Stockman, 1986). Land values declined by 50%, hitting their lowest point in 1987. When Reagan took office, he endeavored to increase exports and reduce federal farm subsidies with the dual aims of solving the agricultural crisis and relieving the tax burdens he felt middle and large sized farms placed on U.S. taxpayers. His attempts at a laissez-faire approach soon included a failed effort to privatize the Farm Credit System, an array of ad hoc production control measures, price supports, and export financing (Stockman, 1986). Yet, his simplified neoliberal approach, combined with the ongoing crisis, led to tense political protests and he quickly backed away from this strategy.

Farm abandonment, low profits, and high debt among medium sized farms exacerbated the transition towards large corporate U.S. farms during this period (Davidson, 1989). By 1987, corporate farm ownership was up 39% from 1979 (a large share of which were foreign investors), and many bankrupt farmers were hired to work their former farms as laborers and managers (Davidson, 1989). In response, several Great Plains and Corn Belt states enacted statutes limiting or prohibiting corporate farm ownership during the 1970s and 1980s. One of these states was Nebraska, whose citizens voted to pass Initiative 300, which amended the state constitution to prohibit corporate farming and ranching in 1982. This was followed in rapid succession with a similar amendment by South Dakota (Davidson, 1989). These laws were seemingly effective: in states with anti-corporate farming and ranching laws, rural unemployment and poverty rates were measurably lower by the early 2000s (Lyson et al., 2001; Lyson and Welsh, 2005).

Even in the face of these anti-corporate laws, corporate farms steadily grew more powerful in the decades following the 1980s largely through their ability to vertically integrate production, processing, and distribution of commodities. By the 2000s, corporate farms successfully challenged states' anti-corporate farming laws. An example was the precedent-setting South Dakota Farm Bureau, Inc. v. Hazeltine (340 F.3d 58; 8th Cir. 2003) which found a voter-approved anti-corporate farming amendment to South Dakota's constitution (Amendment E) to be in violation of the Commerce Clause of the U.S. Constitution; [NALC, n.d.). The defeat of South Dakota's Amendment E opened Nebraska's Initiative 300 to litigation, and the Eighth Circuit Court ruled it unconstitutional in 2006 (CFRA, 2008; Schutz, 2009). I will not provide an analysis of the potential consequence of these rulings on enrollment in the Conservation Reserve Program –and corresponding changes in ecosystem service production –but it is worth noting this trend because farm size and the scale at which it implements management is likely influenced by the trend towards increasingly larger farms and ranches in the Midwest and Great Plains.

The reality of the 1980s crises combined with increasing political opposition to his administration (and the republican party) led Reagan shift his strategy. In the words of Cy Carpenter, president of the National Farmers Union at the time, "Either we rely on the anarchy of the marketplace [...or we...] adopt a rational, coherent policy of supply management with program benefits targeted to the family-scale sector of agriculture" (Eason, 1984). In other words, for the small and medium-scale U.S. farms to remain in existence, federal assistance is requisite (Broder, 1987).

During preparations of the 1985 Farm Bill, the American Farmland Trust, Audobon Society, and Sierra Club lobbied forcefully to ensure a conservation provision, buoyed by mounting urban and suburban support for both environmental issues and farmers (e.g., FarmAid concerts; Visser, 1986). A 1983 report to the Congress by the Comptroller General on the inadequacy of existing soil conservation programs, legal feebleness of existing soil conservation policy (e.g., The Farmland Protection Policy Act of 1981), and a report from the USDA outlining the potential benefits of sodbusting legislation and a reserve program, incentivized the Reagan administration to include a strong conservation measure in the 1985 Farm Bill (Malone, 1986).

In summer 1985, the Ninety-ninth Congress approved a 12 million ha set aside program with "sodbusting" and "swampbusting" provisions that disqualified landowners who farmed highly erodible land and wetlands from receiving federal assistance (Heimlich and Classen, 1998, Whachenheim, 2014). Highly erodible land was defined by the bill as Soil Conservation Service land classes IVe, VI, VII or VIII land (Malone, 1986). Although there was some initial controversy between the House and Senate over the details of the Farm Bill's conservation provisions –the farthest reaching by any measure in U.S. history –they were largely forgotten in chaos over terse debates concerning more controversial provisions like farm subsidies and corporate farm takeovers. This political window of opportunity allowed the Conservation Reserve Program and its sodbuster and swampbuster provisions to be included in the final Farm Bill, with surprisingly little political fanfare relative to the program's scale in history (Malone, 1986).

There are complex social, economic, political, and ecological tradeoffs associated with any Farm Bill, and Reagan's 1985 Bill is no exception. The set aside program his administration initially proposed, for instance, was intended to quickly amplify commodity prices to bolster farm profits. This prototype had no acreage limits or minimum environmental vulnerability enrollment requirements and, argued critics, would most benefit the largest, and richest farms that had large holdings of fertile land, especially if they could quickly enroll during temporary lulls in commodity prices (Malone, 1986). This advantage to corporate farms, which could then increasingly aggregate struggling small farms, would hurt the small U.S. family farmer –a politically toxic move for the administration. It could also put tenant farmers (most of whom were formerly small family farmers) out of work and pass the cost of rising commodities onto consumers during those economic lulls.

Additionally, major seed and fertilizer companies viewed the proposal as a threat to their survival (Malone, 1986). It was also a marked departure from the fiscal conservatism and laissez-faire approach the administration used as foundation for their domestic policy, costing them political capital within their own party. Although family farmers made up less than 3% of the population in the 1980s, they enjoyed record public support during the crises and any move by the administration to revoke aid would have similarly cost political capital (USWNR, 1986; Walljasper, 1986). When the 1985 Farm Bill, entitled The Food Security Act (P.L. 99-198) was finally passed, its set aside program, the Conservation Reserve Program (CRP) was designed principally to conserve vulnerable natural resources and to provide small and medium sized farms with financial assistance, with very weak commodity supply control as a distant secondary objective.

1.2.1 The Conservation Reserve Program: current context

The Conservation Reserve Program, now in its 30th year, is administered by the Farm Service Agency (FSA) through the United States Department of Agriculture (USDA) and supported by the NRCS, state forestry agencies, local soil and water conservation districts, and state fish and wildlife agencies. In 2015, the CRP provided rental payments for the continuous and new enrollments of 9.5 million ha, which amounts to ~8% of the nation's potential cropland being maintained under grassland, savannah, or forest cover (Sullivan et al., 2004). In addition to the \$2 billion year⁻¹ in direct rental payments to farmers, the CRP may provide \$1.1 billion year in added, indirect financial benefit to local economies by stimulating job growth and supporting retired farmers (USDA News Release, 2016).

In 2017, The Conservation Reserve Program (CRP) remains the largest soil conservation initiative in U.S. history in terms of acres enrolled, and provides a range of ecosystem services. However, the reliable production of these services is uncertain in the face of enrollment variability, conflicting management objectives, and the effects of global change. An assessment of ecosystem production from land enrolled in the Conservation Reserve Program provides a way to assess these uncertainties so that policy, management, and science can better support the benefits obtained by this large-scale program.

Within the first decade of its inception, the CRP is estimated to have reduced erosion by between 626 and 2420 million tons, with ongoing annual erosion reduction estimated at

roughly 19 tons acre⁻¹ year⁻¹ (Feather et al., 1999). Its wildlife recreation benefits are estimated at \$428 million year⁻¹ (Feather et al., 1999; Sullivan et al., 2004). Other ecosystem services include sedimentation and runoff reduction, water purification and retention, habitat restoration for upland game birds, waterfowl, songbirds; and pollinator ecosystem services.

Wetlands (including sloughs and wet meadows) are a common cover class in the Great Plains, and their elimination during conversion to row crop agriculture represents a major loss of ecosystem services that is unlikely recoverable. Wetlands are among the most valuable land cover types in terms of their ecosystem service production per unit area (Zedler and Kercher, 2005), and while the CRP and swampbuster provision led to the reflooding of thousands of former wetlands in the late 1980s, it is unlikely that all wetland ecosystem services can be restored following years of cropland cover. A study in the Minnesotan prairie pothole region assessed the restoration of such re-flooded wetlands on CRP land over twenty years. Within the first few years of restoration, many native wetlands plants reappeared, although this response was more gradual in wetland patches isolated from other wetlands in highly fragmented matrices of row crop agricultural cover, i.e., wetlands isolated from potential seed banks. After a decade, however, nearly all sites were dominated by a few nonnative and invasive species. By year 19, most of the wetlands' species richness had stabilized (i.e., flat rate of species additions and losses). Rare species found in native wetlands were poorly or not represented in the restored site. Perhaps more importantly, the carbon and nutrient dynamics and hydrology, which are core to wetland ecosystem service production, did not recover in the re-flooded CRP wetlands to that of their native analogs (Zedler and Kercher, 2005).

In upland, terrestrial grasslands, similar species community and biogeochemical dynamics cast uncertainty over the ability of CRP lands to function like native grasslands. However, even if CRP lands cannot function like their native analogs, they can still generate valuable ecosystem services. As a result, understanding how to manage these lands for is essential. Nested programs, or state-level efforts through the Conservation Reserve Enhancement Program (CREP) were added with successive iterations of the Farm Bill, and specifically targeted many different ecosystem services. One such program is the CP-25, which is an enrollment option in the CRP designed to provide "Rare and Declining Habitat" for birds and pollinators through nesting, escape cover, and food resource vegetation. CP-25 is offered during general CRP sign-up and in return for landowner participation the Farm Service Agency (FSA) provides additional annual rental payments, cost share payments for establishing the restoration, and mid-contract management cost share (USDA CP25, n.d). CRP cover is typically prioritized for low cost, long-term erosion prevention. As a result, most standard CRP seeds mixes are composed of a few native perennial grass species and few forbs. In contrast, CP-25 programs that prioritize pollinator and upland game bird habitat use seed mixes with more grass species (annual and perennial) and a greater relative abundance of forb species.

Whether the CRP can effectively mitigate another social-ecological crises such as the Dust Bowl or the 1980s farming crisis remains unknown. The CRP provides an abundance of ecosystem services, yet it rarely receives empirical social-ecological assessments. Like the other conservation programs it replaced and joined, the CRP has

multiple –sometimes conflicting –objectives that are have varying levels of success due to a diversity of complex social-ecological variables. Provisions like swampbuster and sodbuster, for instance, have been only partially effective due to lack of a common definition or measurement framework and local variability, haphazard enforceability, and because fluctuating commodity prices continue to overwhelm conservation payments in determining land use conservation rates (Heimlich and Classen, 1998; Schnepf, 2008). Indeed, the decision to enroll, re-enroll, or remove land from the CRP relies on a complex combination of economic and social drivers. Due to the large spatial scale of CRP land, enrollment changes can have major consequences for ecosystem service provisioning from CRP lands. Understanding the variables that influence enrollment changes can therefore provide insight into shifting ecosystem service production from Conservation Reserve Program lands.

Although there are about two dozen similar voluntary conservation programs in the United States that receive federal funding, roughly 40% of these funds are devoted to easement programs through the CRP. In 2016, enrollment was 9.5 million ha, down roughly 5.3 million ha from 2007 (USDA/FSA/EPAS, 2016). The sheer size of this program means that even percentage change in enrollment can have profound impacts on land use/land cover change, and associated ecosystem services. In some instances, the processes of interest may misalign with CRP contract length. For example, at some sites local conditions mean that soil carbon sequestration requires centuries to achieve the same results measured in decades at other sites (e.g., Baer et al., 2010). The spatial extent of a CRP field may not be able to accommodate multiple concurrent ecosystem services, depending on the suite of ecosystem services of interest (Birge et al., 2016b).

As a result, an assessment of the economic drivers underlying CRP enrollment provides insight into potential shifts in grassland versus agricultural ecosystem service tradeoffs.

The feedbacks that influence enrollment are largely economic, and these economic effects are rapid. Models investigating the effect of rising corn prices on CRP enrollment in Iowa show that an increase of \$2 to \$3 bushel⁻¹ of corn would result in the removal of half of the state's CRP acreage (Secchi and Babcock, 2007). Under a scenario where corn prices increased to \$4 bushel⁻¹, a doubling of annual CRP payments would be necessary to retain all CRP lands (Secchi and Babcock, 2007). Another model including all of the Corn Belt states (Indiana, Illinois, Iowa, Missouri, Nebraska, Ohio, and Kansas) showed 13-22% decreases in enrolled acres for every dollar increase bushel⁻¹ between 1986 and 2010 (Gill-Austern, 2011). According to the model, the minimum period after which changes in commodity prices affect enrollment is three years (Gill-Austern, 2011). This is likely attributable to the enrollment tradeoffs farmers must assess, including current and potential future commodity prices, ethanol policy, policy details, emergency having provisions, vulnerability to erosion, value of adjacent land, penalties for early-opt-out (i.e., breaking a CRP contract), and rental payments (Cooper and Osborn, 1998; Hellerstein and Malcolm, 2011). CRP rental payments are adjusted based on a variety of factors, with land valuation primary among them. Yet property taxes are also adjusted based on land value, adding further complexity. While these variables influence CRP enrollment, commodity prices remain the primary determinant of CRP enrollment, even after accounting for rental payment adjustments (Wachenheim et al., 2014).

1.3 RESILIENCE AND MANAGEMENT OUTCOMES

The Conservation Reserve Program in the North Central Great Plains is comprised of wetland, grassland, savanna, and forested ecosystems, where complex within and crossscale interactions give rise to ecosystem services that support societal survival and well being within and beyond the Great Plains. Historically, grasslands covered approximately 50% of terrestrial earth surface, a number that now more closely resemble 26% (Sterling and Ducharne, 2008; World Bank, 2017), due almost entirely to agricultural intensification (Sterling and Ducharne, 2008). Remaining grasslands are heavily utilized for rangeland production, supporting 1800 million livestock units (Kemp and Michalk, 2007). Remaining grassland ecosystems are vulnerable to conversion for crop production, and in cases like the Dust Bowl or salinization events for instance, vulnerable to nonlinear loss of functioning following such conversion so that even if restoration is attempted they can never fully return to their grassland state (Birge et al., 2016a). Conservation Reserve Program grasslands are managed partly in an effort to protect society from the undesirable effects of crossing such thresholds, but doing so requires reducing uncertainty surrounding complex ecological scales of interaction in natural resources management plans.

Ecosystems are complex adaptive systems, which are systems with nontrivial emergent (not deducible from the sum of its parts) and self-organizing behaviors (Mitchell, 2009). Complex adaptive systems are made up of components connected through a network of interactions with no central controller. Adaptation to external information inputs (e.g., extreme weather events or nutrient inputs) arises from simple rules of operation giving rise to complex behaviors and sophisticated information processing, without an internal

or external controller (Holland, 1992; Levin, 1998). Patterns of feedbacks and information processing in complex systems can, however, give rise to important processes at some specific scale that defines an operational space for a complex adaptive system. This functioning cannot be reduced to the sum of its parts, because it emerges from the interactions among components at smaller, nested scales.

In systems with low functional redundancy and/or inability to withstand certain disturbances, even a small alteration to a single process can trigger enough shifts from negative (stabilizing) to positive (runaway) feedbacks throughout the system to cause a systemic reconfiguration. The alternative stable state of the complex system is often persistent and unable to deliver the type and quantity of pre-shift ecosystem services. Systems highly vulnerable to reconfiguration are described as having low resilience, because their alternative states are typically persistent and resistant (at least to reversibility). As such, resilience is an emergent system property that describes the amount of disturbance a system can withstand before the loss of key processes trigger the reconfiguration of its components, not a normative description of a pristine ecosystem or a management objective.

While the Conservation Reserve Program typically makes use of ten or fifteen year contracts with a single management ("mid-contact management") event midway through the lease, limits enrollment acreage per landowner, and has minimum vulnerability criteria; ecological processes occur across greater variability, ranging from microbial to millennial (Figure 1.3a). It is impossible to incorporate all of these scales into a single study, but by measuring multiple aboveground and belowground ecological processes in

response to common mid-contract management treatments on a Conservation Reserve Program grassland (Figure 1.3b) and linking these processes to ecosystem services and social perceptions, I attempt a more thorough assessment of the complex social-ecological tradeoffs associated with Conservation Reserve Program grasslands, and the implications for the Program's long-term ecosystem service production.

1.4 FIGURES



Figure 1.1 The United States Great Plains ecoregion (yellow) and a subsection of United States Midwest (orange) where prairie was the historic land cover. Across these regions, from east to west, the prairie cover is tallgrass, mixed grass, and short grass. The boundaries between cover types are porous and dynamic based on large scale (climatic) and local scale (e.g., soil type, topography, hydrology, land use) variables.

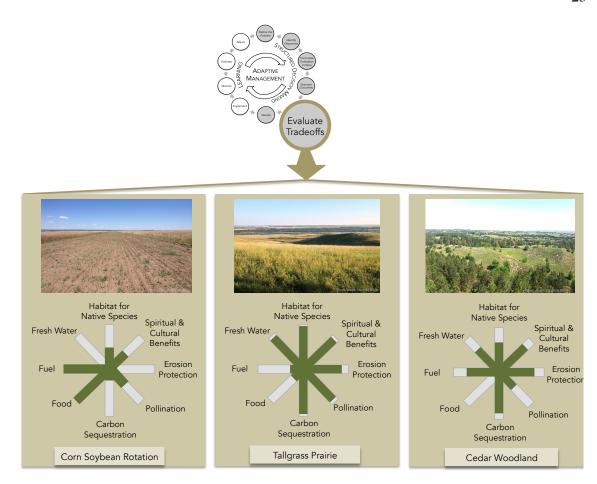


Figure 1.2 An example of different potential suites of ecosystem services and the tradeoffs associated with different cover types in a Great Plains landscapes (from Birge et al., 2016b).

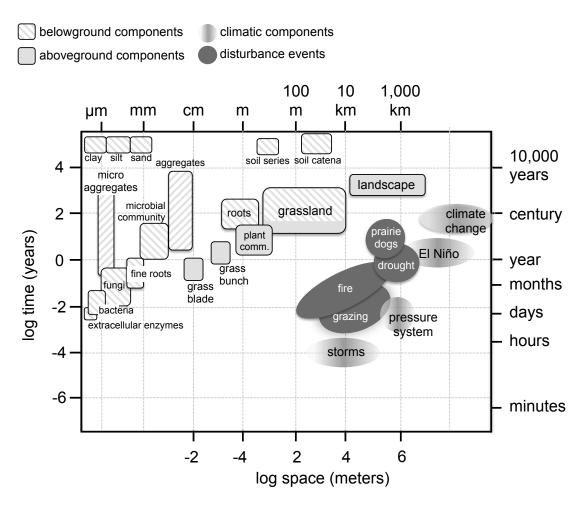


Figure 1.3a. A Stommell diagram of structures and processes in a North Central Great Plains grassland system, including belowground, aboveground, climatic, and disturbance regime components.

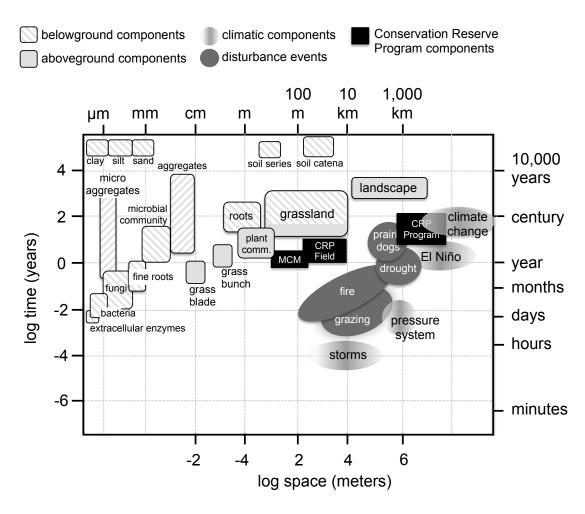


Figure 1.3b. A Stommell diagram showing components of the Conservation Reserve Program on a North Central Great Plains grassland.

2 ECOSYSTEM SERVICES FROM THE CONSERVATION RESERVE PROGRAM:

LANDOWNER PERCEPTIONS AND PRACTICES IN NEBRASKA

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ABSTRACT: Conservation Reserve Program (CRP) lands in Nebraska comprise a vast gradient of environmental variables, past land uses, and management objectives, yet little is known regarding individual landowner practices and perceptions of their management.

To address this uncertainty, I designed survey questions to assess which management

practices were most commonly used in the Nebraska CRP, landowner-desired ecosystem

service outcomes, and how those actions and preferences compare to scientific outcomes.

Ecosystems services can be defined as "benefits people obtain from ecosystems" and

emerge from complex ecological interactions that can be clarified through adaptive

management to avoid surprising, non-linear system response to management. By

assessing landowner responses, I can frame the results of my field study to uncover how

the more common management practices across the state might lead to a non-linear loss

of the ecosystem services that landowners identify as most important. I sent an IRB

approved questionnaire containing questions investigating CRP management practices,

perceptions of ecosystem services, perceptions of ecosystem disservices, landowner

perceptions of management effectiveness, and reasons for choosing among management

practices to over 10,000 CRP enrollees in the state of Nebraska. The survey response rate

was roughly 23%. The majority of respondents (n=730) reported interseeding on their

CRP lands (which was unsurprising given that interseeding is often used in conjunction

with other practices), followed by herbicide application (n=634), burning (n=597), disking (n=384). Respondents ranked burning as the most effective management practice, followed by herbicide application, interseeding, and then disking. While considered most effective, only 26% of respondents reported that they used burning as a management practice. Respondents overwhelming attributed their decision to use a specific practice to agency recommendation, rather than to ease, cost, or past practice. Respondents reported "erosion reduction" as the CRP ecosystem service with highest importance, followed closely by "habitat for pheasants and quail". The respondents generally disagreed that the CRP provided ecosystem disservices, with the exception of the disservice of "invites noxious weeds". These survey results reduce uncertainty surrounding landowner perceptions and behavior, specifically that while landowners perceive burning as effective, they are not using it as management practice in proportion to its perceived effectiveness. By capitalizing on agency influence and the perceived effectiveness of burning, there is an opportunity for a statewide, agency-administered adaptive management plan to test how burning versus herbicide application on CRP lands influence soil and upland game bird ecosystem services.

2.1 INTRODUCTION

Conservation Reserve Program (CRP) lands in Nebraska comprise a vast gradient of environmental variables, past land uses, and management objectives, yet little is known regarding individual landowner practices and perceptions of their management. As of May 2017, Nebraska had 324,311 ha enrolled in the CRP across 21,521 contracts (104,674 ha of which are under continuous enrollment) (FSA, 2017). In Nebraska, 21,481 of those ha are planted to pollinator habitat (CP42), and 8,693 ha are considered high erodible lands, although the amount of acreage on which these designations co-occur is not available. Individual landowner decisions across Nebraska CRP lands represent uncertainty in the social-ecological system that can be reduced using standard survey methods, which was the objective of this study.

Working with the survey designers, I developed questions to investigate Nebraska CRP enrollee perceptions of ecosystem services and disservices (classified using the ecosystem-focused rather than Millennium Assessment classification; discussed below) associated with the CRP and outcomes from mid-contract management practices I assessed in a field study (results discussed in Chapters 3, 4, and 5). This provided me with a way to explore which practices were most commonly used in the Nebraska CRP, which CRP ecosystem services where most valued by landowners, which CRP ecosystem disservices were most undesired by landowners, and how management practices and preferences align vis-à-vis the scientific outcomes I obtained from my own field campaign.

2.1.1. Ecosystem services: history, definition, and classification

The ecosystem services concept was formalized during the 1960s and 70s to leverage environmental concerns during policy decision-making (Ehrlich and Ehrlich, 1981). In the early 21st century, the United Nations' Millennium Assessment provided the now commonly used definition of ecosystem services as "benefits people obtain from ecosystems" (MEA, 2003; 2005), and classified them into four categories: supporting, provisioning, regulating, and cultural services (Figure 2.1). Supporting ecosystem services are foundational to provisioning, regulating, and cultural services, and together all ecosystem services by definition contribute to human wellbeing.

The Millennium Assessment classification scheme informs research, ecosystem services valuation, and policy applications, although its shortcomings have inspired alternative approaches (Carpenter et al., 2009). Specifically, other methods have been proposed to improve consistency in ecosystem service valuation (e.g., Fisher and Turner, 2008), establish common indicators for comparison across ecosystems and institutions (Fisher et al., 2009), and explicitly separate end products from their underpinning ecological processes (Boyd and Banzhaf, 2007; Wallace, 2008). These alternative approaches, experts argue, better reflect the complex realities of social-ecological systems (Haines-Young and Potschin, 2010) (Figure 2.2). The Millennium Assessment's tendency to confound ecosystem service end products with their means of production is exemplified by the "supporting services" classification (Boyd and Banzhaf, 2007; Wallace, 2007). Inability to distinguish between a shared underlying process and multiple end products could result in unintentionally imbalanced valuation of services. In management schemes

where tradeoffs must be carefully weighed to achieve multiple objectives using finite resources, this can be problematic (Wallace, 2007).

The "ecosystem-focused" approach to ecosystem service assessment addresses some of the issues arising from the Millennium Assessment's classification scheme by distinguishing the "final products" that are consumed or used and their underpinning ecological structures and processes (Haines-Young and Potschin, 2010). This distinguishes ecological components central to the simultaneous production of multiple ecosystem services (multifunctionality). This approach is also well suited to the uncertainty I attempted to address with the survey, by listing ecosystem services that are end products, rather than underlying processes, or midpoints between the two.

2.1.2 Adaptive management

Adaptive management provides a way to clarify otherwise concealed relationships among management actions, ecological processes, and the production of ecosystem services. Holling (1978; further developed by Walters, 1986) introduced adaptive management as part of a growing recognition that complex systems of people and nature do not predictably return to an equilibrium state following disturbance but instead adapt through novel or altered feedbacks (i.e., persist in their initial state), or fail to adapt (i.e., reconfigure into alternative state) (Allen and Gunderson, 2011). Adaptive management was designed to identify essential structures and functions and their response to external stressors to avoid critical thresholds. Management that optimizes the production of a single or few ecosystem services may eventually erode the very structures and functions that maintain the state needed to produce the services of interest, eventually leading to an

abrupt and persistent loss of those ecosystem services (Scheffer et al., 2001). When applied in the appropriate contexts (i.e., high controllability and high uncertainty; Peterson et al. [2003]), adaptive management provides a way to avoid non-linear loss of ecosystem services while proceeding with management. By assessing landowner responses, my objective was to frame the results of my field study to uncover how the more common management practices across the state that might lead to a non-linear loss of the ecosystem services that landowners identified as most important.

2.1 METHODS

I included questions regarding CRP management practices, perceptions of ecosystem services, perceptions of ecosystem disservices, landowner perceptions of management effectiveness, and reasons for choosing among management practices in a larger survey sent to every CRP enrollee in the state of Nebraska. Surveys were sent to over 10,000 participants by way of an IRB approved invitation letter that included a paper survey with a weblink for an option to fill out the survey online. The paper survey and web survey were both designed using SNAP survey software. Returned and completed paper surveys were scanned and digitized.

I assessed landowner perception of ecosystem services using a Likert scale (i.e., Not at all important, Not important, Indifferent, Important, Very important) using the prompt "How important are each of these benefits of CRP to you?" for the following ecosystem services: (1) provides habitat for pheasants and quail, (2) restores diverse native prairies, (3) reduces erosion, (4) decreases water runoff, (5) provides better quality soil for the future, (6) reduces the impact of drought, (7) improves water quality, (8) provides

hunting opportunities, (9) provides wildlife-viewing opportunities, (10) provides places for recreation, (11) increases pollinators. To assess how landowners perceived negative effects, or ecosystem disservices, associated with the CRP, I again used a Likert scale (i.e., Strongly disagree, Disagree, Neither agree nor disagree, Agree, and Strongly Agree) using the prompt: "Although the CRP provides benefits, it may cause negative effects as well. How much do you agree with each of the following statements regarding potential negative effects of CRP to your land?" for the following ecosystem disservices (1) invites noxious weeds, (2) harbors predators of livestock, (3) neighbors have a bad perception of CRP, (4) increased pressure to open access to hunting, (5) source of weed seed for adjacent lands, (6) harder to farm in the future, (7) loss of aesthetics, (8) harbors pests, (9) reduces moisture for crops. I also asked what type of management pratice land owners conducted: (1) burning, (2) disking, (3) herbicide treatment, (4) interseeding, and/or (5) none; and to select primary reason they chose to implement those management practices: (1) cheapest option, (2) easiest option, (3) what they've always done, or (4) recommended by the management agency. Using a Likert scale, I also asked landowners to rank the effectiveness of aforementioned management practices (i.e., Not at all effective, Not effective, Neutral, Effective, Very effective).

2.2 RESULTS

I received 2,285 completed responses largely through the mail from 659 zip codes across Nebraska. At roughly 10,000 surveys sent to nearly all of Nebraska's 1182 zip codes, this represents a response rate of 22.85% and represents 55.75% of Nebraska's zip codes. The majority of respondents (730) reported interseeding on their CRP lands which is unsurprisingly as interseeding is often conducted in conjunction with other management

practices, followed by herbicide application (634), burning (597), disking (384), or no management (171) (Figure 2.5). When asked to rank the effectives of all practices (not just those they apply on their CRP enrolled land), respondents ranked burning as the most effective, followed by herbicide application, interseeding, and then disking (Figure 2.6). Generally, the respondents considered burning, herbicide (Figure 2.7), and interseeding on the whole to be effective, but considered disking on the whole to be less effective. Interestingly, while burning was considered to be the most effective treatment for achieving management objectives, only 26% of respondents reported using this treatment. Herbicide had a surprising effect on plant and soil dynamics in the field portion of my study (see Chapters 3 and 4), which is why I examined herbicide users more closely (Figures 2.7 and 2.8).

When asked why they chose to implement their chosen management action, respondents overwhelming attributed their decision making to agency recommendation, rather than ease, cost, or past precedence (Figure 2.8). The decision to apply herbicide followed a similar trend to the other treatments, but with a relative higher proportion in users whose primary reason to apply management was past precedence, and a relatively lower proportion of herbicide users who choose a management practice based on cost or ease (Figure 2.8). In other words, herbicide use is more attributable to agency recommendation and past precedence rather than ease or cost of use, relative to the other practices. Overall however, agency recommendation is still the most influential reason for using any management practice.

With the exception of "provide places for recreation", the respondents generally ranked all the CRP ecosystem services listed on the survey as more important than not important (Figure 2.9). Respondents reported "erosion reduction" as the CRP ecosystem service with highest importance, followed closely by "habitat for pheasants and quail", with "better quality soil for the future" and "decreased water runoff" roughly tied for the third. While "restoring diverse native prairies", "increase pollinators", and "provide wildlife-viewing opportunities" were generally ranked as more important than not important, they did not receive as high importance ranking as the other ecosystem services (again, with the exception of recreation, which was ranked lowest and had more respondents ranking it, on the whole, as not important than important).

The respondents were generally neutral or disagreed that the CRP provided the ecosystem disservices listed on the survey (Figure 2.10), with the exception of the disservice of "invites noxious weeds", which respondents agreed was an ecosystem disservice associated with the CRP. Following "invites noxious weeds", respondents also disagreed the least (i.e., agreed that the CRP provided the ecosystem disservice) with "increased pressure to open access to hunting", "source of weed seed for adjacent lands", "harder to farm in the future", and then "harbors pests". Respondents disagreed most strongly that the CRP "harbors predators of livestock", drives a "loss of aesthetics", and "reduces moisture for crops" (i.e., they disagreed that the CRP provided those ecosystem disservices).

2.3 DISCUSSION

The respondents in this survey surprisingly revealed that, as a group, they think burning is the most effective mid-contract management practice for meeting their objectives, even though only about a quarter implement the practice. Instead, they are more commonly applying herbicide and interseeding (although interseeding is likely used in conjunction with the other mid-contract management practices). Just as surprisingly, respondents attribute their choice of management practice to agency recommendations rather than ease or cost, revealing the leverage of agencies to direct management in the state. This provides a rare opportunity for agencies to have a profound influence on Nebraska's CRP ecosystem services provisioning, by capitalizing on the high controllability necessary for adaptive management to proceed. It is rare for an opportunity to use adaptive management for ecosystem services on such a large spatial scale, and amenability to burning combined with the influence of agency personnel –and current low agricultural commodity prices driving high demand for CRP enrollment –provides such an opportunity in the Nebraska CRP.

Herbicide application is a commonly used practice in Nebraska, perceived as effective, and is more likely to be used than the other practices due to agency recommendation. This, more specifically, provides an opportunity for state agencies to design county or state level adaptive management plans to assess how burning versus herbicide influence different suites of ecosystems services among CRP fields in Nebraska. A shifting mosaic of herbicide and burning might, for example, produce a wider array of ecosystem services than would be available at a single burned or herbicide patch in space and time (Figure 2.4). Alternatively, such an investigation might reveal that one practice is superior over

the other in some, most, or all contexts and scales for eliciting certain ecosystem services. An opportunity for such a plan is especially strategic given that survey respondents mirrored the CRP in identifying soil health and upland gamebird habitat production as leading management priorities. They also identified unwanted species, and the spread of unwanted species to adjoining land, as leading undesirable ecosystem disservices associated with CRP enrollment. Burning may be the most effective method for dealing with many undesirable grassland plant species—notably eastern redcedar, which rapidly spreading in the state—even though herbicide is commonly against unwanted plant species. By creating a burning and/or herbicide schedule to elicit different size and timings of burns or herbicide treatments among CRP fields in the state, agencies could directly test management objectives related to soil health, upland gamebird habitat, and nonnative species in a structured decision making approach that improves field, county, and state level CRP management.

2.4 CONCLUSION

These survey results reduce uncertainty surrounding landowner perceptions and behavior, specifically that while landowners perceive burning as effective they are not using it as a management practice in proportion to its perceived effectiveness relative to other practices. This appears attributable to the influence of agency personnel, which is ranked higher than cost or ease when it comes to landowners choosing among management practices. By capitalizing on the influence of agency personnel and perceived effectiveness of burning among landowners, there is an opportunity for a statewide CRP adaptive management plan to test how burning versus herbicide elicit different suites of ecosystem services through space and time on Nebraska CRP lands.

2.5 FIGURES

Provisioning

- Food
- Fresh water
- Fuel
- Fiber
- Biochemical products
- Genetic product
- Pharmaceuticals

Regulating

- Climate
- Water cycling
- Water purification
- Disease mitigation
- Air purification
- Nutrient retention
- Carbon sequestration

Cultural

- Spiritual
- Religious
- Recreational
- Aesthetic
- Cultural
- Scientific

Supporting

- Soil formation
- Nutrient cycling
- Primary production

Figure 2.1 The Millennium Assessment's Framework for Classifying Ecosystem Services (modified from the Millennium Assessment [2005]). The three consumable or usable classes of ecosystem services (provisioning, regulating, and cultural) rely on supporting ecosystem services, which are not directly consumed or used.

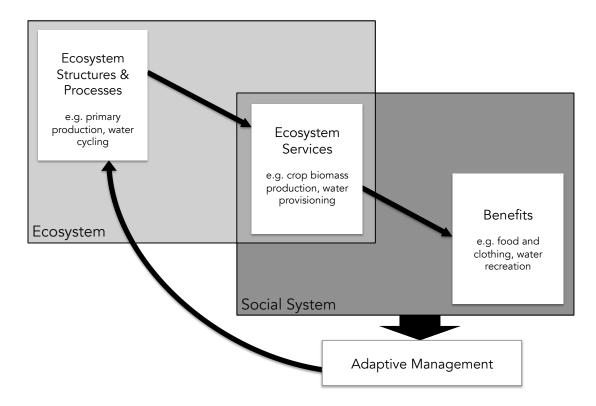


Figure 2.2 An ecosystem services classification scheme that distinguishes between means (ecosystem structures and processes) and end products (ecosystem services and benefits), and illustrates how adaptive management may be used to manage the ecosystem to affect the flow of services to the social system (modified in part from Haines-Young and Potschin [2010]).

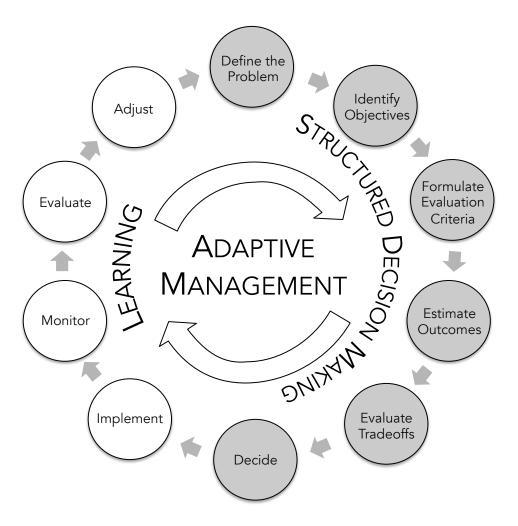


Figure 2.3 The adaptive management cycle (from Allen et al. [2011]).

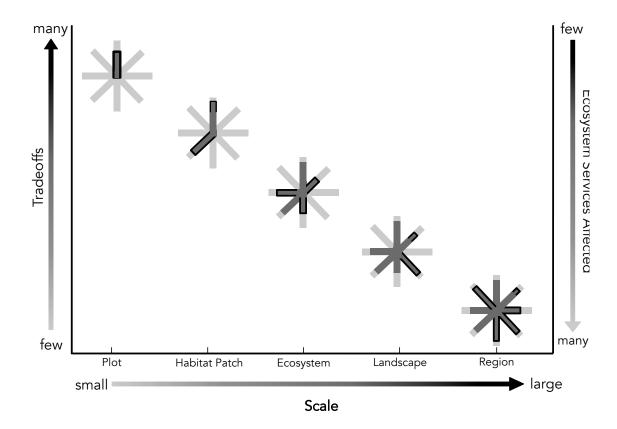


Figure 2.4 Model illustrating inherent tradeoffs in ecosystem services from management actions as influenced by scale. Black outlines highlight changes in tradeoffs with increasing scale.

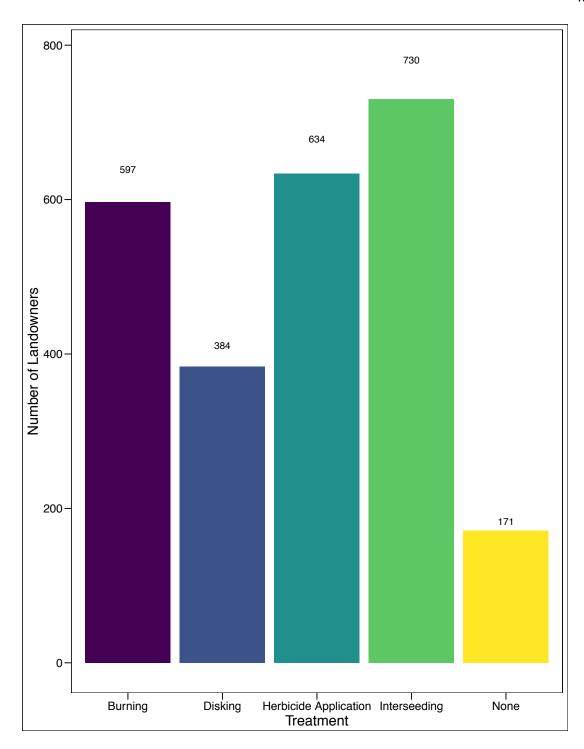


Figure 2.5 The number of respondents who reported implementing the different mid contract management treatments on their CRP enrolled acreage.

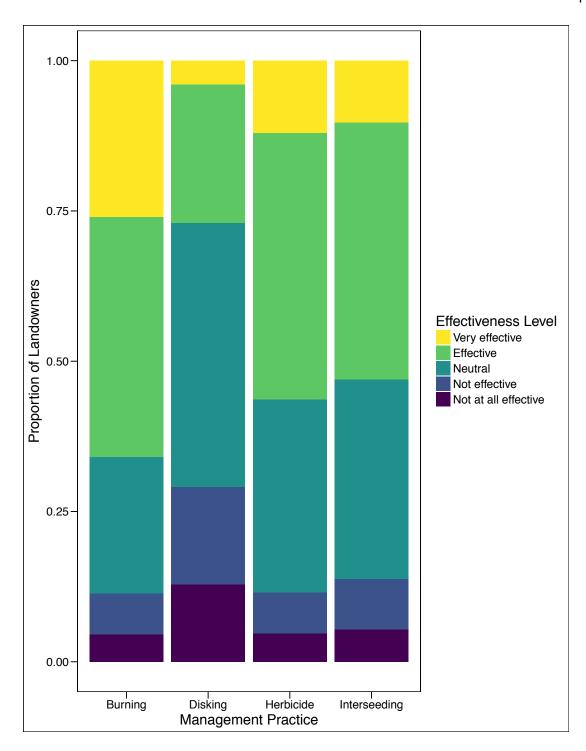


Figure 2.6 The proportion of effectiveness rankings respondents assigned to the four management practices.

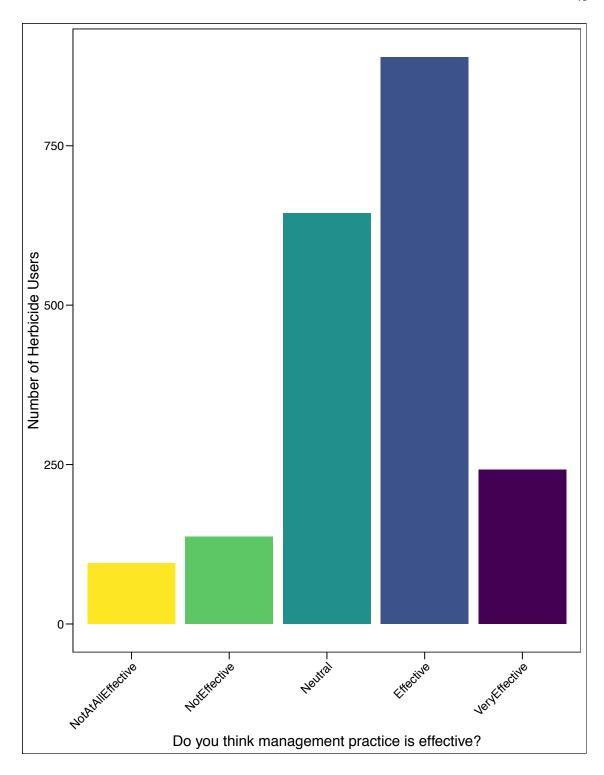


Figure 2.7 The number of respondents according to how they ranked the effectiveness of herbicide applications.

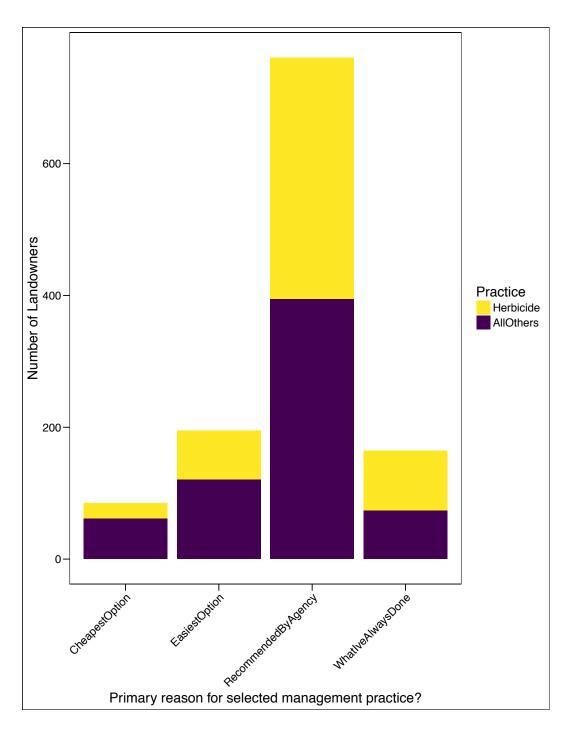


Figure 2.8. The number of respondents according to the primary reason they applied a specific management practice, with herbicide application highlighted.

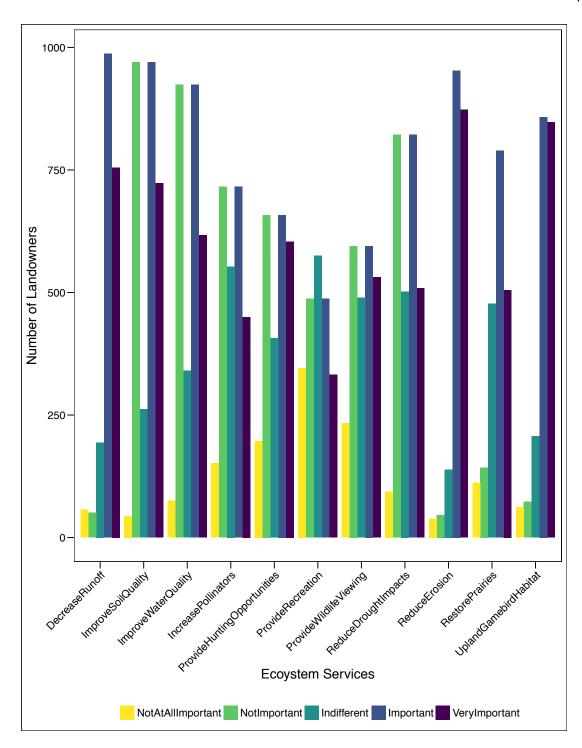


Figure 2.9 The importance respondents assigned to ecosystem services associated with the CRP.

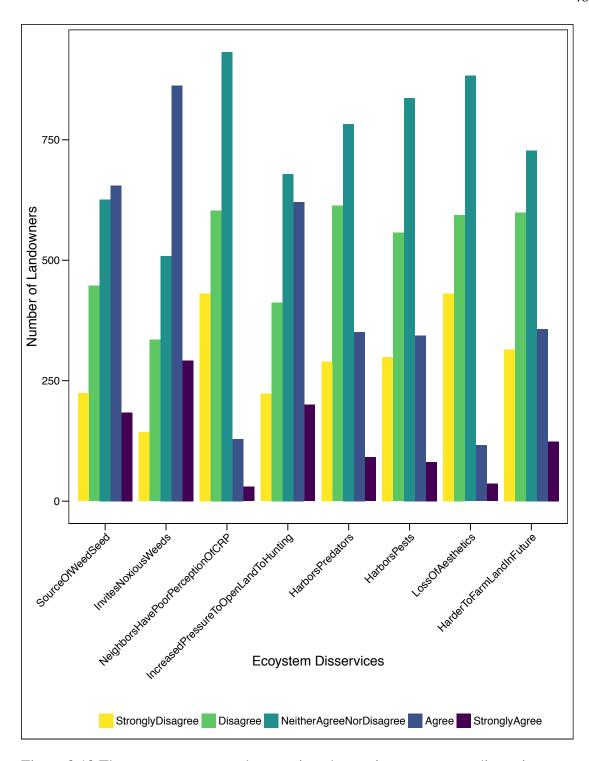


Figure 2.10 The agreement respondents assigned to various ecosystem disservices associated with the CRP.

3 PLANT COMMUNITY RESPONSE TO COMMON MANAGEMENT PRACTICES ON A NORTH CENTRAL GREAT PLAINS CONSERVATION

RESERVE PROGRAM GRASSLAND

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University of Nebraska, 2017

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ABSTRACT: Since European settlement in the U.S. Great Plains and Midwest, it is estimated that native tallgrass prairie cover has declined by as much as 99.9%, with losses largely attributed to conversion to cropland and alteration to the historical disturbance regime. The Conservation Reserve Program (CRP) enrolls over 9.7 million ha of the nation's agricultural lands most vulnerable to erosion, converting them back to perennial vegetation cover in order to protect the nation's soil resources against erosion. However, CRP grasslands removed from the historical disturbance regime are susceptible to dominance of late successional plant species. To remedy this, a mid-contract management (MCM) is required in nearly all CRP contracts. Importantly, however, midcontract management mimics disturbance events, while attempting to elicit ecological outcomes that emerge from disturbance regimes. An explicit desired management outcome of such practices is higher biological diversity. Whether more diverse plant communities are more stable or resistant to invasion is a long running debate in ecology. There is growing evidence, however, that more multifunctional plant communities generate a higher flow of ecosystem services like food, fuel, and fiber production; carbon sequestration; pollinator resources; game habitat; and medicine. But managing for the moving target of biological diversity is not always simple due to the inherent uncertainty and complexity of ecosystems. By measuring biodiversity and more broad plant

groupings (native versus nonnative; graminoids versus forbs and shrubs; annuals versus perennials) in response to four commonly used mid-contract management practices of burning, disk tillage, herbicide application, and a high diversity interseeding, I sought to reduce this uncertainty. My results reveal that while management had no influence on species diversity, it can influence ecological multifunctionality by selecting for broader plant groupings of interest to managers.

3.1 INTRODUCTION

3.1.1 The Conservation Reserve Program: using management to elicit diversity

Since European settlement in the U.S. Great Plains and Midwest, it is estimated that
native tallgrass prairie cover has declined by as much as 99.9%, with mixed and
shortgrass prairie declining by 20-80% (Samson and Knopf, 1996). Conversion to
cropland and changes to the historical disturbance regime drove much of this decline,
contributing to a profound loss of landscape heterogeneity and biological diversity in the
modern Great Plains (Risser 1988; Sterling and Ducharne, 2008).

The Conservation Reserve Program (CRP) enrolls over 9.7 million ha of the nation's agricultural lands most vulnerable to erosion, converting them back to perennial vegetation cover in order to protect the nation's soil resources against erosion. Within its first decade, the CRP was estimated to have reduced erosion by between 626 and 2420 million tons, with ongoing annual erosion reduction estimated at roughly 19 tons acre-1 year-1 (Feather et al., 1999). While not initially an explicit objective of the program, the program also provides wildlife habitat and pollinator resources. However, CRP grasslands removed from the historical disturbance regime are susceptible to dominance of late successional plant species, including shrubs and nonnative grasses, leading to low diversity grasslands incapable of supporting a high flow ecosystem services, including habitat provisioning.

To remedy this, federal policymakers added mid-contract management requirements to CRP contracts with the assumption that the addition of a disturbance event meant to simulate historical disturbance elicits plant diversity and corresponding ecosystem

services. Importantly, however, mid-contract management mimics disturbance *events*, the commonly accepted definition of which is given by Pickett and White (1985) as "any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment", while attempting to elicit ecological outcomes that emerge from disturbance *regimes*, which include the spatial and temporal characteristics of disturbances over long periods and across broad spatial scales.

In the Great Plains, the last glaciation ended 12, 000 years ago, making a meaningfully "long period" many millennia. Spatial interactions that structure most terrestrial ecological communities range from microbial to regional (Birge et al., 2016b).

Disturbance regimes are defined over such periods and extents by disturbance frequency, return interval, spatial distribution, size, intensive, severity, rotation period, and residuals (biotic legacies) (Turner, et al., 1998). Under current land use patterns, however, historic disturbance regimes are profoundly altered, with many disturbance events diminished in frequency, intensity, and size on the Great Plains (Fuhlendorf and Engle, 2001). In their place are new sets of anthropogenic disturbances —or lack thereof.

Mid-contract management offers a way to reintroduce disturbance on CRP grasslands, but whether it can elicit high diversity grassland cover is not well tested. In addition to serving as more disturbance event than as part of a disturbance regime, there is reason to predict mid-contract management may not stimulate high diversity grasslands. Individual manager and landowners are guided by their own management objectives (i.e., cost, ease of application) and are constrained by CRP regulations, being forced to make use of

treatments including herbicide application, disk tillage, and drill interseeding or some combination thereof—clearly none of which are native grassland disturbances—in addition to small extent, low intensity burning. It is infeasible that these serve as direct substitutes for native disturbances which include low to high intensity wildfires, droughts, floods, grazing inundations, and prairie dog activity that varied along all facets of the disturbance regime over millennia across the Great Plains (Biondini et al. 1989, Vinton et al. 1993, Hartnett et al. 1996, Fuhlendorf & Smeins 1998). However, the Conservation Reserve Program enrolls 9.3 million ha, so understanding how management influences plant diversity could provide important insight into the ecosystem services emerging from plant community dynamics across this large area of perennial grassland vegetation.

3.1.2 Why is biodiversity a management target? The diversity-function debate

The question of how biological diversity (i.e., species, functional, response) influences
ecosystem function and resilience to disturbance is a long-standing research theme in
ecology. The original iteration of this question surrounds the effect of species diversity on
ecosystem "stability". Elton (1923, 1958) was an early pioneer of this work, arguing that
high biological diversity provides resistance against environmental stressors. Early
mathematical models (e.g., Gause, 1934) of ecosystems seemingly supported this
relationship. These models, along with work from Odum (1953) and MacArthur (1955),
added further (mostly theoretical) support to the diversity-stability relationship, arguing
that simple communities are more vulnerable to dramatic oscillations and extinctions, and
that these oscillations provided an opening for invaders to successfully establish.

However, there is far from scientific consensus that species diversity leads to stability. This is partly attributable to language: According to Chapin et al. in 2002, ecological "stability" had over 160 different definitions in the literature. Indeed, there is little attempt to isolate and measure any mechanism of species diversity from whence a commonly understood metric of stability emerges. In recent years, there seems to be recognition of this problem, as a growing body of work from Tilman (1994, 1997, 2001), Hooper et al. (2005) and others has begun arguing for a link between biodiversity and ecological *functioning*, more broadly. Much of this work supports the idea of complementarity, in which different functional groups contribute to different ecological tasks to more fully utilize resources, and thus increase gross ecosystem production. In grassland systems, a more consistent relationship is emerging between trait diversity and biomass production (Zavaleta and Hulvey, 2006). Another idea in of this iteration of the diversity-stability debate is "multifunctionality".

Ecological multifunctionality refers to the simultaneous production of numerous ecosystem services, and relies on a diverse community of species with a variety of functional traits (Wall et al., 2004; Gamfeldt et al., 2008; Maestre et al., 2012; Wagg et al., 2014). To maintain multifunctionality through time, a diverse community includes functional replacements for species excluded by shifting conditions ("functional redundancy"), or species with high plasticity (Isbel et al., 2011; de Vries et al., 2012). The link between multifunctionality and biodiversity is especially apparent in communities with low diversity or for a highly specialized function, where the loss of one functional group can be especially impactful (Nielsen et al., 2011). Multifunctional plant communities continue to generate ecosystem services like food, fuel, and fiber

production; carbon sequestration; pollinator resources; game habitat; and medicine. It's no wonder managers aim for biodiversity as a target. But managing for the moving target of biological diversity is not always simple due to the inherent uncertainty and complexity of ecosystems.

The objective of this study was to assess how plant biodiversity indices of species richness, evenness, and Shannon-Wiener diversity, and well as broader functions like growth form (graminoid, forb, subshrub, or shrub), growth duration (annual, biennial, perennial), and native status (native or nonnative) respond to common management practices on a North Central Great Plains CRP grassland. I hypothesized that the different management practices would select for different plant communities and traits due to their different mechanisms of disturbance, and that these impacts would have different legacies over time. Specifically, I hypothesized that both the community response and successional patterns would vary in response to the different treatments used to mimic common mid-contract management practices used on Conservation Reserve Program grasslands.

3.2 METHODS

3.2.1 Study area

The study site was located approximately 2 km southeast of Annear, Nebraska (Holt County; 42°47'26.83"N, 98°43'29.57"W) on 220 ha of privately owned land enrolled in the Conservation Reserve Program (CRP). Mean annual air temperature was 8.61°C and 10.83°C in 2014 and 2015, and annual precipitation (cumulative) was 51.35 and 60.86, centimeters (cm) in 2014 and 2015, respectively (High Plains Regional Climate Center,

2017). Land cover was mixed and tallgrass prairie, and according to aerial imagery it was under center pivot rowcrop agriculture in 1983 and what appears to be non-center pivot cropland in 1954 (USGS EarthExplorer, 2017; Figure 3.1).

The field was enrolled into CRP likely sometime between the late 1980s and 1990s, and has been continuously enrolled throughout the duration of the study. Prior to enrollment, there is aerial imagery evidence that the field was under irrigated rowcrop agriculture (Figure 3.1), and prior to that dry land rowcrop as far back as 1946. Along the southern border of the field, there are trees planted in two rows to form a windbreak, with a ~30 m interspace between the rows that was untilled and uncultivated since at least 1946 according to aerial imagery, but possibly 1930 (conversations with a local landowner).

The study site is bordered to the south by a windbreak composed of mixed deciduous and eastern redcedar trees, to the east by privately owned pasturelands, to the north by CRP grassland and deciduous woody riparian vegetation along Niobrara river, and to the east by an irrigated cornfield. Eastern redcedar windbreaks partially border the field along the middle portion of the east border, and the most easterly edge of the northern border. Biennially planted winter wheat firebreaks border the entire study area.

Soils at the site are of Eolian sands parent material. The dominant soil associations that constitute the site's soil series were Valentine-Dunday loamy fine sand, Simeon loamy sand, and Valentine fine sand. Together, their typical profiles are an A-horizon ($\sim 0-30$ cm), a possible AC-horizon (18-36 cm), and a C-horizon (36-200 cm). Slope on the field ranged from 0-9%. Fine and loamy sands dominate the upper horizon, with sand

more commonly found at lower horizons (> 15 cm). This soil series is excessively drained, with little to no frequency of flooding or ponding, low available water storage in the profile, and are considered nonsaline $(0.0 - 0.2 \text{ mmhos cm}^{-1})$ (Soil Survey Division Staff, 1999).

3.2.2 Treatments and Experimental Design

In summer of 2012, the entire study site was emergency hayed in response to drought. In fall of 2012, the 220 ha field was divided into nine areas separated by firebreaks planted with winter wheat. In each of these nine sections, a 2.4 ha plot was lightly disked and seeded with a CR42 pollinator seed mix using a drill seeder at the NRCS recommended seeding rate. The rest of the site was planted with a standard CRP tallgrass prairie seed mix (CP25 mix, 15 species) using a drill seeder at the NRCS recommending seeding rate (~40 seeds ft⁻¹).

In April 2014, I applied three additional treatments to the study site in a randomized block design, with nine 20 m x 20 m blocks in each of the nine sections made by the interseeded plots and windbreak design in the field, and each block containing four plots assigned to the three treatments plus a control (Figure 3.2). Treatments consisted of: 1) burning, 2) disking, and 3) herbicide application. The herbicide replicates were sprayed on April 14, 2014 with a glyphosate herbicide 32 oz acre⁻¹, or at half-label-rate (which is generally as effective as full label rate; Knezevic, 2008). The burn replicates were burned on April 17, 2014. The temperature was 6 ° C, relative humidity was 30%, and wind speed was 13 MPH. The disk replicates were heavily disked to ~ 30 cm on April 20, 2014 with a disc harrow pulled behind a tractor.

The treatments (burn, disk, herbicide, and a control) were arranged with 20 x 20 m replicates joining the interseeding treatment of field matrix (Figure 2.4).

3.2.3 Data Collection

In 2014 and 2015, I sampled plant communities with two 1 m x 1 m quadrats in each field replicate, twice throughout the growing season. At each field replicate, the 1 m x 1 m quadrat was placed randomly within the replicate (using a random number generator to determine the exact sampling location), and item (bare ground, litter, or plant species) and abundance (measured as canopy cover) was recorded. This was repeated within the replicate for a total of two 1 m x 1 m quadrats per sampling period, and data were combined for that field replicate (i.e., abundance per replicate was on a 2 m² basis). This was repeated for each replicate a total of four times: twice per year in 2014 and 2015. Plants were identified to the species level with the following exceptions, which were identified to genus level: *Ambrosia*, *Andropogon*, *Carex* (combined with *Cyperus*), *Chenopodium*, *Helianthus*, *and Solidago*. At this site, *Andropogon gerardii* and *Andropogon hallii* showed evidence of hybridization, so while they were often recorded separately, they were combined for analysis.

Each plant was assigned a grouping according to its growth habit, native status, and growth duration using assignations from the USDA NRCS PLANTS Database (accessed 2016). Growth habits assignments were graminoid, forb, or shrub. Subshrubs versus shrubs are a delineation that I eliminated due to low sample size in each group resulting in weak statistical power. As a result, I reclassified two subshrub species (*Rosa*

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arkansana and Yucca glauca) as shrubs. When plants had a naturalized assignation

(i.e., Chenopodium), I assigned them as "nonnative" and not as "native". Plants' growth

duration was assigned as annual, biennial, or perennial.

3.2.4 Analysis

I used multi-model inference to assess my hypotheses, i.e., compared treatment, time,

field block the combination (i.e., global), or simply a null model against one another, to

assess which model best fit data for species richness, evenness, Shannon-Wiener Index

(SHI), bare ground, and litter cover. I also compared how these models explained broad

level community traits (growth habit, native status, and growth duration). The following

models were included in multi-model inference (MMI) frameworks, with the response

variable (Y) for each MMI as species richness, diversity, evenness, growth habit, native

status, growth duration, bare ground abundance, or litter abundance (i.e., eight MMIs in

total):

Treatment model: Y ~ Treatment

Time model: Y ∼ SamplingTime

Block model: Y ~ Block

Global model: Y ~ Treatment+SamplingTime+Block

Null model: $Y \sim 1$

I set two AICc as criteria for models being equal a priori.

3.3 RESULTS

Average species richness (± SD) (Figure 3.3), evenness (Figure 3.4), and Shannon

Wiener (Figure 3.5) index for all replicates across the entire study (whole field, over two

years) was 12.94 ± 6.31 , 0.80 ± 0.18 and 1.91 ± 0.54 , respectively. The multimodel inference framework showed that the sampling time model –and not treatment –was the best model for species evenness (Table 3.1), species richness (Table 3.2), and species diversity (Table 3.3). Species richness was higher in 2014, evenness higher in 2015, and Shannon-Wiener diversity higher in 2014.

The models that best fit forb abundance (Figures 3.6 and 3.7) in the multimodel inference framework were the global (AICc = 0.52) and treatment models (AICc = 0.36) (Table 3.4). Time was the third best fitting model (AICc = 0.09). The summary of the global model (Table 3.5) revealed that the interseed treatment resulted in significantly (P < 0.05) higher forb abundance than all other treatments and control (Figure 3.6). A summary of the time model showed that forb abundance was also significantly higher in 2014 versus 2015 (Figure 3.7). The model that best fit graminoid (grass) abundance was the time model (AICc = 0.99) (Table 3.6; Figure 3.6), a summary of which showed significantly increased abundance from 2014 to 2015. None of the candidate models I selected fit the shrub abundance data better than the null model (AICc = 0.69), although the time model (AICc = 0.21) was within two AIC of the top (null) model (Table 3.7), with higher shrubs in 2015 versus 2014.

Treatment was the model that best fit abundance of nonnative species (AICc = 0.44) in the multimodel inference (Figure 3.8; Table 3.8) although it was tied (within two AIC) with the null model (AICc weight = 0.32) so care must be taken when interpreting these results. Nevertheless, a summary of the treatment model showed that the abundance of nonnative species was significantly higher in the herbicide plots (Table 3.9). The model

that best fit native species abundance was time (AICc = 0.93), with higher native species abundance in 2015 versus 2014 (Figure 3.9; Table 3.10). The next model was the null (AIC = 0.03), with all others falling below.

The model that best fit annual plant abundance was that global model (AICc = 0.86), followed by the time model (AICc = 0.1) (Figure 3.10; Table 3.11), and a summary of the global model revealed that annual plant abundance was nominally significantly (P < 0.1) higher in the herbicide and interseed treated plots (Figure 3.10), and in 2014 (Figure 3.11). Because I had few models in my MMI framework, that my global model was the best fit for the data does not mean I should reject this result as my models being a poor fit. This is especially true in light of none of the blocks being significant predictors of annual plant abundance. The time model was by far the best fit for perennial plant abundance (AICc = 0.99), with higher cover in 2015 (Table 3.12), and all other models falling below the null. The candidate models that best fit biennial plant abundance, which was low throughout the study, were the null model (AICc = 0.67) and the (with the time model (AICc = 0.3) which tied (within two AIC of one another) (Table 3.13).

The best fit for bare ground percent cover was the global model (Table 3.14), the summary (Table 3.15) of which revealed higher bare ground in the disking treatment, and lower bare ground herbicide treatment and slightly lower bare ground in the control (Figures 3.12). The summary also revealed higher bare ground in 2014 versus 2015 (Figures 3.13). None of the blocks had higher bare ground, with the exception of blocks, five and six which had nominally significantly (P < 0.1) higher bare ground. The treatment model was by far the best fit for litter percent cover (AICc = 1), with

significantly higher litter cover in the herbicide treatment, significantly less in the interseed treatment, and nominally significantly less in the disk treatment (Table 3.17; Figure 3.12).

3.4 DISCUSSION

The standard management treatments applied to this mixed grass Conservation Reserve Program field did not elicit plant communities with greater species diversity, but did shift communities towards different broader functional groupings. In contemporary grassland communities experiencing increased representation of species undesirable from a management perspective (i.e., nonnative and woody species), managing for higher species richness or Shannon-Weiner diversity may not support management objectives typically assumed to be reliant on high biological diversity. This is exemplified by the interseed treatment, which had no effect on Shannon-Weiner diversity, but did elicit higher forb abundance –a management goal of the treatment. This indicates that plant community targets not coupled to Shannon-Weiner diversity may be a more effective management objective.

Management also played a significant role in other broad scale plant dynamics that are often of interest to managers but were independent from species identity. Herbicide treatment led to higher abundance of nonnative species in my study, even though it is frequently administered to produce the opposite outcome. Bare ground is thought to invite invasive, nonnative species, but in the treatment that elicited the highest bare ground, disking, this did not occur. Instead, the treatment with the lowest bare ground cover, herbicide, had the highest abundance of nonnative species. Bare ground and litter

cover are often used as proxies for other management objectives, including upland game bird habitat and various soil processes (sometimes collective referred to as "soil health"). My results indicate that bare ground cover may not always be an appropriate gauge of resource availability in the system.

It appear that in my study a flush of reactive nitrogen, rather than bare ground, provided a foothold for nonnative species. Many nonnative species successfully colonize a system as a result of their ability to quickly capitalize on resources following the release stage of a disturbance event (i.e., the 'fluctuating resource hypothesis'; Davis et al., 2000). However, as the system restructures, they are outcompeted by more resource efficient (often native) species. In the herbicide treatment, initially elevated soil nitrogen, possibly due to lack of plant re-uptake, root necromass mineralization, and/or glyphosate-induced priming effects (see Chapter 4), could give a continued advantage to low nitrogen efficiency nonnative invaders, which might then perpetuate their advantage through mineralization low carbon to nitrogen litter tissue content (Ehrenfeld, 2003).

My results indicate that while management may not be able to simply elicit higher species diversity, it can still influence ecological multifunctionality through selecting for broad functional plant community groupings rather than at the species scale. To maintain multifunctionality through time, communities require functional replacements for species excluded by shifting conditions ("functional redundancy"). Because no species-level trends emerged across the site in response to treatment, and/or over time, yet broader groupings including growth form (graminoid, forb, or shrub), native status, and growth duration (annual, biennial, or perennial) did respond to treatment, my work provides

tentative evidence for possible functional redundancy at the species level in this North Central Great Plains CRP grassland.

3.5 CONCLUSION

For managers and landowners seeking to improve functional redundancy and high multifunctionality on similar grasslands, my work supports the use of monitoring programs that measure broad groupings such as native versus nonnative and forbs versus graminoids, rather than individual species identities. By incorporating this broader level information, the collection of which is more efficient than species level assessments, into management programs, managers can design plans that better navigate the complexity and uncertainty of grassland community dynamics while balancing multiple management objectives.

3.7 TABLES AND FIGURES

Table 3.1 Multimodel inference table showing the time model as the best fitting model of the candidate set for plant species evenness per two m².

	Model	K	AICc	Delta AICc	AICc weight	log-Likelihood
2	Time	3	-57.38	0	0.84	31.83
5	Null	2	-53.38	4	0.11	28.76
3	Block	3	-51.59	5.79	0.05	28.94
1	Treatment	6	-47.14	10.23	0.01	30.08
4	Global	21	-34.95	22.42	0	45.37

Table 3.2 Multimodel inference table showing the time model as the best fitting model of the candidate set for plant species richness per two m².

	Model	K	AICc	Delta AICc	AICc weight	log-Likelihood
2	Time	3	468.86	0	0.98	-231.29
4	Global	21	477.2	8.34	0.02	-210.7
5	Null	2	584.59	115.73	0	-290.22
3	Block	3	586.67	117.81	0	-290.19
1	Treatment	6	592.11	123.25	0	-289.54

Table 3.3 Multimodel inference table showing the time model as the best fitting model of the candidate set for plant species Shannon-Weiner diversity index per two m².

	Madal	IZ.	AIC.	Dalta AICa	AICa waight	log-
	Model	K	AICc	Delta AICc	AICc weight	Likelihood
2	Time	3	123.76	0	1	-58.74
4	Global	21	142.22	18.46	0	-43.21
5	Null	2	146.16	22.4	0	-71.01
3	Block	3	148.15	24.39	0	-70.93
1	Treatment	6	154.43	30.68	0	-70.7

Table 3.4 Multimodel inference table showing the global and treatment models as tied for the top model (within two AIC) out of the candidate model set for forb abundance per two m^2 .

	Madal	V	AICa	Dalta AICa	AICa vyajalat	log-
	Model	K	AICc	Delta AICc	AICc weight	Likelihood
4	Global	17	6249.64	0	0.52	-3107.48
1	Treatment	6	6250.43	0.78	0.36	-3119.17
3	Time	5	6253.11	3.47	0.09	-3121.52
2	Block	10	6256.56	6.91	0.02	-3118.16
5	Null	2	6257.37	7.73	0.01	-3126.68

Table 3.5 Summary of the treatment model from the forb abundance multimodel inference framework per two m².

	Estimate	Std. Error	t value	Pr(>ltl)
(Intercept)	4.9766	0.5446	9.14	0
Control	-0.3109	0.7691	-0.4	0.6861
Disk	-0.2858	0.7461	-0.38	0.7017
Herbicide	0.9401	0.7605	1.24	0.2167
Interseed	1.9868	0.7376	2.69	0.0072

Table 3.6 Multimodel inference table showing the time model as the best fitting model of the candidate set for graminoid abundance per two m².

	3.6.1.1	**	A.T.C.	D 1. A70	170	log-
	Model	K	AICc	Delta AICc	AICc weight	Likelihood
3	Time	5	10902.23	0	0.99	-5446.09
1	Treatment	6	10913.66	11.43	0	-5450.79
5	Null	2	10914.59	12.37	0	-5455.29
4	Global	17	10914.78	12.55	0	-5440.13
2	Block	10	10927.6	25.37	0	-5453.71

Table 3.7 Multimodel inference table showing the null model as the best fitting model of the candidate set for shrub abundance per two m².

	N. (1.1)	17	AIC	Dolto AICo	AIC : 14	log-
	Model	K	AICc	Delta AICc	AICc weight	Likelihood
5	Null	2	163.02	0	0.69	-79.21
3	Time	5	165.38	2.36	0.21	-75.93
2	Block	10	167.28	4.26	0.08	-64.47
1	Treatment	6	171.37	8.35	0.01	-77.06
4	Global	22	Inf	Inf	0	-36.16

Table 3.8 Multimodel inference table showing the treatment and the null model as tied (within two AIC) for the best fitting model of the candidate set for nonnative plant abundance per two m^2 .

	Model	K	AICc	Delta	AICc	log-
	Wiodei	IX	THEC	AICc	weight	Likelihood
1	Treatment	6	1123.82	0	0.44	-555.66
5	Null	2	1124.49	0.67	0.32	-560.21
2	Time	5	1126.31	2.49	0.13	-557.98
3	Block	10	1127.16	3.34	0.08	-552.92
4	Global	17	1129.07	5.25	0.03	-545.61

Table 3.9 Summary of the Treatment model for nonnative plant abundance per two m² from the multimodel inference.

	Estimate	Std. Error	t value	Pr(>ltl)
(Intercept)	3.4259	1.0907	3.14	0.002
Control	0.9907	1.5034	0.66	0.5108
Disk	1.6366	1.4116	1.16	0.2479
Herbicide	3.6149	1.3583	2.66	0.0085
Interseed	0.9289	1.4919	0.62	0.5343

Table 3.10 Multimodel inference table showing the time model as the best fitting model of the candidate set for native plant abundance per two m².

	Model	K	AICc	Delta AICc	AICc weight	log-Likelihood
2	Time	5	17145.71	0	0.93	-8567.84
5	Null	2	17152.36	6.65	0.03	-8574.18
1	Treatment	6	17152.4	6.68	0.03	-8570.18
4	Global	17	17158.61	12.9	0	-8562.15
3	Block	10	17165.5	19.79	0	-8572.69

Table 3.11 Multimodel inference table showing global model as the best fitting model of the candidate set for annual plant abundance per two m².

	Model	K	AICc	Delta AICc	AICc weight	log-Likelihood
4	Global	17	5509.78	0	0.86	-2737.5
2	Time	5	5514.03	4.25	0.1	-2751.98
1	Treatment	6	5515.88	6.1	0.04	-2751.89
5	Null	2	5524.37	14.58	0	-2760.18
3	Block	10	5525.08	15.3	0	-2752.4

Table 3.12 Multimodel inference table showing the time model as the best fitting model of the candidate set for perennial plant abundance per two m².

					AICc	log-
	Model	K	AICc	Delta AICc	weight	Likelihood
2	Time	5	11572.13	0	0.99	-5781.04
5	Null	2	11584.03	11.9	0	-5790.01
1	Treatment	6	11584.47	12.34	0	-5786.2
4	Global	17	11587.28	15.15	0	-5776.4
3	Block	10	11597.65	25.53	0	-5788.74

Table 3.13 Multimodel inference table showing the null and time models tied (within two AIC) as the best fitting models of the candidate set for biennial plant abundance per two m^2 .

	Model	K	AICc	Delta AICc	AICc weight	log-Likelihood
5	Null	2	438.68	0	0.67	-217.23
2	Time	3	440.27	1.59	0.3	-216.91
1	Treatment	6	445.02	6.34	0.03	-215.69
3	Block	9	451.23	12.54	0	-214.74
4	Global	16	465.18	26.5	0	-209.96

Table 3.14 Multimodel inference table showing the global model as the best fitting model of the candidate set for percent bare ground cover per two m².

	Model	K	AICc	Delta AICc	AICc weight	log-Likelihood
4	Global	17	1035.36	0	1	-497.9
1	Treatment	6	1074.22	38.86	0	-530.77
3	Time	5	1093.12	57.76	0	-541.31
5	Null	2	1118.64	83.28	0	-557.27
2	Block	10	1133.76	98.4	0	-555.94

Table 3.15 Summary of the global model for percent bare ground per two m² from the multimodel inference.

	Estimate	Std. Error	t value	Pr(>ltl)
(Intercept)	25.9286	4.297	6.03	0
Time - August2014	-2.4095	3.0429	-0.79	0.4301
Time - July2015	-21.2261	3.3459	-6.34	0
Time - August2015	-18.3248	3.1288	-5.86	0
Control	-12.5808	3.7729	-3.33	0.0012
Disk	17.7944	3.125	5.69	0
Herbicide	-13.2373	3.9531	-3.35	0.0011
Interseed	-4.2493	3.339	-1.27	0.2058
Block2	0.8684	4.6065	0.19	0.8508
Block3	2.7321	4.8255	0.57	0.5724
Block4	-0.9474	5.0393	-0.19	0.8512
Block5	7.8594	4.6557	1.69	0.0942
Block6	7.5494	4.4843	1.68	0.0951
Block7	-2.7347	5.7371	-0.48	0.6345
Block8	0.8297	4.6747	0.18	0.8594
Block9	2.9152	5.0471	0.58	0.5647

2.1.3

Table 3.16 Multimodel inference table showing the treatment model as the best fitting model of the candidate set for percent cover litter per two m² AIC table.

	Model	K	AICc	Delta AICc	AICc weight	log-Likelihood
1	Treatment	6	1403.77	0	1	-695.65
2	Time	5	1429.08	25.3	0	-709.37
5	Null	2	1433.45	29.68	0	-714.69
3	Block	10	1445.11	41.34	0	-711.92
4	Global	166	4651.03	3247.26	0	-528.81

Table 3.17 Summary of the Treatment model for percent litter cover per two m².

Estimate	Std. Error	t value	Pr(>ltl)
15.0694	1.7928	8.41	0
2.9514	2.5354	1.16	0.2459
-4.6694	2.5534	-1.83	0.0691
8.2708	2.5354	3.26	0.0013
-5.4658	2.4569	-2.22	0.0274
	15.0694 2.9514 -4.6694 8.2708	15.0694 1.7928 2.9514 2.5354 -4.6694 2.5534 8.2708 2.5354	15.0694 1.7928 8.41 2.9514 2.5354 1.16 -4.6694 2.5534 -1.83 8.2708 2.5354 3.26

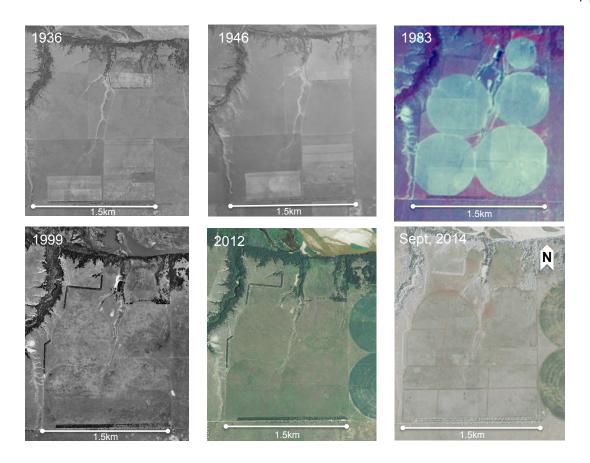


Figure 3.1 Aerial photos of the study area from USGS indicating different land use and the presence of the southern border windbreak, starting in 1936 and until 2014. The 2014 photos show the mid-contract management treatments applied in this study.

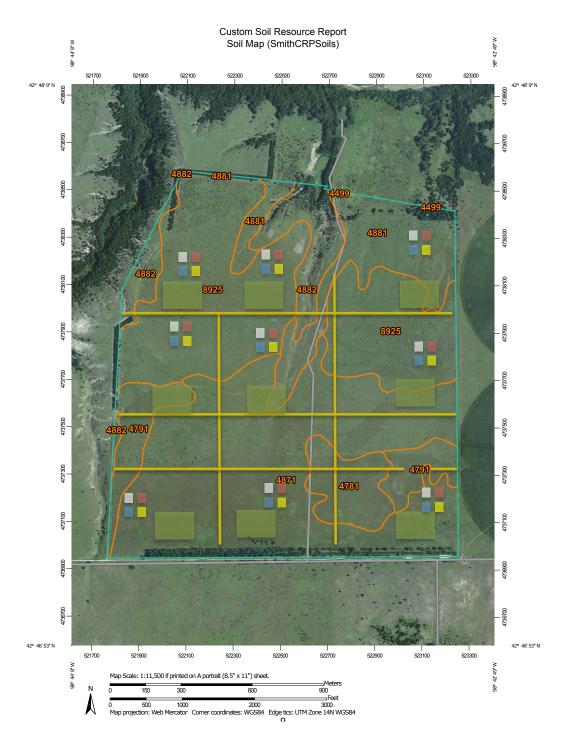


Figure 3.2 A custom soil report from the NRCS Web Soil Survey with a map of the 220 ha study area with the 2.4 ha interseed (green rectangles) and other mid-contract management treatments (20 x 20 m white, red, blue, and yellow squares) indicating the relative position and size of the nine replicates on the field. Although here they are shown

in the same order, the mid-contract management squares (save the interseed replicates) were randomized on the field. The yellow lines were planted in winter wheat in 2013 and 2014 as a firebreak. Map unit legend for the orange numbers, which indicate soil types are as follows, with percent cover of the study area in parentheses: 4499 – Dunday loam sand, 3-6% slope (0.1%); 4781 – Valentine fine sand, 0-3% slope (4.6%); 4791 –Valentine fine sand, 3-9% slope (6.3%); 4871 – Valentine-Dunday loamy fine sands, 0-3% slope (39.0%); 4881 – Valentine-Simeon sands, 3-9% slope (11.4%); 4882 – Valentine-Simeon sands, 9-30% slopes (6.9%); 8925 – Simeon loamy sand, 0-3% slope (31.7%).

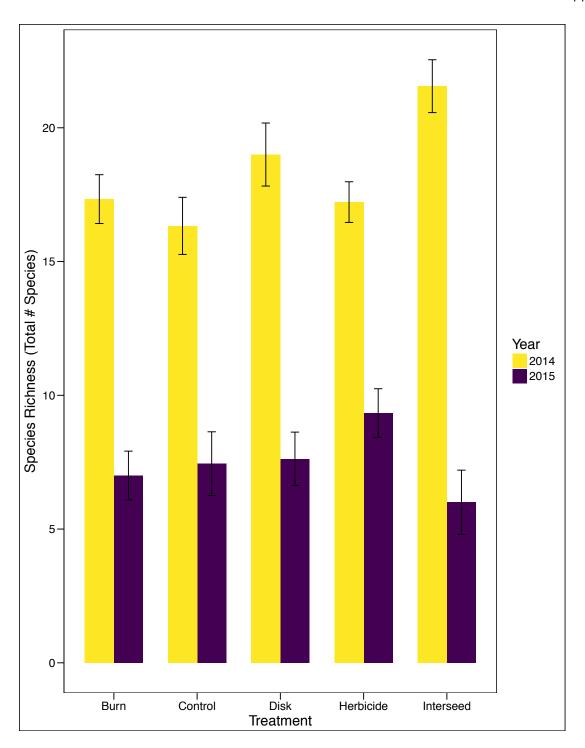


Figure 3.3 Mean species richness per two m^2 by year in the treatments and control. Error bars are $\pm SE$.

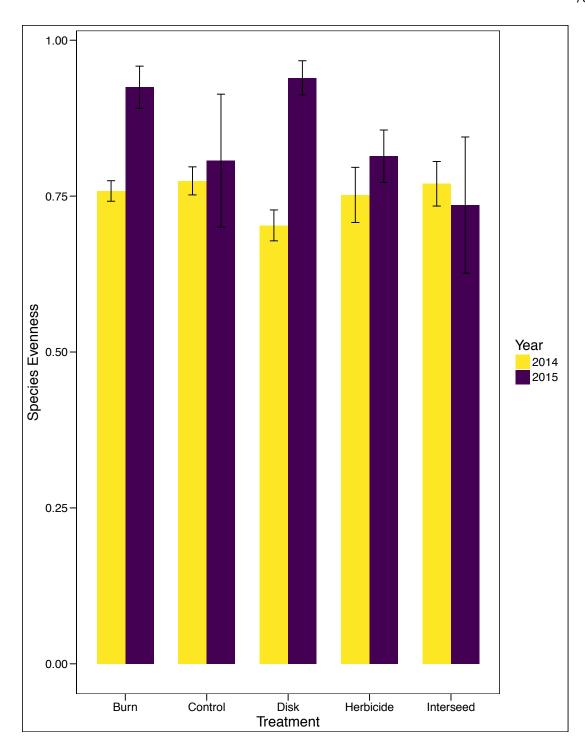


Figure 3.4 Mean species evenness per two m^2 , by year in the treatments and control. Error bars are $\pm SE$.

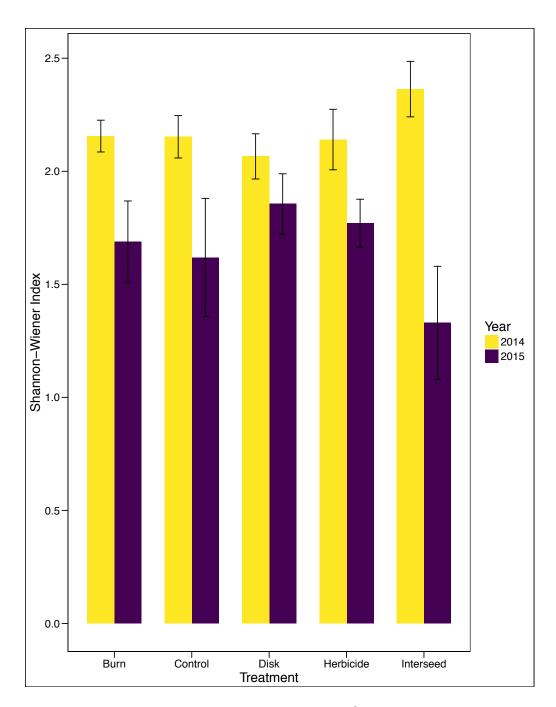


Figure 3.5 Mean Shannon-Weiner Index per two m^2 , by year in the treatments and control Error bars are $\pm SE$.

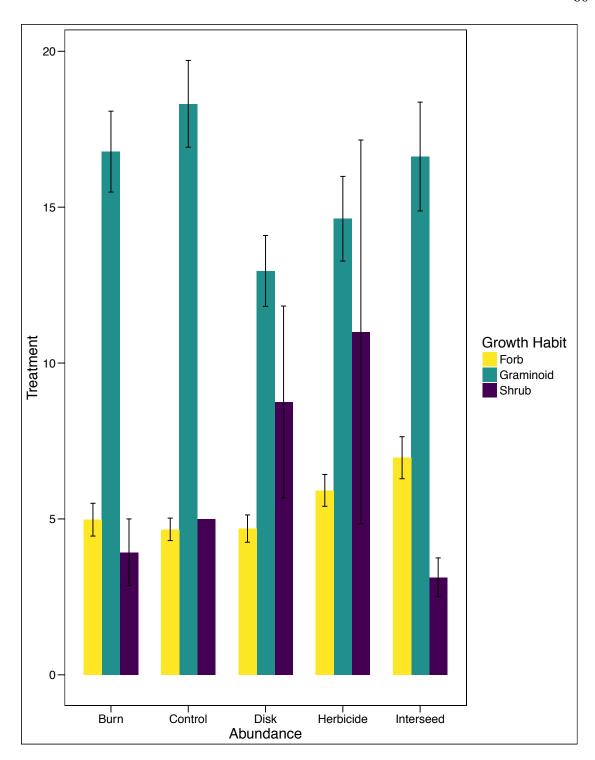


Figure 3.6 Mean abundance of plants per two m^2 grouped by growth forms (forb, graminoid, and shrub/subshrub combined into shrub), in the treatments and control. Error bars are $\pm SE$.

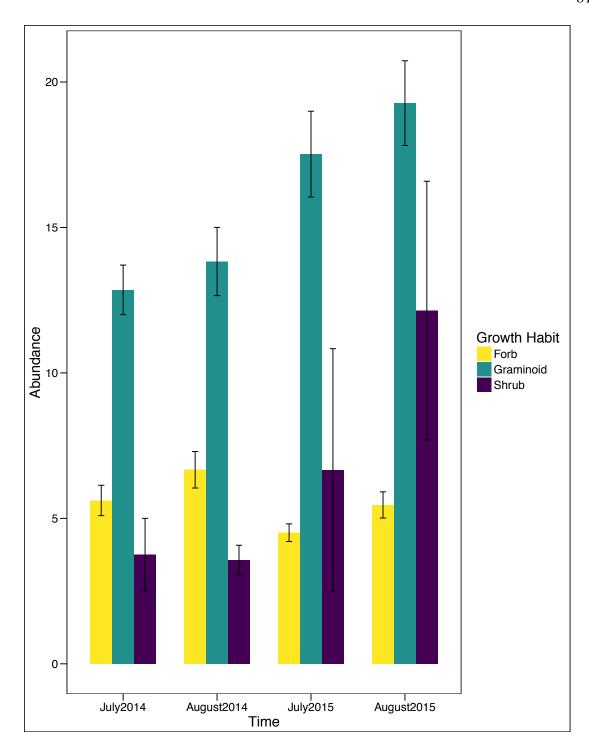


Figure 3.7 Mean abundance of plants per two m^2 grouped by growth forms (forb, graminoid, and shrub/subshrub combined into shrub) over the four sampling periods. Error bars are $\pm SE$.

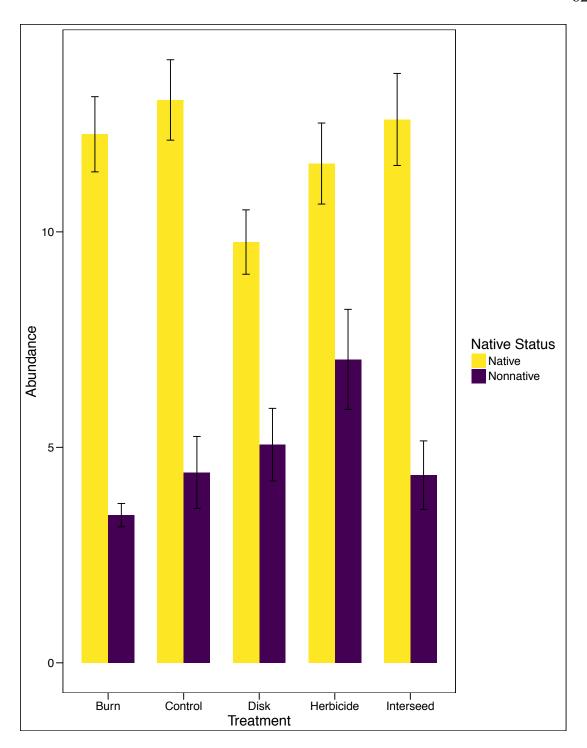


Figure 3.8 Mean abundance of plants per two m² grouped by native status (nonnative or native), in the treatments and control. Error bars are ±SE.

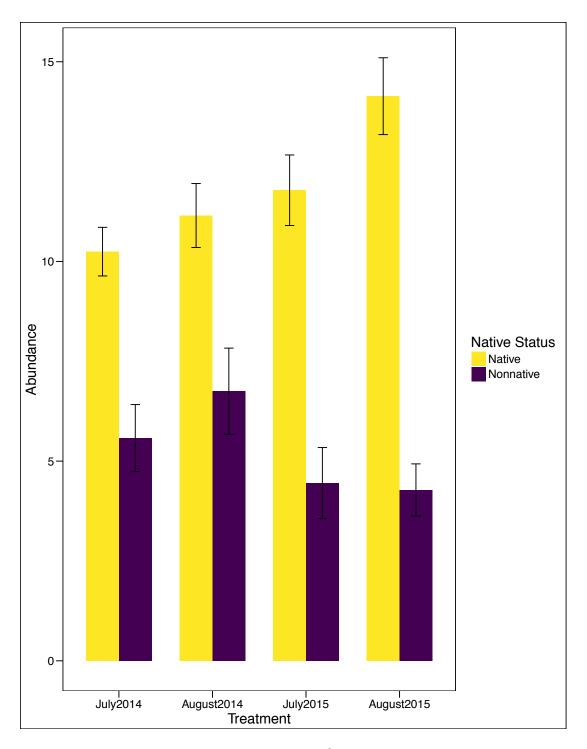


Figure 3.9 Mean abundance of plants per two m² grouped by native status (nonnative or native) by sampling time. Error bars are ±SE.

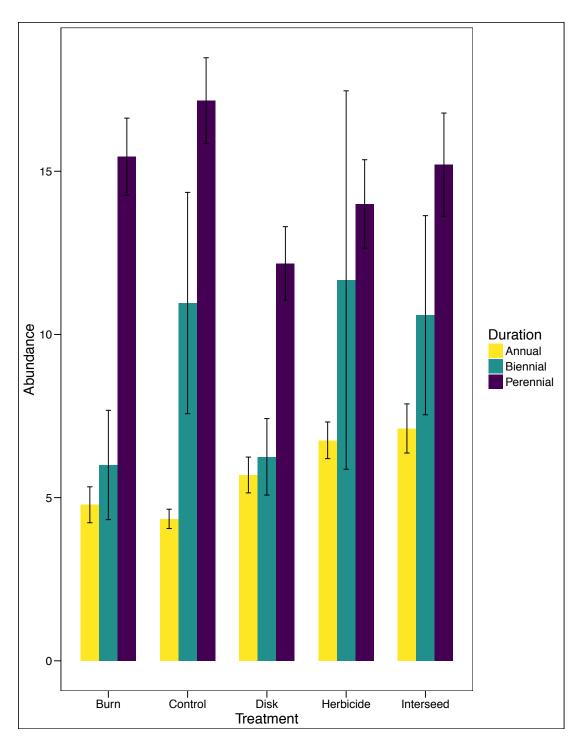


Figure 3.10 Mean abundance of plants per two m² grouped by growth duration (annual, biennial, or perennial) by treatment and control. Error bars are ±SE.

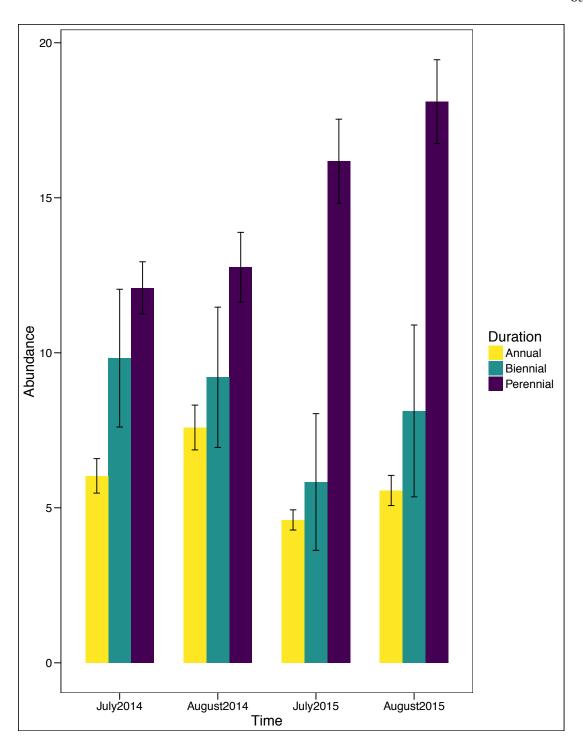


Figure 3.11 Mean abundance of plants per two m² grouped by growth duration (annual, biennial, or perennial) over sampling times. Error bars are ±SE.

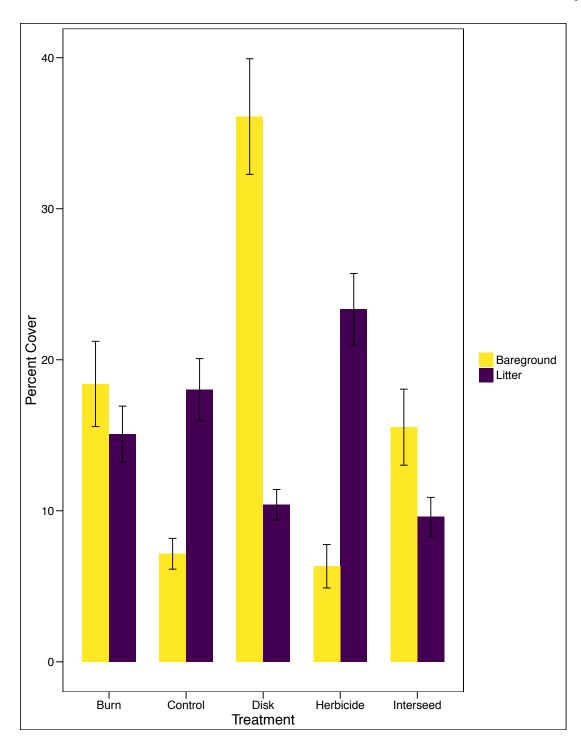


Figure 3.12 Percent cover of bare ground and litter per two m^2 grouped by treatments and control. Error bars are $\pm SE$.

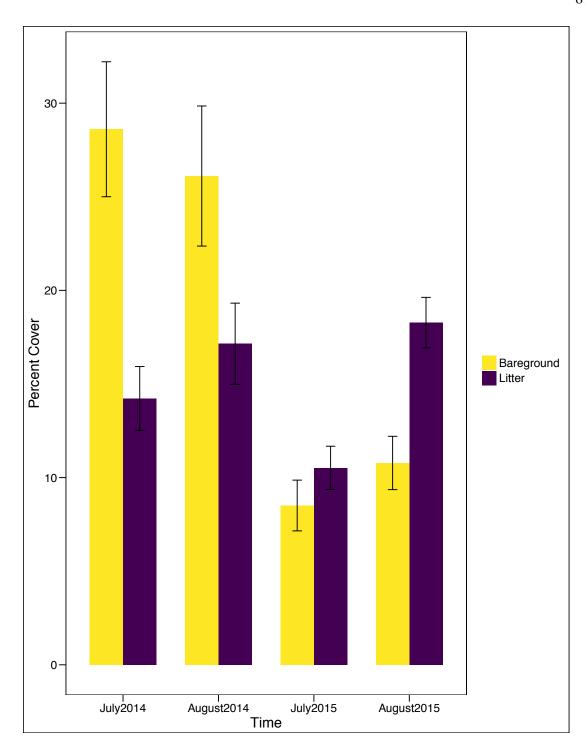


Figure 3.13 Percent cover of bare ground and litter per two m² grouped by sampling period. Error bars are ±SE.

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4 COMMON CONSERVATION RESERVE PROGRAM MANAGEMENT PRACTICES HAVE VARIABLE EFFECTS ON SOIL DYNAMICS IN A NORTH CENTRAL GREAT PLAINS GRASSLAND

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University of Nebraska, 2017

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ABSTRACT: A chief objective of the Conservation Reserve Program is to protect soil resources, yet conflicting secondary management objectives using management practices that disrupt the soil may lead to an inadvertent loss of soil ecosystem services, ultimately undermining the Program's overarching objective. Burning, herbicide application, disk tillage, and drill interseeding are approved mid-contract management (MCM) practices meant to elicit diverse plant communities. While these management practices are allowed as interchangeable, they use different mechanisms and ostensibly influence the belowground differently. To investigate these potential differences, I measured soil organic matter (assessed by total carbon, labile carbon, soil nutrients, and aggregation) and microbial community structure and function (assessed by PLFA and extracellular enzymes) in response to the four management practices on a Conservation Reserve Program grassland in North Central Nebraska. I found that soil carbon was slightly higher in the herbicide relative to the disked plots, which represent the treatments with the least and highest bare ground, respectively. However, soil carbon was also slightly in the herbicide treatment relative to the control, which had the second highest percent litter cover, so it is unlikely that litter cover drove soil carbon storage in my study. Mean weighted diameter also did not appreciable change in response to the treatments. Soil nitrogen was significantly elevated in the herbicide treatments, which is likely

attributable to lack of plant nitrogen uptake upon herbicide-induced death, mineralization of root necromass, microbial priming in response to the herbicide chemical I used, or some combination thereof. There was weak evidence for shifts in microbial community in response to treatments, yet it appears that herbicide-induced elevated soil nitrogen shifted the belowground towards carbon and phosphorus limitation, evidenced by elevated production of carbon and phosphorus acquisition enzymes. Additionally, enzyme activity Q₁₀, which indicates lability of soil organic matter (SOM), was significantly lower in burn treatment, potentially due to fire adapted grassland plants releasing labile carbon to stimulate mineralization of SOM to release nutrients for regrowth following burning. The soil is directly and indirectly responsible for numerous ecosystem services upon which society depends for its survival and wellbeing. While the belowground is often ignored in management plans, my study reveals the complexity of its role in mediating management outcomes.

4.1 INTRODUCTION

A chief objective of the Conservation Reserve Program is to protect soil resources (Gebhart et al., 1994; Karlen et al., 1998, Staben et al., 1997), yet conflicting secondary management objectives using management practices that disrupt the soil may lead to an inadvertent loss of soil ecosystem services, ultimately undermining the Program's overarching objective. Soils contribute directly and indirectly to multiple ecosystem services, such as regulation of the atmosphere and climate, primary (including agricultural) production, waste processing, decomposition, nutrient conservation, water purification, erosion control, medical resources, pest control, and disease mitigation (Wall et al., 2004; Bardgett, 2005; de Deyn and van der Putten, 2005; Wall et al., 2015). Standard Conservation Reserve Program (CRP) contracts are ten to fifteen years in duration, with a "mid-contact management" provision requiring management intervention on at least a portion of the enrolled acreage around the contract's mid point, the goal being a reduction in the dominance of late-stage successional or nonnative plants.

Burning is one of the approved mid-contract management (MCM) practices, along with herbicide application, disk tillage, and drill interseeding, the last of which is often used in conjunction with other management techniques to establish a specific plant community. While these management practices are allowed as interchangeable, they use different mechanisms to elicit an early successional plant community and ostensibly influence the belowground differently both directly and indirectly through aboveground response to management, due to the tight coupling between aboveground and belowground functioning (de Deyn and van der Putten, 2005).

The overarching objective of this study was to assess how four common CRP MCM practices actions of herbicide application, low intensity burning, disk tillage, and drill interseeding on a Conservation Reserve Program grasslands affect the soil. I hypothesized that, due to their different mechanisms of action, the four different practices would have different effects on soil carbon, nutrients, and microbial communities.

4.1.1 Soil Organic Matter and Grassland Soil Functioning

Soil organic matter (SOM) is central to soil structure and function. SOM is made up of decomposing plant material and soil microbiota, and confers multiple ecological properties including nutrient, water, and mineral retention, energy and nutrients for the belowground food web, soil structure necessary to support numerous soil functions, and a stable reservoir of non-greenhouse gas carbon. Due to the ecosystem services it directly and indirectly provides, SOM sequestration is a common objective in management plans for systems ranging from ecological restorations to intensive agroecosystems. However, the complex mechanisms responsible for the formation, transformation, and loss of SOM are not entirely understood (Horwath, 2007), creating uncertainty in management plans targeting SOM sequestration.

The quantity of SOM in ecosystems is the long-term result of a net primary production (NPP) minus the rate of decomposition, i.e., net ecosystem production. In native temperate grasslands, annual aboveground NPP is largely allocated to litter fall and standing dead biomass (Schlesinger, 1990; Schlesinger and Bernhardt, 2013), but much of grassland production occurs belowground, allocated to the growth and turnover of deep, dense, fibrous, grassland root systems. In grasslands, moisture limitations help

reduce the two major sources of carbon loss from the system: microbial respiration of SOM to CO₂, and dissolved organic carbon (DOC) leaching. Mineralization of SOM also releases soil nitrogen and phosphorus, which are taken up by microbiota and plants, leached, reduced to N₂ gas in the case of reactive nitrate, or gradually occluded in minerals in the case of bioavailable phosphorus. As a result, undisturbed grassland soils accumulate large SOM pools, and while they are generally nitrogen limited, grasslands tend to become increasingly more phosphorus limited as they age.

An important control on SOM transformation and loss is microbial accessibility (Dungait et al., 2012; Birge et al., 2015b). SOM can be isolated from microbial attack due to occlusion within aggregates, low rate of material movement among pores, or strong physico-chemical bonding to soil clay minerals (the "Abiotic Gate Hypothesis"; Kemmitt et al., 2008). As a result, tillage and irrigation of temperate grassland soils leads to rapid loss of carbon from the soil (Jenny, 1933; Bauer & Black, 1981; Parton et al. 1983; Mann, 1986; Parton et al. 1987; Davidson and Ackermann, 1993; Reeder et al., 1998; David et al., 2000; Mikhailova, 2000). Tillage disrupts soil carbon protected in aggregates and redistributes soil carbon so that it is exposed to decomposing extracellular enzymes and organisms. Cropping reduces aboveground residue (i.e., harvest) and reduces belowground inputs as vegetation is shifted towards annual shallow-rooted crop cover (Elliott, 1986; Burke et al., 1995). Irrigation relieves water limitation on soil respiration, and altered soil structure and hydrology from tillage accelerates flushing of dissolved organic carbon (typically the lighter fraction) out of the system or to greater depths (> 200 cm) (David et al., 2000). The loss of soil carbon to CO₂ associated with land use change from native cover to crop (e.g., Burke et al., 1991) occurs in all

ecosystem types, but the greatest SOM losses occur associated with land use change from former grasslands (Guo and Gilford, 2002).

Whether SOM can be recovered through enrollment in the Conservation Reserve Program remains unknown, although there is growing evidence that quantity recovery is possible. The soil carbon saturation hypothesis (Six et al., 2002) posits that all soils have a limited amount of carbon they can store due to a variety of interacting constraints, and that rate of accrual will vary depending on how far a soil is from its saturation, with highest rates of accrual occurring in the most depleted soils, and rates slowing as saturation approaches. It should follow that recently restored grassland soils, which again generally lose the most carbon in response to conversion to cropland, gain the most carbon the fastest relative to other native ecosystems converted back from cropland. A metaanalysis exploring how various management activities influence soil carbon storage, including "improved" rotational grazing strategies, different vegetation cover, and chronosequences of cropland to grassland or forest restorations indeed found that the fastest soil organic matter accumulation indeed occurred in the cropland conversion to grassland or forest treatments (Conant et al., 2001). Additionally, carbon accrual in these restorations occurred fastest in the first forty years following conversion, and in the top 10 cm of soil (Conant et al., 2001).

SOM quality, as opposed to quantity, is often defined by how easily it is mineralized. Recently inputted materials with low lignin to nitrogen ratio, exposed to less chemical and physical processing, not adsorbed onto minerals or protected within aggregates are often used as examples of high quality SOM in conceptual models. Whether the soils at

my study site appreciably accumulated carbon and nitrogen that was lost in response to a heavy mid-contract management disking treatment is an uncertainty that I address by measuring total carbon, Solvita carbon (which is a measure of the high quality, labile SOM, and microbial fraction), nitrogen, and phosphorus. I also measured aggregation to assess whether the various treatments significantly altered this potential SOM-storage structure, using soil undisturbed for at least 80 years from between rows of shelterbelt trees at the southern edge of the study area as a comparison. This soil also served as a potential measure of soil carbon that the soil could store at their saturation point.

While the effect of tillage on soil carbon, nutrients, and the microbial community that rely on these resources is well studied, burning has a less well understood mechanistic effect on the belowground (e.g., Michelsen et al., 2004; Preston & Schmidt, 2006). Fire volatilizes potential future aboveground litter inputs, and may accelerate belowground inputs through increased root necromass and labile inputs meant to stimulate microbial mineralization of nutrients needed for regrowth (Michelsen et al., 2004). Fire also keeps at bay woody encroachers that may alter soil physical, chemical and biological properties (e.g., Haugo et al., 2013) Recalcitrant "black carbon" or "biochar" inputs resulting from high intensity, low oxygen condition fires could confer added nitrogen and water retention, altered pH, water repellant soil surfaces and decomposition-resistant soil carbon (Hamer et al. 2004; Preston & Schmidt, 2006; Zimmerman, 2010).

The effect of interseeding with a high diversity seed mix –or any of the treatments eliciting higher aboveground diversity –on the soil is difficult to predict. The positive effect of plant diversity on soil organic matter accumulation has received empirical

support in recent years (e.g., Zavaleta et al., 2010; Eisenhauer et al., 2013) although disentangling the complex linkages between aboveground and belowground species and functional diversity, and how these relationships influence soil carbon, is not yet fully understood (de Deyn and Van der Putten 2005; Bradford et al., 2014).

Even less is known about herbicide effects on soil functioning (Bunemann et al., 2006; Rose et al., 2016) largely due to the lack of empirical studies. The evidence that does exist shows small and ephemeral effects on soil biota, with responses specific to the class of herbicide, taxa, and process of interest (Rose et al., 2016). Glyphosate, belonging to the glycine class of herbicides, is the most widely used herbicide on earth (Duke and Powles, 2008) and was the herbicide used in my study. It is non-selective (for photoautotrophic taxa), has high sorption affinity (i.e., strongly binds to soil minerals), and easily undergoes xenobiotic transformation (i.e., it is biodegradable; Rose et al., 2016). Soil microbial growth is apparently unaffected *in situ* at typical application rates (Drouin et al., 2010), and may even stimulate microbial soil respiration (personal communication with J. Megan Steinweg). This could be due to higher microbial respiration of recent root necromass, or from microbial breakdown of glyphosate through xenobiotic "co-metabolism" (i.e., "accidental" metabolism that does not support growth, cellular repair, or reproduction).

4.1.2 Microbial Community Structure and Function

Relative to the rest of the ecosystem, microbial biomass (i.e., bacteria, fungi, protists, archea) is small, yet their transformations of materials and energy in the rhizosphere

influence whole ecosystem functioning (Alphei, 1996; de Deyn and Van der Putten 2005). Microbiota mineralize nutrients for plant uptake, permanently reduce reactive nitrogen in the system, remediate toxins, alter gas and water flow around roots by increasing soil aggregation (Jastrow, 1987; Kennedy, 2005; Kibblewhite et al., 2008), and are a food source for soil fauna, like protozoa and nematodes (Griffiths, 1990). Plants exude up to 40% of their fixed carbon (C) into the rhizosphere as easily decomposable carbon, which is the major "currency" for the belowground system (Lynch and Whipps, 1990; Brussard, 2012). Most soil microbes are found concentrated within 2 - 5 mm of plant roots (Kennedy, 2005), and their activity in turn influence aboveground functioning (de Deyn and Van der Putten 2005), creating complex linkages between the aboveground and belowground.

Hydrolytic extracellular enzymes are excreted by the microbial biomass to cleave nutrient and carbon molecules from soil organic matter for uptake, mediating belowground energy and nutrient cycling, and reflecting relative nutrient and carbon limitations of the microbial community as a snapshot in space and time (Sinsabaugh and Shah, 2011). Extracellular enzymes are targeted, accelerating the hydrolysis reactions of specific types of bonds, e.g., sulfatases cleave carbon-SO₄²⁻ bonds in organic molecules. While they are energetically expensive to produce, especially in low nitrogen environments (enzymes are proteins), extracellular hydrolytic enzymes play an essential role in the accessibility and uptake of nutrients and carbon to the microbial biomass. The abundance of different extracellular enzymes in the soil combined with soil nutrient status and microbial community structure provides insight into microbial community functioning and potential outcomes for the aboveground. By conducting enzyme assays at multiple temperatures, I

can also calculate Q_{10} (the reaction rate sensitivity to an increase of 10 ° C) in response to the management treatments. These provide additional insight into soil carbon quality dynamics, because more biochemically recalcitrant soil carbon should be more temperature sensitive (have a higher Q_{10}) (Conant et al., 2011). The enzymes I measured included two carbon acquisition enzymes, a nitrogen, a phosphorus, and a sulfur acquisition enzyme (Table 4.1).

In conjunction with measuring soil carbon and nutrients, I tested the hypothesis of whether microbial community structure and function responded differently in response to the four management practices due to their different mechanisms of actions, using microbial PLFA and extracellular enzyme assays to assess microbial structure and function, respectively.

4.2 METHODS

4.2.1 Study area

The study site is located approximately 2 km southeast of Anncar, Nebraska (Holt County; 42°47'26.83"N, 98°43'29.57"W) on 220 ha of privately owned land enrolled in the Conservation Reserve Program (CRP). Mean annual air temperature was 8.61°C, and 10.83°C in 2014 and 2015 respectively. Annual precipitation (cumulative) was 51.35, 60.86 cm in 2014 and 2015, respectively (High Plains Regional Climate Center, 2017). Land cover is mixed and tallgrass prairie, and according to aerial imagery the study area was under center pivot rowcrop agriculture in 1983 and what appears to be non-center pivot cropland in 1954 (USGS EarthExplorer, 2017; Figure 4.1).

The field was enrolled into CRP likely sometime between the late 1980s and 1990s, and was continuously enrolled throughout the duration of the study. Prior to enrollment, there is aerial imagery evidence that the field was under irrigated rowcrop agriculture (Figure 4.1), and prior to that, dry land rowcrop agricultural cover as far back as 1946. Along the southern border of the field, there are trees planted in two rows to form a windbreak, with a ~30 m interspace between the rows that was untilled and uncultivated since at least 1946 according to aerial imagery (Figure 4.1), but possibly 1930 (according to conversations with a local landowner).

The study site is bordered to the south by a windbreak composed of mixed deciduous and eastern redcedar trees, to the east by privately owned rangeland, to the north by CRP grassland and food plots and deciduous woody riparian vegetation along Niobrara river, and to the east by an irrigated corn-soybean rotation. Eastern redcedar windbreaks partially border the field along the middle portion of the east border, and the most easterly edge of the northern border. Biennially planted winter wheat firebreaks border the entire study area.

Soils at the site are of Eolian sands parent material. The dominant soil associations at the site are Valentine-Dunday loamy fine sand, Simeon loamy sand, and Valentine fine sand. Together, their typical profiles are an A-horizon ($\sim 0-30$ cm), a possible AC-horizon (18 -36 cm), and a C-horizon (36-200 cm). Slope on the field ranges 0-9%. Fine and loamy sands dominate the upper horizon, with sand more commonly found at lower horizons (> 15 cm). This soil series is excessively drained, with little to no frequency of

flooding or ponding, low available water storage in the profile, and is classified as non-saline $(0.0 - 0.2 \text{ mmhos cm}^{-1})$ (Soil Survey Division Staff, 1999).

4.2.2 Treatments and Experimental Design

In summer of 2012, the entire study site was emergency hayed in response to the 2012 drought. In fall of 2012, the 220 ha field was divided into nine areas separated by windbreaks planted with winter wheat. In each of these nine sections, a 2.4 ha plot was lightly disked and seeded with a CP42 pollinator seed mix (exact mix unknown; conversation with Nebraska Game and Parks agency personnel) using a drill seeder at the NRCS recommended seeding rate. The rest of the site was planted with a standard CRP tallgrass prairie seed mix (CP25 mix, 15 species) using a drill seeder at the NRCS recommending seeding rate (~40 seeds ft⁻¹).

In April 2014, I applied three additional treatments to the study site in a complete randomized block design, with nine 20 m x 20 m blocks in each of the nine sections made by the interseed plots and firebreak design in the field, and each block containing four plots assigned to the three treatments plus a control (Figure 4.2). Treatments consisted of: 1) burning, 2) disking, and 3) herbicide application. The herbicide replicates were sprayed on April 14, 2014 with a glyphosate herbicide 32 oz acre⁻¹, or at half-label-rate (which is generally as effective as full label rate; Knezevic, 2008). The burn replicates were burned on April 17, 2014. The temperature was 6 ° C, relative humidity was 30%, and wind speed was 13 MPH. The disk replicates were heavily disked to > 30 cm on April 20, 2014 with a disc harrow pulled behind a tractor. The mid-contract management

treatments ("burn", "disk", "herbicide", "interseed") were arranged with nine 20 m x 20 m replicates of field matrix that served as a control ("C") (Figure 4.2).

4.2.3 Sample Processing

A composite sample of ten cores (diam: 2 cm; depth: 10 cm) were taken from treatment and control replicate plus the windbreak interspace (herein "N" for native) for soil carbon, Solvita C, soil N, soil P, PLFA, and extracellular enzyme analysis. For the aggregate mean weighted diameter analysis samples, I cored deeper (depth: 20 cm) and wider (diam: 10cm), using a dutch style auger designed for sandy soils (SoilMoisture Equipment Corp., Goleta California) and collected four composite cores instead of ten at each field replicate due to the greater depth and diameter of the auger to achieve a representative sample without removing overly large samples.

Samples were collected at following times for soil carbon and phosphorus; August 2014 and August 2015; aggregation and extracellular enzymes: August 2015; soil nitrogen and microbial PFLA: May 2014, August 2014, and August 2015. Upon collection, samples were stored at 4 ° C and split into equal subsamples with one transferred to University of Nebraska-Lincoln and the other transferred to Ward Laboratories, in Kearney, NE. Upon arrival in Lincoln they were pushed through a 2.00 mm sieve (or 4.75mm in the case of the aggregation samples), and mineral and organic fragments or the rare mineral fragment on the mesh surface were discarded. Samples were stored at 4 ° C until analysis for extracellular enzymes or aggregation.

Soil samples at Ward Laboratory were subdivided. One subsample was stored at –20 °C until the time of lipid PLFA extraction. The other was stored at 4 °C until analysis for soil carbon, and H3A inorganic nitrogen (NO₃ and NH₄), inorganic phosphorus, and Solvita carbon analysis. No inorganic carbon (CaCO₃) was present in the soil, using standard methods (Allison and Moodie, 1965), so total organic carbon is equal to total carbon (presented here as percent carbon).

4.2.4 Laboratory Analysis – H3A Nitrogen, Phosphorus, Total Percent C, Solvita C

Total inorganic nitrogen, nitrate, ammonium, and phosphate were analyzed according to Haney et al., (2006) and modified by Haney et al. (2010) (the so called "H3A", method after the authors). Four grams of soil were placed in a 50 mL centrifuge tube and a mixture of 40 mL of the following extractant was added: 2 g L⁻¹ lithium citrate, 0.6 g L⁻¹ citric acid, 0.4 g L⁻¹ malic acid, and 0.4 g L⁻¹ oxalic acid. The mixture was shaken for 5 minutes and then filtered through a cone fitted with Whatman 2V filter paper. The filtrate was divided for total inorganic nitrogen and phosphorus. Ammonium, and nitrate were analyzed in the filtrate using an IO Analytical rapid flow analyzer (RFA, colorimetric). Units were expressed as ppm (mg nitrogen as nitrate or ammonium per kg dry soil). Phosphate in the filtrate was analyzed using a Varian Vista-MPX axial flow ICP (as mg phosphorus per kg dry soil). Total soil carbon was analyzed on a Tru Mac LECO as expressed as percent carbon on a dry soil basis.

Solvita carbon burst methods were conducted according to Franzluebbers (2015). 100 grams of 4.75 mm sieved soil, oven dried (60 ° C for two days) soil was wetted to 50% water filled pore space and placed into a sealed jar containing a 10 mL vial of 1 M NaOH

(CO₂ trap) and a vial of water to maintain headspace humidity. Jars were incubated for three days at 25 ° C. Blank jars with vials of 1 M NaOH were included for every 25 samples. Following the incubation, the NaOH vial was removed and sealed until titration, at which point 1.5 M BaCl₂ solution was added to precipitate the CO₂ as bicarbonate (BaCO₃), along with phenolphthalein as a color indicator that binds to the bicarbonate. The vial was placed on a stir plate with a mini stir bar to mix the solution as 1 M HCl was slowly added to return the solution from pink to clear. CO₂ (mg C kg ⁻¹ soil) was calculated using the following formula:

$$CO_2 = (mL_{[blank]} - mL_{[sample]}) \times N \times M / S$$

Where $N = \text{normality of acid (mol L}^{-1})$, $M = \text{mass conversion from cmol}_c \text{ to g C}$, and S = soil weight (i.e., 100 g).

4.2.5 Laboratory Analysis - Aggregates

A 10 g subset of soil was oven dried for two days at 40 ° C to determine soil moisture. The rest of the field moist soil samples were cold air dried under low humidity (~20%) at 4 ° C until they reached gravimetric water content of 100 g water kg⁻¹ soil (approx. 7-14 days) based on methods described by Sainju (2006). I used this cold air drying method rather than oven or air drying to reduce potential microbial activity that might affect aggregation by decomposing carbon substrates adhering aggregates. I used the dry sieving method of aggregate separation based on methods described by Schutter and Dick (2002) and Sainju (2006) rather than wet sieving to protect delicate aggregates in the sandy soils. I placed 100 g soil on nested sieves (diam.: 20 cm) on a Retsch AS 300 Control 8" Sieve Shaker Table (Palm Bay, FL) to capture large macroaggregates (> 4 mm mesh), macroaggregates (2-4 mm mesh), small macroaggregates (2.00-0.25 mm mesh),

and microaggregates, silt, and clay (< 0.25 mm mesh). The nested sieves shook at 200 oscillations minute⁻¹ for three minutes. The (negligible) fragments of identifiable vegetation/litter retained on the topmost sieve were discarded. The retained fractions were weighed, air-dried and stored at room temperature for potential future analysis of total C and N (pending; not presented here).

Mean weighted diameter (MWD) of aggregates was calculated using the following equation, where \bar{x}_i is the mean diameter (mm) of that soil aggregate size fraction and w_i is the proportion of each aggregate relative to the total weight of the sample (g):

$$MWD = \sum_{i=1}^{n} w_i \, \bar{x}_i$$

Samples with less than 90% recovery on a mass basis were discarded from the analyses

4.2.6 PLFA - Laboratory Analysis

The phospholipid fatty acid (PLFA)/fatty acid methyl ester (FAME) extraction and analysis I used was according to methods from Clapperton et al. (2005). 9.5 mL of a dichloromethane:methanol:citrate buffer (1:2:0.8 v/v) was added to each 4 g dry weight equivalent frozen soil sample in a test tube, and shaken for two hours. After the two hours was complete, 2.5 mL dichloromethane and a 10 mL saturated NaCl solution were added to each of the test tubes, which were then shaken for an additional five minutes. Tubes were centrifuged for ten minutes at 3000 RPM, and the organic fraction transferred to new vials. Five mL of a methanol:citrate (1:1 v/v) solution was added to the original samples in the test tubes, and the mixture was again shaken for 15 minutes and

centrifuged for ten minutes at 3000 RPM. The organic fraction was combined with the organic fraction extracted earlier in the corresponding vials. The organic fractions were dried in a fume hood under heat (37 ° C) and a flow of N_2 gas. 2mL of dichloromethane was added to the dry samples to dissolve the organic fraction for storage at -20 ° C and eventual analysis (within 14 days). Samples were loaded into silica gel columns, pipetting dichloromethane into the vials to rinse any residual sample from the vial into the column. Lipid-class separation was conducted as follows: neutral, glycolipids, and phospholipids fractions were eluted using sequential leaching with ~2 mL dichloromethane, 2 mL acetone or methanol, respectively. The neutral and phospholipids fraction was retained in separate vials, and glycolipids fraction discarded. The phospholipid and neutral fraction samples were dried in the hood under heat (37 ° C) and a flow of N_2 gas and then dissolved in ~2 mL of methanol or dichloromethane, respectively, and stored at -20 ° C.

Fatty acid methyl esters analyzable on a gas chromatograph (GC) were generated from these samples through mild acid methanolysis. The neutral and phospholipid fractions were thawed and again dried in the hood under heat (37 ° C) and N_2 gas flow, and all samples in their vials received ~1 mL methanol/ H_2SO_4 (25:1 v/v) and were placed in an oven for ten minutes at 80 ° C. After removal from the oven, samples were left to cool to room temperature upon which they received 2 mL hexane, were vortexed for thirty seconds, and left to sit for five minutes. After five minutes, settling allowed the aqueous fraction of the mixture to be removed carefully and discarded. After adding 10 μ L methyl nonadecanoate fatty acid (19:0; Sigma Aldrich), samples were dried in the hood under

heat (37 ° C) and a flow of N_2 gas. Fifty μL hexane was added to the dried samples, which were immediately transferred to 100 μL glass inserts placed into a GC vial.

Samples were analyzed using a flame ionization detector, a 50-m Varian capillary Select FAME # cp7420, and helium as the carrier gas (30 mL min⁻¹). 2 μL samples were injected at 5:1 split mode at 250 °C, and the flame ionization detector was held at 300 ° C. The oven was held at 140 ° C for five minutes, raised to 210 ° C at a rate of 2 °C min⁻¹, at which point the heating rate was increased to 5 ° C min⁻¹ until the temperature reached 250 ° C, and then held at 250 ° C for twelve minutes. Peak identification was conducted by comparing retention times to the standards (Supelco Bacterial Acid Methyl Esters #47080-U, and MSJ Biolynx #MT1208 for 16:1ω5). The 19:0 standard peak values was used to calculate relative area under specific peaks corresponding to known PLFAs to determine abundance of PLFAs in each sample. The nomenclature for PLFAs is as follows: the number of carbon atoms, followed by a colon, followed by the number of double bonds, the lower case omega (ω) , and the position of the first double bond from the methyl end of the molecule. If stable cis and trans configurations of the PLFA molecules (isomers) exist, they are indicated with c or t. Methyl and hydroxyl groups are indicated with (meth) and (OH) before the number of carbon atoms, and if the PLFAs are isoforms or anteisoforms, an "i-" or "a-", respectively, is added at the beginning of the name. The PLFAs we measured and the microbial groups to which they are assigned can be found in Table 4.2. The abundance of PLFAs was reported as ng PLFA g⁻¹ soil. 16:1ω7c:cy17:0 and 18:1ω7c:cy19:0 were used to calculate the ratio of monounsaturated to cyclounsaturated PLFAs, and gram-negative to gram-positive ratios, bacteria to fungal ratios, and community structure were calculated from PLFAs in Table 4.2.

4.2.7 Extracellular Enzyme Activity

Modifying a protocol developed by Steinweg and McMahon (2012), I mixed 1.375 g of soil with 45 mL of 50 mM sodium acetate buffer with a pH adjusted to match that of the soil sample (~5.5-7) in a metal cup (vol: 475 mL) using a Cuisinart® SmartStickTM immersion hand blender on high for 60 seconds. The soil solution was placed on a weigh boat with a stir bar on a stir plate at medium rotations to keep the solution suspended and then pipetted into deep-well plates using a multichannel pipette. Fluorescently-tagged substrates BG, CB, NAG, P, and S (see Table 4.1 for descriptions) were added to in excess in order to measure potential activity.

The deep-well plates containing the soil sample solution and substrate were covered, shaken gently on a shaker table for two minutes, and incubated at 35 ° C for 1.5 hours. The same was repeated for an additional replicate at 20 ° C but for 4.5 hours to maintain equal degree hours. The fluorescent tags on the substrates only absorb electromagnetic radiation and fluoresce when separated from the substrate, which occurs when extracellular enzymes catalyze the mineralization of the fluorescently labeled substrate. Using a plate reader, I analyzed the amount of fluorescence emitted by the incubated slurries. Known amounts of fluorescent substrate 4-methylumbelliferone (MUB) was added to a concurrent set of standard plates to account for natural fluorescence in the soils, and data from samples with corresponding high slope, low slope, and total slope standard curves below a threshold ($R^2 < 0.999$) for any temperature were discarded and both samples and standards were resampled at both temperatures. I used the standard Q_{10} formula to

determine the temperature sensitivity of the reaction i.e., the ratio of rate increase with a temperature increase of 10 degrees:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10^{\circ}/(T_2 - T_1)}$$

I assessed potential enzyme activity rate in μ mol activity g soil⁻¹ h⁻¹ at the high laboratory incubation temperatures (35 ° C), and calculated Q₁₀ using enzyme activity rates (μ mol activity g⁻¹ soil h⁻¹) at the low (25 ° C) and high (35 ° C) assay incubation temperatures.

4.2.8 Data Analysis

I assessed the effect of year, treatment, and block on percent soil carbon (% C), labile carbon (Solvita C), soil inorganic N (H3A NO₃, H3A NH₄, and total inorganic H3A nitrogen which is the sum of H3A NO₃ and H3A NH₄), soil P, aggregation, PLFA biomass, ratio of PLFA fungal to bacterial ratios, and enzyme dynamics using an analysis of variance (ANOVA). Prior to analysis, I checked normality of residuals using a visual inspection of applots. If heteroscedasticity was present, I used a Box-Cox (Box and Cox, 1964; Osborne, 2010) transformation. Significance was decided a priori as P < 0.05, with nominal significance set at P < 0.1. My study design was a randomized complete block design with only one replication per block by treatment combination, meaning I had no way to directly measure experimental error. As a result, I applied the Tukey 1-df test for non-additivity to make sure the block-treatment interaction was not significant and that the means square error (error variance) could be used to estimate experimental error. When the Tukey 1-df rejected the null hypothesis (i.e., P < 0.05), I included block as an explanatory variable; otherwise I assumed that treatment alone was a sufficient explanatory variable.

To generate the model residual and predicted values needed to test assumptions, I first performed an analysis of variance using treatment, time, and block as the explanatory variables. I used a Shapiro-Wilk normality test of residuals (significance level set at P < 0.05) and visual inspection of the plot of residuals versus predicted values (the latter of which, in this case of a complete randomized block design, are the sum of the overall mean) to assess whether errors were normally distributed. In the second ANOVA (without or without block; depending on the Tukey 1-df test for non-additivity), if treatment was significant (P < 0.05) or nominally significant (P < 0.1), I performed a Tukey HSD as a post-hoc analysis to find which treatment means were significantly different from one another.

4.3 RESULTS

There was no evidence to include block in the models (because I did not reject the null hypothesis of Tukey's 1-df test for non-additivity) for percent carbon (P = 0.09), H3A total nitrogen (P = 0.08), H3A nitrate (P = 0.43), H3A ammonium (P = 0.30), and phosphorus (P = 0.31). There was however evidence non-additivity for Solvita C (P < 0.001), and I included block in that ANOVA as an explanatory variable.

Almost immediately following treatment (the first samples were collected within two weeks of treatments) inorganic nitrogen (mostly in the form of NO₃⁻) was significantly elevated in the herbicide treatments relative to other treatments and controls. Total H3A inorganic nitrogen and H3A NO₃⁻ were highest in the first two sampling periods (spring and summer 2014) and declined in the summer 2015. H3A NH₄⁺ was much lower than

H3A NO₃, and did not vary significantly over time. The ANOVA assessing total H3A inorganic nitrogen showed that treatment and time were significant (P < 0.01)explanatory variables. A post-hoc Tukey HSD analysis revealed differences between the herbicide versus control and the herbicide versus disk H3A total inorganic nitrogen treatment means (see Appendix I) (Figure 4.3). There were also nominally significant differences (P < 0.1) between herbicide versus burn, and interseed and control disk H3A total inorganic nitrogen treatment means. Unsurprisingly (total H3A inorganic nitrogen is the sum of NO₃ and NH₄⁺), I found a similar pattern for H3A NO₃ (Figure 4.4) and NH_4^+), (Figure 4.5). Treatment and time were significant explanatory variables for H3A NO_3^- (P < 0.01) and treatment was a significant explanatory variable for NH_4^+ (P < 0.01). A post-hoc Tukey HSD analysis revealed differences between herbicide versus control and herbicide versus disking for H3A NO₃ treatment means (see Appendix I). The only significant difference treatment means for H3A NH₄ occurred between interseed versus burn, and I found nominally significant differences between the interseed versus control, interseed versus disk, and herbicide versus burn treatments means. Neither time nor treatment was a significant explanatory variable for total soil phosphorus.

Soil carbon did not vary over time (P = 0.67), and while treatment was significant (P = 0.05) soil carbon was only slightly higher in the herbicide treatment relative to the disking plot, and (nominally) higher relative to the control in the post-hoc Tukey HSD (see Appendix I) (Figure 4.6). Soil carbon in the control and treatments was lower (\pm SE) $0.65 (\pm 0.02)$, versus the windbreak interspace, which had an average percent soil carbon of $1.65 (\pm 0.14)$. Neither time nor treatments were significant explanatory variables for Solvita carbon, but block was (P < 0.01), with higher carbon in blocks 1, 4, and 7 (the

southern most blocks that are closest to the nearest road and farthest from the Niobrara) (Figure 4.7). There was no evidence to include block in the ANOVA for aggregate mean weighted diameter (Tukey 1-df Test for non additivity P value of 0.73). However, treatment was not a significant explanatory variable in the ANOVA (P = 0.15). The windbreak interspace soils did not differ in their mean weighted diameter from that of the control and treatment soils.

Even though it appear as though there was a decline in fungal to bacterial ratios in the herbicide treatment in summer 2014 and 2015, it was not captured by this analysis, which found no differences in fungal to bacterial ratios in response to treatment or over time (Figure 4.8). PLFA biomass, however, was significantly higher in the interseed treatment relative to the control treatment, and nominally higher biomass in the interseed relative to the disk (see Appendix I for post-hoc Tukey HSD analysis results) (Figure 4.9). There was no evidence to include treatment block in the PLFA ANOVAs, because I did not reject the null hypothesis of Tukey's 1-df test for non-additivity for microbial PLFA (P = 0.101) or for the fungal to bacterial biomass (P = 0.2509). Treatment was a significant explanatory variable in the ANOVA for microbial PLFA biomass (P = 0.01).

The herbicide treatment shift microbial functioning towards higher CB and especially P activity. There was no evidence to include treatment block in the following enzyme activity ANOVAs, because I did not reject the null hypothesis of Tukey's 1-df test for non-additivity for BG activity (P = 0.22), NAG (P = 0.42), P (P = 0.22), and S (P = 0.08). I did include block for CB, because I rejected the null hypothesis of Tukey's 1-df test for non-additivity (P = 0.045). Treatment was not a significant explanatory variable

for BG in the ANOVA (P = 0.11) or NAG (P = 0.33). Treatment was significant for P activity (P < 0.01), S activity (P = 0.04), and nominally significant for CB (P = 0.054). Block was not a significant explanatory variable in the CB ANOVA (P = 0.37). A post-hoc Tukey HSD analysis for CB activity (see Appendix I) showed significant differences between the herbicide versus disk, and nominally significant differences between the herbicide versus interseed treatment means yet did not show meaningful differences among blocks even though that explanatory variable was included in the ANOVA (Figure 4.10). The post-hoc Tukey for P activity showed significant differences between in the herbicide versus burn, herbicide versus disk, and herbicide versus interseed treatments, with nominally significant differences between the herbicide versus control treatment means. The only significant difference for S activity was in the disk versus control treatment means (see Appendix I).

The burn treatment significantly reduced Q10 for BG, CB, and NAG relative to other treatments, indicating higher labile carbon in response to that treatment. There was no evidence to include treatment block for any of the enzyme Q10 ANOVAs, because I did not reject the null hypothesis of Tukey's 1-df test for non-additivity for BG Q10 (P = 0.83), CB (P = 0.26), NAG (P = 0.72), P (P = 0.97), or S (P = 0.56). Treatment was significant for Q10 for BG (P = 0.01), CB (P = 0.01), NAG (P < 0.01) but not for P (P = 0.21) or S (P = 0.14). A post-hoc Tukey HSD showed significant difference between the burn versus disk treatment means for BG, the burn versus herbicide treatment means for CB, burn versus herbicide and disk treatment means for NAG, and nominally significant (P < 0.1) differences between the interseed versus disk means for NAG (see Appendix I).

4.4 DISCUSSION

The different mid-contact management practices influenced soil differently, as I hypothesized, but in some unexpected ways. Disking did not select for bacteria over fungi or appreciably drive declines in soil carbon. Soil carbon also did not increase over time, even though higher levels in the windbreak interspace indicated that they are far from potential carbon (C) saturation points. Instead, the herbicide treatment most strongly and surprisingly influenced the belowground by eliciting high soil inorganic nitrogen, likely through suppressed plant uptake, mineralization of root necromass, and/or glyphosate induced priming of soil organic nitrogen.

Soil C, both total C and the Solvita C (a measure of labile C) fraction, did not change appreciably over time. While soil carbon was slightly higher in the herbicide relative to the disked plots, which represent the treatments with the least and highest bare ground, respectively, the herbicide treatment also had significantly higher mean percent carbon than the control, which had the second highest litter cover (see Chapter 3). So it is unlikely that litter cover is a driver of carbon sequestration in my study. Moreover, it is unclear whether higher soil carbon in the herbicide treatment is a result of any process that I measured. Soil carbon was also (much) higher in the undisturbed soils from the shelterbelt area in the field, yet without concurrently higher aggregation. The carbon saturation hypothesis posits that soils most depleted of carbon should store carbon fastest when they are furthest from their saturation point, which did not occur in my study, even with varying levels of disturbance to possible aggregate formation and differences litter cover. This may be attributable to low large aggregate formation, which is a mechanism for carbon storage in other studies of grassland soils but which may be inhibited in sandy

soils (Baer at el., 2010). Interestingly, the three experimental blocks closest to the windbreak had significantly higher Solvita C, perhaps indicating a legacy effect of the Niobrara River to the north or from the road or shelterbelt of trees along to the south of the study area. So it is inconclusive whether mechanisms related to lack of physical mixing disturbances are alone responsible for higher carbon in the windbreak interspace. It is therefore possible that the legacy of low soil carbon was driven by other mechanisms including fewer inputs under rowcrop systems, and activities that accelerate decomposition, like irrigation.

The elevated nitrogen in the herbicide treated is likely attributable to either lack of plant uptake upon death, root necromass turnover, microbial priming of soil organic matter in response to glyphosate, or some combination thereof. Priming is a short-term increase in microbial turnover of soil organic matter in response to relatively moderate increases in available labile substrate (Kuzyakov, 2000). If the microbial community was primed by glyphosate as a labile substrate, elevated soil nitrogen could be attributable to mineralization of SOM. Fortunately, studies examining the effect of glyphosate on microbial communities under glyphosate-resistant crops disentangle somewhat the effect of plant death from direct non-target herbicide impacts. Newman et al. (2016) found increases in Proteobacteria and attributed this to increases in members of the Proteobactera family Xanthomondacadeae. The authors noted that, because in a different study (Campbell et al., 2010) Xanthomondacadeae increased in response to fertilizer treatments, soil disturbance in general may give the taxa a competitive advantage over other microbiota. However, Campbell et al. 2010 assessed mineral nitrogen fertilization on arctic tundra microbial communities, and did not include glyphosate or glyphosateresistant plants in their assessment. Additionally, Newman et al. did not assess soil nutrient status in their study, so it is feasible that glyphosate stimulated mineralization of soil nitrogen, which in turn selected for Xanthomondacadeae (a bacteria). This line of reasoning points to glyphosate-induced priming as a potential mechanism for elevated soil nitrogen. While my statistical approach could not detect shifts towards bacterial dominance in the multiple replicates and treatments over time, it does appear that while fungi increasingly dominated the belowground in all treatments as time progressed, the trend was moderated somewhat by elevated nitrogen in the herbicide treated soils.

It also appeared that the herbicide treatment functionally shifted the belowground towards carbon and phosphorus limitation, evidenced by elevated increased production of CB and P, which are carbon and phosphorus acquisition enzymes, respectively. The phosphorus atoms in glyphosate molecules may be available for microbial uptake, which further underlines the shift away from nitrogen limitation that may have occurred in response to the glyphosate treatment. Additionally, because enzymes are nitrogen rich molecules, excess nitrogen in the herbicide treated soils could have provided additional microbial currency needed to mineralize the now non-nitrogen limiting resources from soil organic matter.

Another interesting microbial functional response was that of enzyme activity Q_{10} , which is the amount of increased reaction rate due to an increase by 10 ° C, or the temperature sensitivity of a reaction. It can be used to detect the lability or recalcitrance of soil carbon, as more biochemically complex organic matter is more sensitive to increases in temperature (Conant et al., 2011). The enzymes from the burn treatment had lower Q_{10} ,

which could be due to plants releasing labile carbon in an effort to stimulate mineralization of organic matter to release nutrients for regrowth following fire.

However, this is speculative, as I did not find concurrently higher PLFA biomass, Solvita or total C, which would support this hypothesis.

Herbicide is commonly used to control undesirable plant species. In this study, it elicited increased soil nitrogen, which may have influenced belowground community structure and more likely influenced functioning by shifting the belowground towards greater phosphorus and carbon demand. Additionally, the aboveground consequences of herbicide (discussed in Chapter 3) included higher nonnative plant abundance —a result not uncommon in response to elevated soil nitrogen. These coupled aboveground and belowground responses to the herbicide treatments reveal complex feedbacks that can arise from management practices seeking to optimize for a few ecosystem services (e.g., eliminating nuisance plant species) ultimately influencing the initial management objective in surprisingly ways.

4.5 CONCLUSION

Herbicides are the most common agricultural pesticides on earth (Grube et al., 2011), at an estimated 1.35 million metric tons per year applied by 2017. While the soil is directly and indirectly responsible for numerous ecosystem services upon which society depends for its survival and well-being, this study on a single field in the North Central Great Plains reveals how much we have yet to learn about the cryptic belowground and its role in mediating management outcomes. While soil carbon was much higher in the nevertilled windbreak interspace, the mechanism for this difference could not apparently be

explained by differences in aggregate size between the never tilled and field matrix soils. Without this understanding, managing such soils for high contents of organic matter —which is central to soil functioning and ecosystem services production —is relegated to guesswork. Fortunately, scientific knowledge of the soil system is continuously expanding, providing opportunities to test mechanisms in a variety of settings so that we can understand how best to manage soils for multiple, simultaneous ecosystem services.

4.6 TABLES AND FIGURES

Table 4.1 Extracellular hydrolytic enzymes assessed in the study, the target organic matter component they hydrolyze, and the synthetic substrate used in the assay for their assessment (MUB: 4-methylumbelliferone). Adapted from German et al. (2012) and Steinweg and McMahon 2012.

Enzyme	Target	Synthetic Substrate	
β-glucosidase (BG)	Cellulose degradation	4-MUB-b-D- glucopyranoside	
Cellobiohydrolase (CB)	Cellulose degradation	4-MUB-b-D-cellobioside	
N-acetyl-β-D-glucosaminidase (NAG)	Chitin degradation	4-MUB-N-acetyl-b-D-glucosaminide	
Phosphatase (PHOS)	Phosphate acquisition	4-MUB phosphate	
Sulfonatase (S)	Sulfate acquisition	4-MUB sulfate	

Table 4.2 The PLFA/FAME biomarkers used to assess fungi, bacteria, Gram-negative and Gram-positive bacteria, and more specific taxonomic groups

PLFA/FAME Biomarkers	Specific Group	Family	Class
10:0 2OH		Gram -	Bacteria
10:0 3OH		Gram -	Bacteria
11:0 iso 3OH		Gram -	Bacteria
12:0 2OH		Gram -	Bacteria
14:0 iso		Gram +	Bacteria
14:0 2OH		Gram -	Bacteria
14:0 iso 3OH		Gram -	Bacteria
15:0		Gram +	Bacteria
15:0 iso		Gram +	Bacteria
15:0 anteiso		Gram +	Bacteria
16:0 iso		Gram +	Bacteria
16:1 w5c	Arbuscular Mycorrhizal		Fungi
16:1 w7c		Gram -	Bacteria
16:1 w9c		Gram -	Bacteria
16:0 2OH		Gram -	Bacteria
16:0 10-methyl	Actinomycetes	Gram +	Bacteria
17:0	•	Gram +	Bacteria
17:0 iso		Gram +	Bacteria
17:0 anteiso		Gram +	Bacteria
17:0 10-methyl	Actinomycetes	Gram +	Bacteria
17:0 cyclo	•	Gram -	Bacteria
18:0 10-methyl	Actinomycetes	Gram +	Bacteria
18:1 w5c	•	Gram -	Bacteria
18:1 w7c		Gram -	Bacteria
18:1 w9c	Saprophytes		Fungi
18:2 w6c	Saprophytes		Fungi
18:3 w3c	Saprophytes		Fungi
19:0 iso		Gram -/Gram +	Bacteria
19:0 anteiso		Gram -/Gram +	Bacteria
19:0 cyclo w8c	Rhizobia	Gram -	Bacteria
19:0 cyclo w9		Gram -	Bacteria
19:0 cyclo w6		Gram -	Bacteria
20:1 w9c	Arbuscular Mycorrhizal		Fungi
20:2 w3c	j		Protozoa
20:2 w6c			Protozoa
20:3 w3c			Protozoa
20:4 w6c			Protozoa
22:1 w9c	Arbuscular Mycorrhizal		Fungi
20:5 w3c	Saprophytes		Fungi

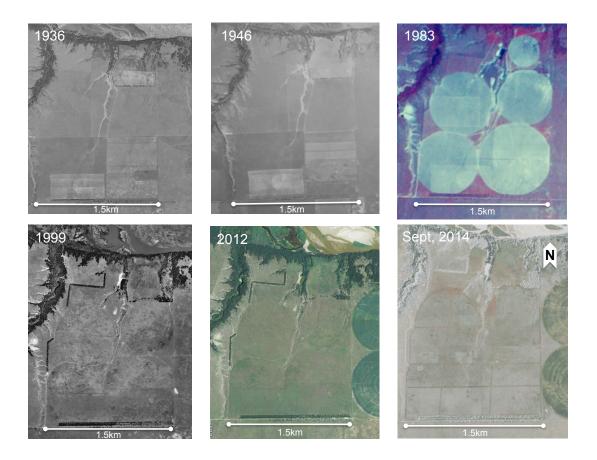


Figure 4.1 Aerial photos of the study area from USGS indicating different land use and the presence of the southern border windbreak, starting in 1936 and until 2014. The 2014 photos show the mid-contract management treatments applied in this study.

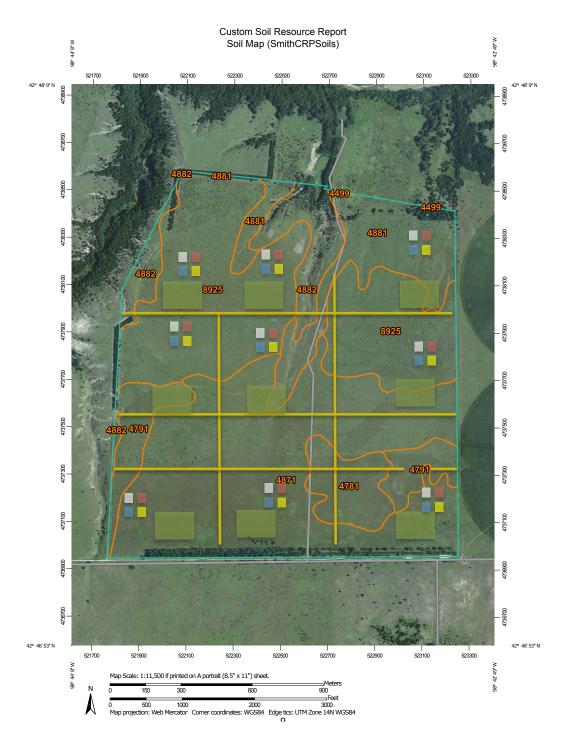


Figure 4.2 A custom soil report from the NRCS Web Soil Survey with a map of the 220 ha study area with the 2.4 ha interseed (green rectangles) and other mid-contract management treatments (20 x 20 m white, red, blue, and yellow squares) indicating the relative position and size of the nine replicates on the field. Although here they are shown

in the same order, the mid-contract management squares (save the interseed replicates) were randomized on the field. The yellow lines were planted in winter wheat in 2013 and 2014 as a firebreak. Map unit legend for the orange numbers, which indicate soil types are as follows, with percent cover of the study area in parentheses: 4499 – Dunday loam sand, 3-6% slope (0.1%); 4781 – Valentine fine sand, 0-3% slope (4.6%); 4791 –Valentine fine sand, 3-9% slope (6.3%); 4871 – Valentine-Dunday loamy fine sands, 0-3% slope (39.0%); 4881 – Valentine-Simeon sands, 3-9% slope (11.4%); 4882 – Valentine-Simeon sands, 9-30% slopes (6.9%); 8925 – Simeon loamy sand, 0-3% slope (31.7%).

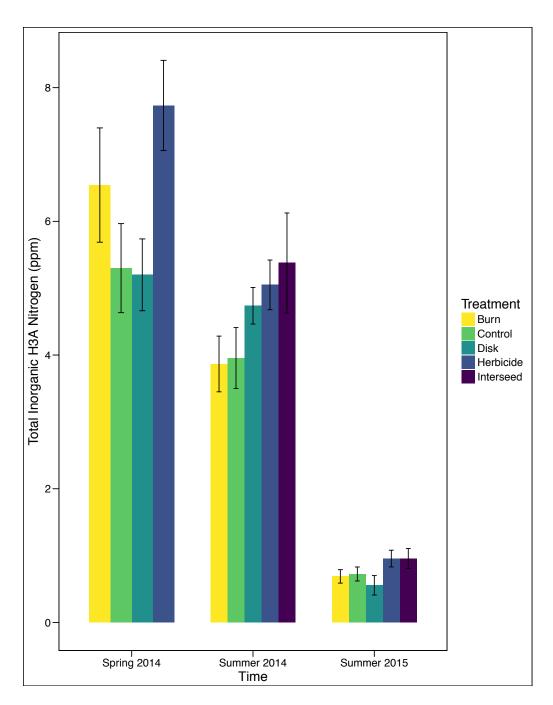


Figure 4.3 Mean H3A inorganic nitrogen (ppm) in the treatments and control from the three sampling period. Error bars are ±SE.

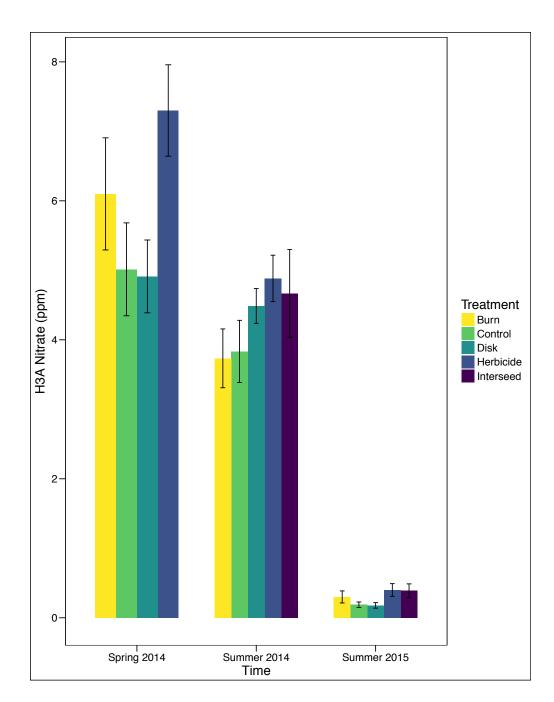


Figure 4.4 Mean H3A nitrate (ppm) in the treatments and control from the three sampling periods. Error bars are ±SE.

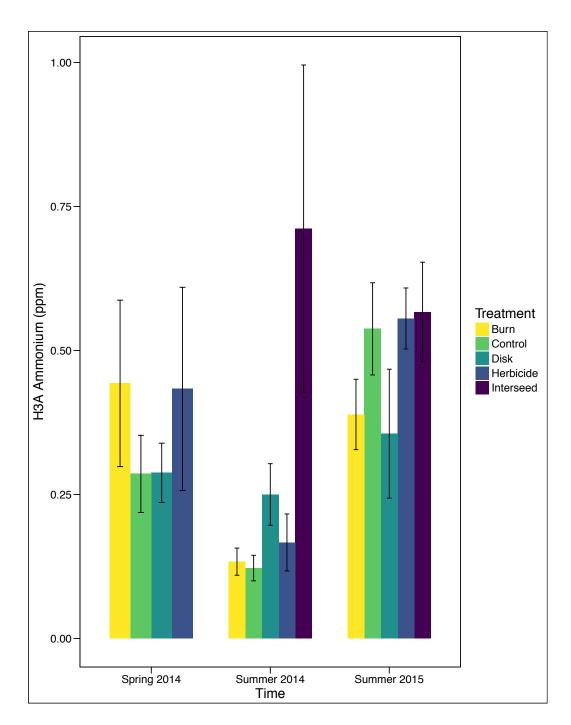


Figure 4.5 Mean H3A ammonium (ppm) in the treatments and control from the three sampling periods. Error bars are \pm SE.

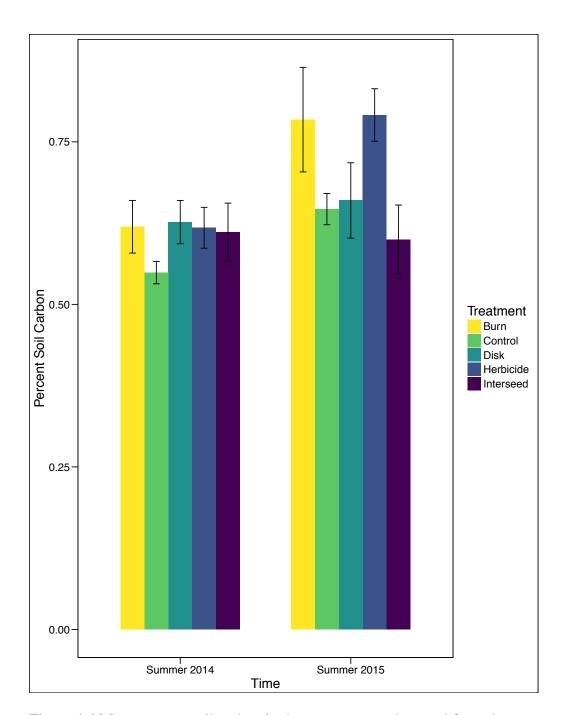


Figure 4.6 Mean percent soil carbon in the treatments and control from the summer 2014 and 2015 sampling periods. Error bars are ±SE.

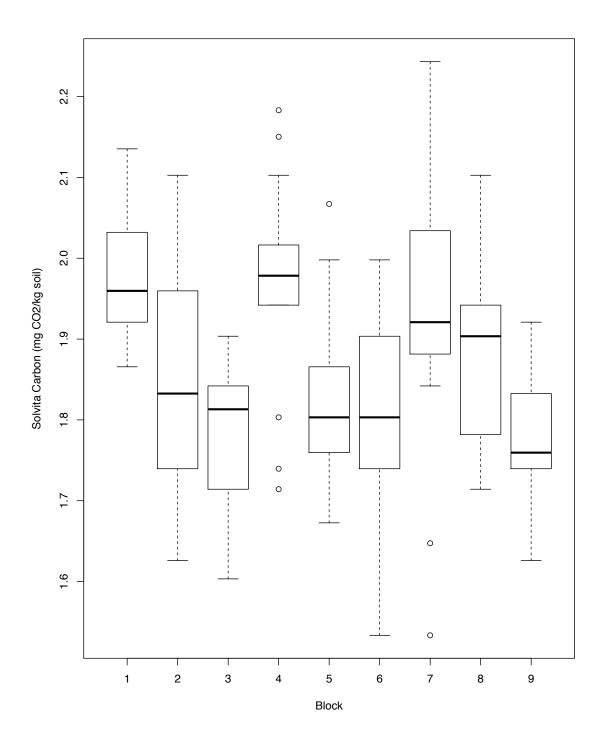


Figure 4.7 Mean Solvita carbon (mg CO_2 carbon per kg soil) in the field blocks, with all sampling periods and treatments combined. Error bars are $\pm SE$.

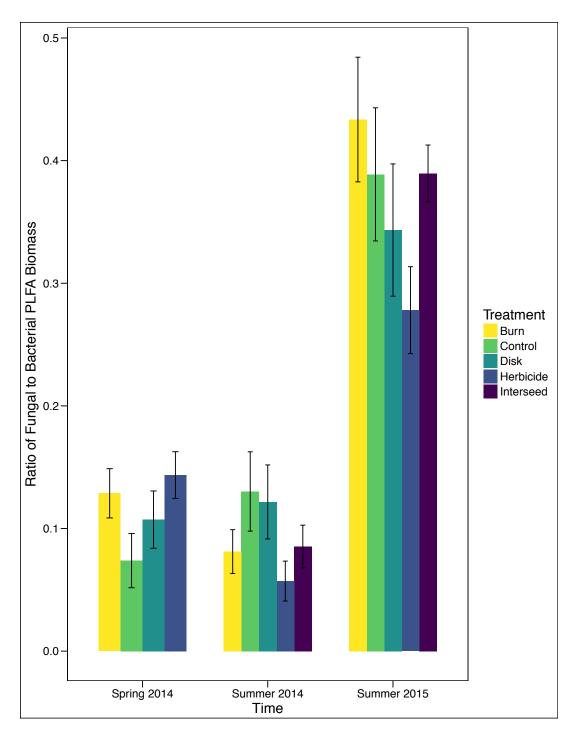


Figure 4.8 The ratio of fungal to bacterial PLFAs (ng g^{-1} soil) in the treatments and control from the three sampling time periods. Error bars are \pm SE.

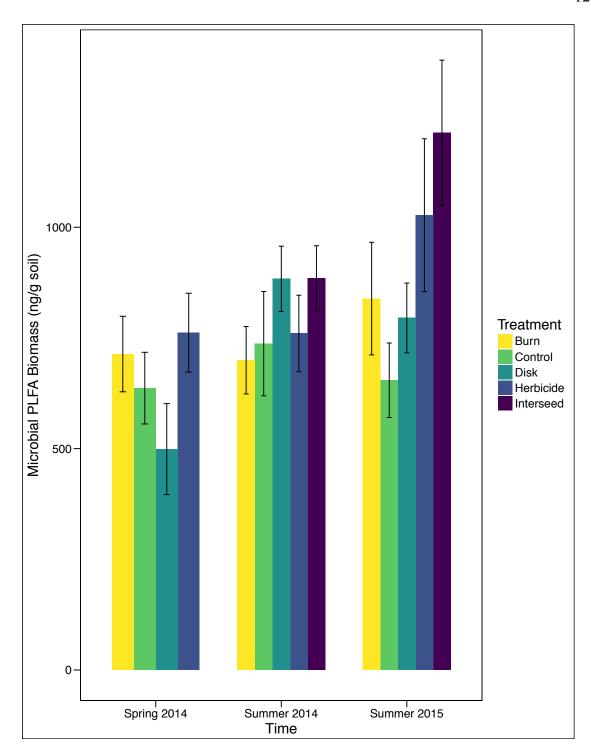


Figure 4.9 Microbial PLFA biomass in the treatments and control over three sampling. Error bars are ±SE.

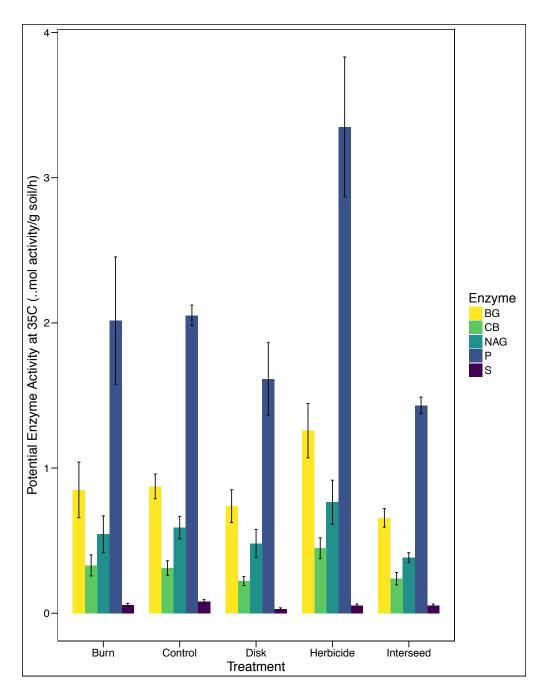


Figure 4.10 Mean enzyme activity (μ mol activity g^{-1} soil h^{-1}) at 35 ° C of β -glucosidase (BG), cellobiohydrolase (CB), N-acetyl- β -D-glucosaminidase (NAG), phosphatase (PHOS), and Sulfonatase (S) extracellular hydrolytic enzymes in the treatments and control. Error bars are \pm SE.

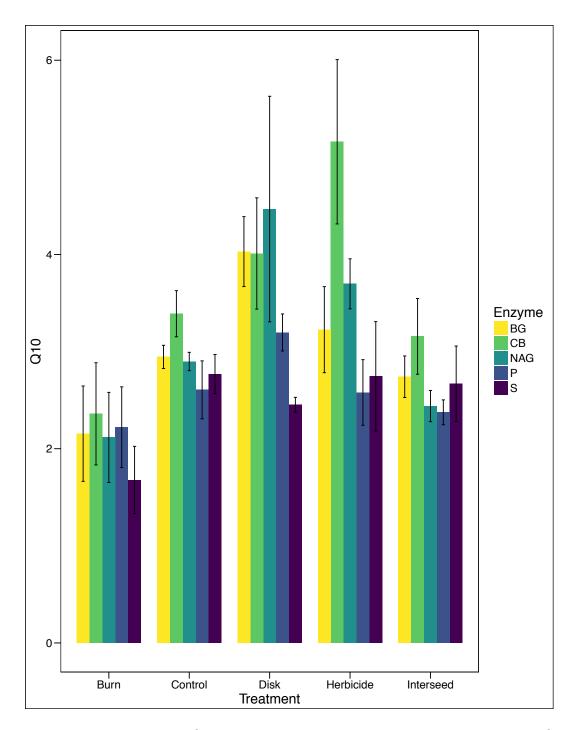


Figure 4.11 Mean Q10 of β -glucosidase (BG), cellobiohydrolase (CB), N-acetyl- β -D-glucosaminidase (NAG), phosphatase (PHOS), and Sulfonatase (S) extracellular hydrolytic enzymes in the treatments and control. Error bars are \pm SE.

5 HABITAT ECOSYSTEM SERVICES FROM THE CONSERATION RESERVE

PROGRAM

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University of Nebraska, 2017

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ABSTRACT: The Conservation Reserve Program (CRP) began in 1985 as an incentive for landowners to take marginal land out of production for the purpose of soil conservation. Yet in the years since the CRP's inception, new programs have been added to target non-soil related management outcomes. The need for species-focused management of CRP lands has become especially apparent in the case of grassland birds and pollinators, as their populations have declined throughout their historic ranges in recent decades despite 9.7 million ha of enrolled CRP grasslands. In addition to grassland birds and pollinators, the effect of CRP grasslands and management on invertebrate communities, which play a central role in ecological functioning including as a critical food source for upland game birds, is uncertain. By measuring invertebrate abundance, blooming forbs, and rearing quail chicks in situ on both the field matrix control plots and plots interseeded with a high diversity pollinator seed mix I attempted to evaluation a common management practice already being used on conservation land within the state of Nebraska for various, simultaneous habitat management objectives. Ground dwelling macroinvertebrate abundance was higher in a pollinator treatment versus the control, with lowest abundance in 2013, followed by peak abundance in 2014, and a slight decline in 2015. Forbs were higher in the pollinator versus control plots, and a blooming forb survey on other common CRP management practices showed significantly higher number of blooms and number of plants with blooms in burn treatment relative to others. A predation event reduced the statistical robustness of the bobwhite quail study, but the primary objective was to develop methodology for habitat assessment, which my methods accomplished. Nevertheless, my less-robust analysis did reveal that bobwhite quail chick weight gain was significantly higher (P < 0.05) in the pollinator treatment versus the control treatment. These results show that a single management treatment may be used to generate habitat for multiple taxa. However, while it appears that the pollinator treatment, intended to provide higher quality for the many taxa, succeeds in its objective, there remain gaps in scientific understanding that must be addressed before such results can be applied more broadly. Specifically, interseeding is typically used in conjunction with other treatments, as was the case in my study as the interseeding followed light disking, and in the year prior to my study the entire field was emergency hayed in response to a regional drought. As a result, care must be taken with the interpretation of these result.

5.1 INTRODUCTION

5.1.1 Habitat Provisioning and The Conservation Reserve Program

The Conservation Reserve Program (CRP) began in 1985 as an incentive for landowners to take marginal land out of production for the purpose of soil conservation (FSA, 2014). In the years since the program's implementation, knowledge to improve the management of natural resources has improved, and new programs have been added to target non-soil related management outcomes. Indeed, while not initially an explicit objective of the Program, its wildlife recreation benefits are estimated at \$428 million year-1 (Feather et al., 1999; Sullivan et al., 2004). As a result, and there is growing interest among policy makers, agency personnel, and private landowners to manage CRP land for multiple purposes, including wildlife habitat (FSA, 2014). The need for species-focused management has become especially apparent in the case of grassland birds and pollinators in recent decades, as their populations decline throughout their historic ranges despite 9.7 million ha of enrolled CRP grasslands (Brennan and Kuvlesky, 2005; Veech, 2006). It is increasingly apparent that simply setting land aside does not meet the diverse habitat requirements for pollinator species and grassland birds, the latter of which have shifting needs unique to specific live stages. Programs tailored to meet the needs of target species on CRP lands are widespread in an effort to retain these populations in North America (Herkert, 2009).

In Nebraska where little public lands are available for hunting access and wildlife management, there is a great deal of interest among landowners, management agencies, and private citizens to increase upland bird populations, especially game species including ring-necked pheasants, prairie chickens, and bobwhite quail. To that end, the

Focus on Pheasants program was established in 2002 in Nebraska to provide research, implementation, and learning opportunities for groups interested in improving habitat for game birds (NGPC, 2011). However, little work has been done to determine which of several possible management strategies will provide optimal forage conditions for game bird chicks. This aspect of habitat management is crucial because of the high mortality rates of young chicks (VDG, 2015). If certain management strategies demonstrably improve survival, this information has the potential to advance management of game bird populations on current CRP lands.

In their Focus on Pheasants 2011-2021 report, the Nebraska Game and Parks

Commission noted that to retain landowner cooperation, habitat management strategies

must not be aesthetically or ecologically disruptive, and to secure government funding
they must be cost-efficient and able to provide demonstrated improvements in habitat

over a no-management strategy (NGPC, 2011). On Conservation Reserve Program lands,
however, mid-contract management requirements may dovetail with those of Focus on
Pheasants.

Several studies have examined the effect of management on bird habitat indicators and residency in restored grasslands and CRP set-asides (Herkert, 2009; Veech, 2006). However, to our knowledge no research has yet assessed the effect of such treatments on weight gain and survival in upland game bird hatchlings –a critical life stage –which could serve as an essential indication of habitat quality in management plans (2015 ISI Web of Science search). The objective of this study was to address this gap, using bobwhite quail chicks as the study organism.

5.1.2 Bobwhite quail as a study organism

Though omnivorous as adults, bobwhite chicks feed exclusively on small ground-dwelling macroinvertebrates for the first three weeks of life (Taylor et al., 1999). Because they weigh only a quarter of an ounce at hatching, the chicks cannot penetrate ground litter when foraging and thus require direct access to the ground in order to forage (VDG, 2015). Studies of bobwhite quail suggest growth rates are highest and most variable in the first thirty days (Lusk et al., 2005), and by six weeks the birds have developed juvenile feathers and begin an omnivorous diet (NGPC, 2015).

Though many management strategies, including burning and tilling, increase bare ground, they may not all improve the availability of the small insects vital to the chicks survival due to insufficient vegetative cover or insect abundance (VDG, 2015). Past habitat management strategies have included expensive feed supplementation (Guthery, 1997) or caused inadvertent biological invasions that undermined manager-landowner relations (NGPC, 2011), thus making them unsustainable according to the constraints outlined by the Nebraska Game and Parks Commission's guidelines (as of 2011). As Guthery (1997) notes in his review of Bobwhite management, the cost of continuous management and feed additions are often prohibitive, and many areas, such as hayfields, which supposedly provide quail habitat are only useful for part of the year as cutting the fields eliminates a large portion of that habitat from use. Additionally, research on the potential for mid-contract management in CRP lands to improve game bird survival has been limited to surveys of wild populations, which are often not abundant enough to provide significant results.

5.1.3 Does a High Diversity CRP Seed Mix Treatment Provide Simultaneous Habitat for Multiple Taxa?

In CRP grasslands, a common management strategy is to seed mixes with high species diversity and high forb abundance to establish habitat for pollinators. Often, light disking precedes the interseeding to release resources sequestered by late successional species. This leads to higher bare ground and high biomass of ground dwelling insects.

Invertebrate communities comprise approximately 94% of all animal species, influence and indicate soil functioning (Rousseau et al., 2013; Schon et al., 2012; Stork and Eggleton, 1991) and are an integral component of soil food webs either directly as prey or indirectly through carbon and nutrient cycling (Stork and Eggleton, 1991; Wiens, 1973). Their dynamic ecological role is pronounced following disturbance such as disking and interseeding, by capitalizing on a flush of resources and rapidly increasing their overall biomass and diversity (e.g., Hodkinson et al. 2002), and playing an important role in restructuring the post-disturbance system (Gunderson and Holling 2002).

By rearing quail chicks *in situ* on both the field matrix control plots and plots interseeded with a high diversity pollinator seed mix, continuing to assess invertebrate abundance, and assessing the number of blooming forbs as a proxy for pollinator habitat, I attempted to systematically assess the value of the common management strategy used on conservation land within the state to accomplish various habitat management objectives.

The results of this study should provide better information about what type of management may be most effective in increasing brood survival, and thus the overall population, of bobwhite quail and other game birds experiencing a loss of habitat

throughout their historic ranges, and will serve as a the first type of study design for assessing ecosystem quality under a variety of management and environmental conditions.

5.2 METHODS

5.2.1 Ground dwelling macroinvertebrate

In summers of 2013, 2014, and 2015, I measured ground dwelling invertebrates in the nine replicate pollinator interseeded treatment (interseeding with a high diversity, high forb seed mix) plots and in the field matrix (control) four times, spanning early June through mid-August. In each plot, I established a 50 m transect, with a pair of pitfall traps spaced every 10 m along the transect. The pairs of pitfall traps were placed 1 m on either side of the transect. At the start of each field season, the traps were installed using a polyvinyl chloride [PVC] sleeve in the ground (diam = 1.7 cm) sleeves placed into a hole excavated by a hand auger so that the top of the PVC tubing was flush with the soil surface. This established a way to repeatedly re-sample the same traps throughout a season.

Labeled, uncapped 15 mL Falcon™ polypropylene conical centrifuge tubes were filled with ~8mL SIERRA® ethylene glycol-free antifreeze and placed in the PVC traps for a rain-free period (very light precipitation permitted) for 72 hours. More than 0.5 cm of rain accumulation resulted in a failed sampling due to potential overflow from the centrifuge tubes (decided *a priori*), but this never at any point over the three years. When necessary, I pushed vegetation and litter closer to the trap for camouflage and protection against sun and light precipitation. At the end of the 72-hour sampling period, I removed

and capped the test tubes, and covered the PVC tubes with a cork to ensure they remain free of debris in the field between sampling times. Upon return to the field house, samples were stored at 4 ° C, and processed within 4 weeks.

At the field house, samples were processed by depositing the entire sample on a plastic tray, picking individual invertebrates out of the sample using soft body tweezers, gently rinsing them free of debris and antifreeze with 75% EtOH, and transferring them to 25 mL glass scintillation vials filled with 75% EtOH. For samples containing an excess of sand, I gently poured the liquid fraction of samples between trays, "washing" them of sand and plant fragments with 75% EtOH. Once in scintillation vials of EtOH, the samples were stored at room temperature and transferred to University of Nebraska-Lincoln, where they were processed within six weeks under a dissecting scope to assess the abundance of species per replicate, combining insects from all ten traps within the field replicate. I used a one-way ANOVA to assess the effect of treatment and year on insect abundance.

5.2.2 Bobwhite quail chick weight gain

To evaluate the effect of different management strategies on bobwhite quail chick growth and survival, for eight hours each day for thirteen days in June 2015 I put hatchling bobwhite quail chicks on two 20 m x 20 m blocks within the fifth pollinator treatment and control replicates (located most centrally in the study area), for a total of four blocks. In both blocks, vegetation was clipped to < 10 cm in height to help us disentangle the effects of vegetation from insect abundance on chick weight gain and survival. I reclipped vegetation in all plots once to maintain < 10 cm height. In these 40 m² plots, quail

had access to fresh water at all times, and a 0.5 m x 20 m strip of burlap across the top of the enclosure along one side to provide shade. In each block, there were 25 chicks, identified with labeled leg bands, for a total of 100 chicks. Individual chicks served as the experimental replicates to ensure accurate measurements, limit the effects of individual mortality or extreme outliers on average group weights, and perform repeated measures ANOVA.

Chicks were transported to and from the field in cardboard boxes. Immediately upon return to the field house, chick weight was recorded using a triple beam balance. After weighing, chicks were placed in 1 m x 1 m enclosures inside of the field house with free access to water and grain, and with both direct overhead heat lamps and shade available for chicks to self regulate temperature overnight. An initial pilot study revealed that without grain available overnight, chicks lost weight, so feed was nonnative part way through the study, rendering the data unusable. The study was thus repeated with grain freely available overnight. Both during transport and overnight, chicks were kept with their own blocks. Both the outdoor plots and overnight enclosures provided well over the recommended density for pen-raised chickens of the same age (which are also significantly larger) to minimize the chance of stress-related health effects due to overcrowding (FASS, 2010).

5.2.3 Plant response to mid-contract management treatments

In summer of 2012, the entire study site was emergency hayed in response to drought. In fall of 2012, the 220 ha field was divided into nine areas separated by windbreaks planted with winter wheat. In each of these nine sections, a 2.4 ha plot was lightly disked and

seeded with a CR25 pollinator seed mix using a drill seeder at the NRCS recommended seeding rate (see appendix for species). The rest of the site was planted with a standard CRP tallgrass prairie seed mix (CP25 mix, 15 species) using a drill seeder at the NRCS recommending seeding rate (~40 seeds ft⁻¹).

In April 2014, we applied three additional treatments to the study site in a randomized block design, with nine 20 m x 20 m blocks in each of the nine sections made by the pollinator replicates and windbreak design in the field, and each block containing four plots assigned to the three treatments plus a control. Treatments consisted of: 1) burning, 2) disking, and 3) herbicide application. The herbicide replicates were sprayed on April 14, 2014 with a glyphosate herbicide 32 oz acre⁻¹, or at half-label-rate (which is generally as effective as full label rate; Knezevic, 2008). The burn replicates were burned on April 17, 2014. The temperature was 6 ° C, relative humidity was 30%, and wind speed was 13 MPH. The disk replicates were heavily disked to > 30 cm on April 20, 2014 with a disc harrow pulled behind a tractor.

The mid-contract management treatments burn, disk, herbicide, and pollinator seed mix interseeding were arranged with 20 x 20 m replicates of field matrix that served as a control. In 2014 and 2015, I sampled plant communities with two 1 m x 1 m quadrats in each field replicate twice throughout the growing season. At each field replicate, the 1 m x 1 m quadrat was placed randomly within the replicate, and item (bare ground, litter, and plant identity) and abundance (as canopy cover) was recorded. This was repeated within the field replicate for a total of two 1 m x 1m quadrats per sampling and data were combined for that field replicate (i.e., abundance per replicate was on a 2 m² basis). This

was repeated for each replicate a total of four times: twice per year in 2014 and 2015.

Nearly all plants were identified to the species level with the following exceptions, which were identified to genus level: *Ambrosia*, *Andropogon*, *Carex* (combined with *Cyperus*), *Chenopodium*, *Helianthus*, *and Solidago*. At this site, *Andropogon gerardii* and *Andropogon hallii* showed evidence of hybridization, so while they were often recorded separately, they were combined for analysis.

Each plant was assigned a grouping according to its growth habit using assignations from the USDA NRCS PLANTS Database (accessed 2016). Growth habits assignments were graminoid, forb, or shrub. Subshrubs versus shrubs are a porous delineation that I eliminated due to low numbers in each group resulting in weak statistical power. As a result, I reclassified two species (*Rosa arkansana* and *Yucca glauca*) as shrubs that are classified as subshrubs on the PLANTS database as of spring 2017.

I also counted each individual blooming forb plant, the total number of blooms, and the plants' identity (to the species level) the on each of the 20 x 20 m mid-contract treatment replicates in mid-July 2014. Blooming forb dynamics were captured only on the 20 x 20 m mid-contract management plots as a proxy of pollinator habitat because actual pollinator assessments were being conducted by a concurrent study on the 2.4 ha pollinator treatment replicates.

5.2.4 Plant response – data analysis

I used multi-model inference to assess how much variability in growth habit was described treatment, sampling year or month, location on the field (site), along with the

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null and global against which the candidate models were tested. The following

models were included in multi-model inference (MMI) frameworks, with the response

variable (Y) for each MMI as species richness, diversity, evenness, growth habit, native

status, growth duration, bare ground abundance, or litter abundance (i.e., eight MMIs in

total):

Treatment model: Y ~ Treatment

Time model: Y ~ SamplingTime

Block model: Y ~ Block

Null model: $Y \sim 1$

I used a one-way ANOVA to assess the effect of treatment on total number of flowering

plants, total number of blooms, and flowering species richness.

5.3 RESULTS

5.3.1 Bobwhite quail

On day seven one of the blocks in the control plot experienced almost 100% mortality

due to a predation event, and high mortality across all other blocks required me to pool

data and simply assess overall day six weight gain in the treatment versus the control

using a one-way ANOVA, removing the blocking and the repeated measures. This

reduced the statistical robustness of the study, but the primary objective of this study was

to develop methodology for habitat assessment, which this method describes. The coarse-

scale analysis did reveal that weight gain was significantly higher (P < 0.05) in the

pollinator treatment versus the control (Figure 4.1).

5.3.2 Ground dwelling macroinvertebrates

Ground dwelling macroinvertebrate abundance varied significantly in response to year and in response to treatment, with the lowest abundance in 2013, followed by peak abundance in 2014, and a slight decline in 2015, and higher abundance in the pollinator treatment relative to the control (Figure 4.2). Separating the datasets into individual years revealed that the higher abundance in the pollinator treatment was significant (P < 0.05) in 2013 and 2015 but only nominally significant (P < 0.1) in 2014. The pitfall traps in field pollinator treatment replicate number 8 were consistently disturbed during the sampling period, likely by a raccoon that was frequently spotted in the area during early mornings and late evenings. The perpetrator dug up PVC tubes, spilled trap contents, and disrupted the ground around the sampling area. After repeated failed efforts to establish a sampling transect in this replicate in both 2013 and 2014, I abandoned the pollinator and control replicate 8 from my study (and from all analyses).

5.3.3 Flowering plants

The models that best fit forb abundance (Figures 5.4a and 5.4b) in the multimodel inference framework were the global (AICc = 0.52) and treatment models (AICc = 0.36) (Tables 5.1 and 5.2). Time was the third best fitting model (AICc = 0.09). The summary of the treatment model revealed that the interseed treatment resulted in significantly (P < 0.05) higher forb abundance than all other treatments and control. A summary of the time model showed that forb abundance was also significantly higher in 2014 versus 2015 (Figure 3.7).

Treatment was not significant for average total number of flowering plants but it was for average number of total blooms, with significantly higher number of blooms on the burned and control plots relative to the disked and herbicide treated plots (Figure 4.5). Richness of flowing plants was also higher on the burned and control plots relative to the disked plots. Additionally, biennial *Oenothera rhombipetala* (four point evening primrose) bloomed in 2013, leading to a high abundance of blooming forbs across the entire study area.

5.4 DISCUSSION

While the hatchling bobwhite quail chicks gained significantly more weight in the pollinator treatments relative to the control in the first 6 days of their life (Figure 5.1), this result must be taken in context: the original experimental design was compromised, and *a priori* analyses were discarded in lieu of a more coarse scale analysis that, for instance, fails to accommodate outlier chicks and non-insect related field variability (blocks were combined). As a result, while this is an interesting result that supports the premise that greater abundance of ground dwelling macroinvertebrates leads to higher weight gain in bobwhite quail chicks, it should serve as a starting point for additional inquiry, rather than a guide for land management practice.

I did, however, find strong evidence that insects responded to the pollinator treatment, with consistently higher abundance in 2013 and 2015, and slightly higher abundance in 2014 (Figure 5.2). Following the drought and haying of 2012, summer 2013 invertebrate abundance was unsurprisingly low in the control and pollinator treatments, but seemed to respond to the pollinator treatment (light disking and interseeding), likely due to insects'

ability to rapidly capitalize on newly available soil resources. In 2014, restructuring of the system through increased nutrient cycling, productivity, and biological diversity likely elicited higher invertebrate biomass, especially in the pollinator treatment. This is possibly due to higher resources as a legacy of the pollinator treatment, positive feedbacks as macroinvertebrates improve and benefit from improving their habitat (e.g., enhancing decomposition or soil porosity), more bare ground and leafy forb cover, or some combination thereof. The slight trend of ground dwelling macroinvertebrates downward in 2015 perhaps supports the legacy resources hypothesis, as it indicates that as resources begin to be tied up in biomass and interactions dictating resource transfer through the ecosystem become more complex (Angeler et al., 2015), invertebrates become more scarce. In patches with slightly higher resources, this is commensurately alleviated, which could explain why the pollinator treatment continues to host higher macroinvertebrate abundance nearly three years post treatment.

While the number of species and species evenness (and, consequently Shannon Weiner diversity) did not respond meaningfully to the pollinator treatment versus the control, the treatment did result in significantly higher forb abundance (Figure 5.4a). This indicates that managing for pollinator habitat should focus on treatments that nudge the system towards forbs, because setting richness targets may be difficult to obtain. In the other treatments (the 20 x 20 m mid-contract management plots), the richness of blooming forbs diverged from the total number of blooms (Figure 5.5) (a possible indicator of the amount of pollinator food available), indicating again that species identity does not predict the abundance of traits that are of interest to managers (Chapter 3), in this case forbs for pollinator sustenance. This is an especially interesting finding because, during

the sampling period, there was a biennial flush of *Oenothera rhombipetala* (four point evening primrose), and it was apparent (visual observations) that some treatments variably influenced primrose specifically (disking seemed to diminish this species' abundance), so there is likely enough diversity in functional response among blooming plant species that overall numbers of blooms were not affected.

5.5 CONCLUSION

My results show that a single management treatment can be used to elicit habitat for multiple taxa. In such systems where uncertainty and controllability are both high, my findings provide insight for future studies seeking to simultaneously generate habitat for taxa ranging from blooming forbs and pollinators, to macroinvertebrates, to bobwhite quail chicks. While it appears that the pollinator treatment, intended to provide higher quality for the aforementioned taxa, succeeds in its objective, there remain gaps in scientific understanding that must be addressed before my results can be applied more broadly (i.e., whether it was the interseeding, the preceding light disking, the 2012 drought, or some combination thereof that elicited the response). It is becoming increasingly clear through this work and that of others that management actions often have multiple, complex, and even conflicting outcomes that must be better understood so that management objectives come into better alignment with management practices.

5.6 TABLES

Table 5.1 Multimodel inference table showing the global and treatment models as tied for the top model (within two AIC) out of the candidate model set for forb abundance per two m^2 .

	M - 1 - 1	IZ.	AIC.	Dalta AICa	A I.C 1.4	log-
	Model	K	AICc	Dena AICC	AICc weight	Likelihood
4	Global	17	6249.64	0	0.52	-3107.48
1	Treatment	6	6250.43	0.78	0.36	-3119.17
3	Time	5	6253.11	3.47	0.09	-3121.52
2	Block	10	6256.56	6.91	0.02	-3118.16
5	Null	2	6257.37	7.73	0.01	-3126.68

Table 5.2 Summary of the treatment model from the forb abundance multimodel inference framework per two m².

	Estimate	Std. Error	t value	Pr(>ltl)
(Intercept)	4.9766	0.5446	9.14	0
Control	-0.3109	0.7691	-0.4	0.6861
Disk	-0.2858	0.7461	-0.38	0.7017
Herbicide	0.9401	0.7605	1.24	0.2167
Interseed	1.9868	0.7376	2.69	0.0072

5.7 FIGURES

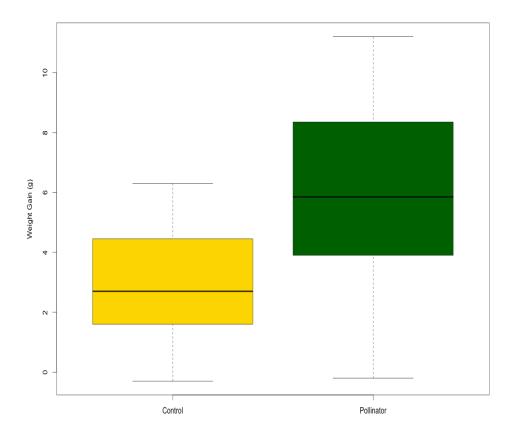


Figure 5.1 Average day-six weight gain (g) of the bobwhite quail chicks on the pollinator treatment versus the control in 2015. Error bars are ±SE.

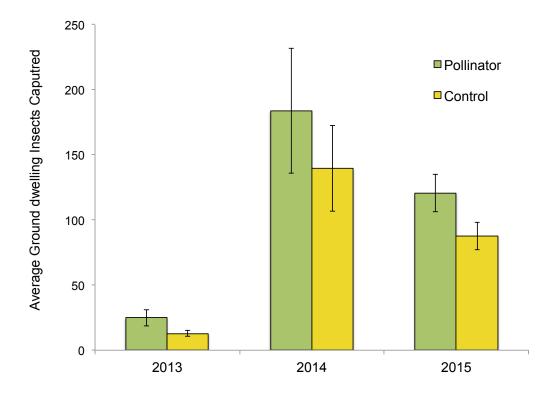


Figure 5.2 Average ground dwelling insect abundance in response to the pollinator treatment (lightly disked + interseeded with a high diversity, high flowering forb seeding mix in late fall 2012) versus controls over three years of data collection. The site experienced an intensive drought and was subsequently hayed in summer of 2012. Error bars are ±SE.

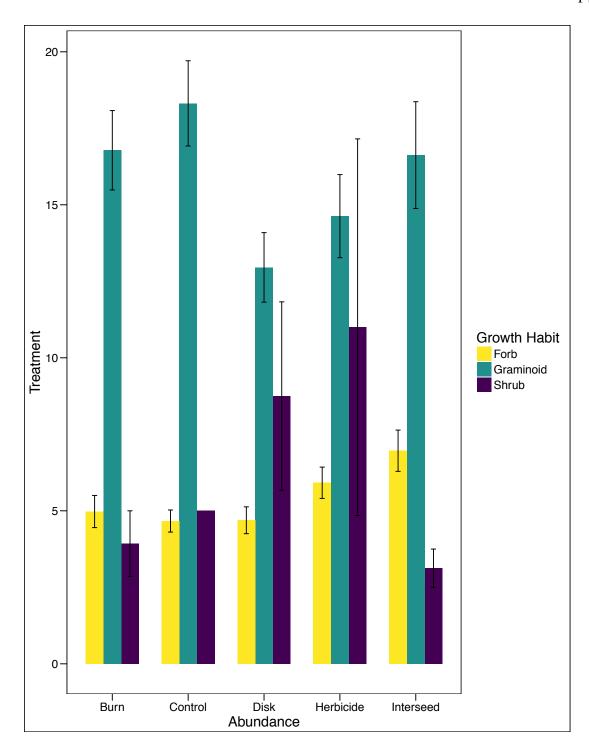


Figure 5.4a Mean abundance of plants per two m² grouped by growth forms (forb, graminoid, and shrub+subshrub combined into shrub), in the treatments and control. Error bars are ±SE.

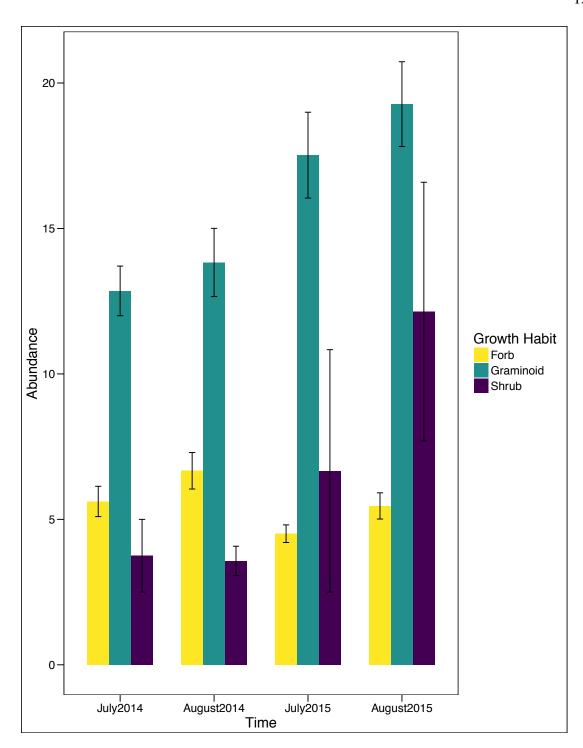


Figure 5.4b Mean abundance of plants per two m² grouped by growth forms (forb, graminoid, and shrub/subshrub combined into shrub) over the four sampling periods. Error bars are ±SE.

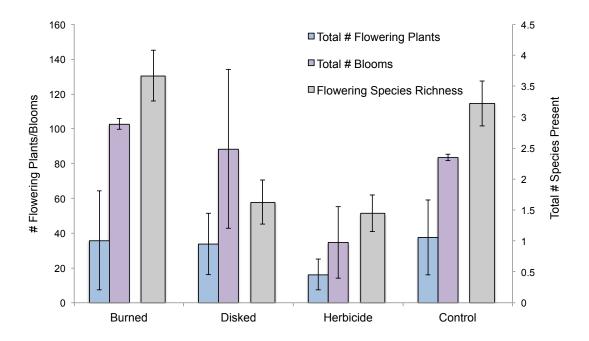


Figure 5.5 Average total number of flowering plants (blue bars), average number of total blooms (purple bars), and species richness (grey bars) in the 20 x 20 m mid-contract management and control plots (nine field replicates of each) in 2014. Error bars are ±SE.

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ADAPTIVE MANAGEMENT FOR SOIL ECOSYSTEM SERVICES

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ABSTRACT: Ecosystem services provided by soil include regulation of the atmosphere climate, primary (including agricultural) production, waste processing, decomposition, nutrient conservation, water purification, erosion control, medical resources, pest control, and disease mitigation. The simultaneously production of these multiple services arises from complex interactions among diverse aboveground and belowground communities across multiple scales. When a system is mismanaged, nonlinear and persistent losses in ecosystem services can arise, such as desertification, soil salinization, or biological invasions. Adaptive management is an approach to management designed to reduce uncertainty as management proceeds. By developing alternative hypotheses, testing these hypotheses and adjusting management in response to outcomes, managers can probe dynamic mechanistic relationships among aboveground and belowground soil system components. In doing so, soil ecosystem services can be preserved and critical ecological thresholds prevented. Here, we present an adaptive management framework designed to reduce the uncertainty surrounding the soil system, even when soil ecosystem services production is not the explicit management objective, so that managers can reach their management goals without undermining soil multifunctionality or contributing to an irreversible loss of soil ecosystem services.

6.1 INTRODUCTION

6.1.1 Managing for Soil Ecosystem Services

Ecosystem services provided by soil include regulation of the atmosphere and climate, primary (including agricultural) production, waste processing, decomposition, nutrient conservation, water purification, erosion control, medical resources, pest control, and disease mitigation (Wall et al., 2004; Bardgett, 2005; de Deyn and van der Putten, 2005; Wall et al., 2015). Many of these services emerge from cryptic processes in the rhizosphere (the interface between soil and plant roots characterized by high biological activity), creating uncertainty for managers seeking to improve or increase the delivery of soil ecosystem services. Adaptive management, a form of learning-while-doing that seeks to reduce uncertainty surrounding key questions in the landscape of interest and to adjust procedure as new information is gained (Allen and Garmestani, 2015), provides the opportunity to manage soils for multiple services while learning what strategies work in individual environments. Here, we discuss the unique challenges soils present to an adaptive management approach and then offer an adaptive management approach for soil service provisioning that can be applied to multiple management contexts.

6.1.2 Multifunctionality: the role of biodiversity in ecosystem service production

Ecological multifunctionality refers to the simultaneous production of numerous
ecosystem services, and relies on a diverse community of species with a variety of
functional traits (Wall et al., 2004; Gamfeldt et al., 2008; Maestre et al., 2012; Wagg et
al., 2014). For example, the multiple functions of nutrient transformation, primary
production, and carbon sequestration arise from the processes and interactions of, and
among, a variety of species in one place in time (de Vries et al., 2012; Bradford et al.,

2014). To maintain multifunctionality through time, a diverse community includes functional replacements for species excluded by shifting conditions ("functional redundancy"), or species with high plasticity (Isbel et al., 2011; de Vries et al., 2012). The link between multifunctionality and biodiversity is especially apparent in communities with low diversity or for a specialized function, where the loss of one biotic group can be especially impactful (Nielsen et al., 2011).

In terrestrial ecosystems, functioning among aboveground and belowground systems is tightly linked through the rhizosphere (de Deyn and Van der Putten 2005) (Figure 6.1). Plants exude up to 40% of their fixed carbon into the rhizosphere as easily decomposable carbon (e.g., glucose), which is the major "currency" for the belowground system (Lynch and Whipps, 1990; Brussard, 2012). Most carbon in soils is protected from microbial metabolism, resulting in a high concentration of soil microbes in the rhizosphere, mostly inhabiting the zone within 5mm of plant roots (Kennedy, 2005). Relative to the rest of the ecosystem, microbial biomass (i.e., bacteria and fungi) is not impressive. However, microbial transformations of materials and energy in the rhizosphere influence ecosystem functioning (Alphei, 1996; de Deyn and Van der Putten 2005). Microbiota mineralize nutrients for plant uptake, permanently remove reactive nitrogen from the system (Schlesinger and Bernhardt, 2013), remediate toxins (Reynolds and Skipper, 2005), alter gas and water flow around roots by increasing soil aggregation (Jastrow, 1987; Kennedy, 2005; Kibblewhite et al., 2008), and serve as a food source for microfaunal grazers, like protozoa and nematodes (Griffiths, 1990). These grazers provide food for higher tropic levels, excrete nutrients for plant uptake, and engineer the soil (Bonkowski, 2004; Ekelund et al., 2009). Availability of nutrients for plant uptake may stimulate root carbon

exudation, creating a potential feedback between aboveground and belowground through the rhizosphere, and affecting where and how a plant allocates its carbon stores (i.e., growth, nutrient mining, or reproduction) (Bonkowski, 2004). In addition to root exudates, plants provide carbon to the soil surface and belowground through aboveground litter fall and large root turnover, stimulating a diverse soil food web through changes in the quality and quantity of inputs (Eisenhauer et al., 2013; Lange et al., 2015; Steinhauer et al., 2015).

Plants also interact directly with various herbivores, pollinators, pathogens, and symbiotic endophytes aboveground, and root herbivores, parasites, pathogens, symbiotic nitrogen fixing bacteria, and arbuscular mycorrhizal fungi belowground (Bezemer and van Dam, 2005; De deyn and Van der Putten 2005; Bardgett and van der Putten; 2014). These interactions affect plant community structure and plant contributions to ecological multifunctionality, such as biomass production, invasion resistance, and belowground carbon sequestration (Zavaleta et al., 2010; Isbell et al., 2011; Eisenhauer et al., 2013). These interactions result in tightly coupled aboveground and belowground functioning. Ignoring the cryptic, complex, multi-scale interactions occurring in soil can result in nonlinear responses to management and irreversible failures. An adaptive management framework for managers seeking to improve soil ecosystem services across a landscape must account for these cryptic and cross-scale interactions in order to avoid undesirable, unrecoverable system behavior.

Given the generally positive relationships between biodiversity and multifunctionality, greater ecosystem service outputs could be achieved by managing for higher plant and soil biodiversity. However, there are spatial and temporal constraints on the provisioning of any ecosystem services (Birge et al., 2016b). For example, intensive agriculture generates valuable textile and food ecosystem services (MA 2005), but reduces soil diversity and multifunctionality (Brussaard 1997; DeFries et al., 2004). The tradeoffs between agriculture and biodiversity may not be apparent until a threshold is exceeded and ecosystem services are lost, and/or significantly reduced (Walker and Salt 2008). In many cases, this unintended loss of ecosystem services is irreversible and sudden (Holling and Meffe, 1996; Scheffer et al., 2011).

Indeed, slowly developing feedbacks between intensive production of a single agroecosystem service and soil functioning have been responsible for multiple social-ecological regime shifts associated with a catastrophic loss of ecosystem services, both now and throughout human history (Pitman, 2002; Peters, 2015). Soil salinization in some arid agricultural areas is catastrophic shift as a result of altered plant—soil feedbacks and/or intensifying irrigation (Smedema, 1990, Folke et al., 2004). In Australia, replacement of native woody vegetation with shallow-rooted wheat crops results in rising groundwater tables. This leads to the mobilization of deep salt stores to shallower soils, reducing plant productivity and soil biological activity (McFarlane et al., 1992; Pankhurt et al., 2001; Gorden et al., 2003). In the arid "Wheatbelt Region" of Australia, continual groundwater recharge combined with low precipitation (i.e., lack of flushing events) means there is no hydrologic mechanism for reversing upper horizon soil salinity.

Irrigation has a similar effect in arid climates and/or for poorly drained soils due to evaporation of irrigation water containing salts or waterlogged soil with natural salt deposits.

The ecological impacts of soil salinization are widespread globally (e.g., Rietz and Haynes, 2003; Houk et al., 2006). Loss of ecosystem services associated with soil salinization as a result of agricultural intensification is not a new problem – it was a contributing factor to the dissolution of the Sumerian nation-state in ~1800 BCE (Jacobsen and Adams, 1958). Irreversible loss of riverine and wetland ecosystem services from saline soil runoff reveals the potential for long-term, watershed-scale impacts of soil salinization (Hart et al., 1991; Delaney et al., 2015). Today, roughly 50% of agricultural soils worldwide are affected by salinization, with associated costs estimated at US \$12 billion annually (Smedema and Shiati, 2002; Pitman and Läuchli, 2002).

Another result of intensive agricultural ecosystem services production is desertification (Peters et al., 2013; Verstaete et al., 2009). Desertification is a broad-scale and persistent reduction in productivity that often arises from climatic, ecological, and social factors and occurs in arid, semi-arid, tropical, temperate, and high-latitude ecosystems (Verstraete et al., 2009). It is often characterized by a shift from native perennial plant cover to high bare ground, annual, non-native and/or xeric shrubby plant cover (Peters et al., 2015). Replacement of deep-rooted, drought tolerant perennial grassland species by drought intolerant wheat crops in the early 20th century U.S. Great Plains by European settlers resulted in a reduced rhizosphere and high bare ground cover, contributing to a loss of soil stability. An especially intense and long lasting drought in the 1930s (Miao et al.,

2007; Cook et al., 2009) was the proximate cause of a desertification event that displaced nearly 39 million ha of topsoil across the Southern Great Plains, USA. In the case of the Dust Bowl, as is common in desertification, a stochastic event triggered a catastrophe by overwhelming other system feedbacks that were previously altered, making it difficult to disentangle the individual drivers of system state changes (Rietkerk and van der Koppel 1997; Peters et al., 2006; Scheffer et al., 2011). Yet, poor land management at least partially contributes to the 12 million hectares of newly desertified land each year (UNCCD, 2011). Losses in agricultural, cultural, hunting, tourism, and carbon sequestration ecosystem services due to desertification (UNCCD, 2013) cost roughly US \$3 trillion globally, or 3-5% of gross world product (Berry and Campbell, 2003).

Non-linear losses of soil ecosystem services also result from alterations to soil nutrients, driving bottom-up changes in the plant community. Even following the cessation of agriculture, high loads of phosphorus acquisition enzyme dynamics did phosphorus acquisition enzyme dynamics did phorus and nitrogen can persist in soils, undermining restoration targets due to their unexpected interactions with biodiversity, carbon sequestration, and water quality (Isbell et al., 2013; Graham and Mendelssohn, 2016). For example, "Hole-in-the-Donut" is a tract of agricultural land formerly surrounded by Everglades National Park, Florida, USA. In 1975, after eighty years of intensive agricultural pesticide and fertilizer inputs, the Hole-in-the-Donut was incorporated into the park. Bedrock plowing, which crushes and mixes the limestone bedrock into the overlying marl and organic horizons, and fertilizer inputs created a deeper, more nutrient rich soil type relative to the surrounding matrix. As a result, the non-native, shrubby

Schinus terebinthifolius (Brazilian pepper or Christmas berry), formerly recorded only in small numbers in southern Florida, found favorable conditions in the well drained, phosphorus rich Hole-in-the-Donut restoration site (Smith et al, 2011; Ewel, 2013). Exacerbating this is Brazilian pepper's beneficial association with mycorrhizal fungi (Figure 6.1), which are obligate aerobes and thus uncommon among native plants inhabiting the hydric soils characteristic of the Everglades ecosystem (Ewel et al., 1982). Despite intensive mechanical tree removal, herbicide application, and prescribed burning on the site, Brazilian pepper persisted for decades, eventually forming a near monoculture on the site (Ewel et al., 1982; Smith et al., 2011). Eventually, managers removed the entirety of the phosphorus rich, rock-plowed soil down to the bedrock over the entire 22 km² expanse of Hole-in-the-donut –an expensive undertaking. Eleven years after soil removal, Hole-in-the-Donut had nearly 4cm of newly formed topsoil, and was dominated once again by native plant cover (O'Hare, 2008; Smith et al., 2011).

As these examples illustrate, when landscapes are optimized for the intensive production of a single service, the system may cross a threshold where not even the desired service can be adequately produced. Soil degradation, such as salinization, erosion, and changes in nutrient cycling are recognized as threats to the security of soil as a global resource for food and fiber production, water purification, a reservoir of biodiversity, and climate regulation (CEC, 2006; Lal, 2010; McBratney et al., 2014). Management of ecosystems is often necessary even when there is uncertainty regarding soil and plant response to management actions because the cost of inaction is too high. As managers seek to improve the output of soil multifunctionality, or at least ensure that their management actions do not contribute to non-linear system shifts arising from feedbacks with or

within the soil system, it is imperative to reduce uncertainty surrounding management decisions. One such approach is adaptive management, which offers managers a method to proceed with management actions while learning about mechanistic system relationships so that soil ecosystem services can be improved and increased, and critical thresholds can be avoided.

6.2 Incorporating soil into an adaptive management framework

In any ecosystem, the amount of services available for production is finite. Top-down constraints such as climate, topography, and soil type dictate the range of services an ecosystem can provide, and management decisions further constrain the realized set of ecosystem services.

No single ecosystem can produce every service possible at its optimized output consistently throughout space and time, but a diverse, functionally connected aboveground and belowground contributes to multifunctionality and safeguards against regime shifts (Wall et al., 2004; Foley et al., 2005). In a management context, stakeholders may not be immediately concerned with ecosystem service losses associated with potential future regime shifts. Yet the costs associated with these shifts are high, and complex soil feedbacks are poorly understood, creating uncertainty around important mechanisms driving these shifts. This uncertainty can be addressed in management plans to avoid an inadvertent loss of soil multifunctionality and ecosystem services. Managers attempting to generate multiple ecosystem services also face tradeoffs – especially if their plans require a reduction in biodiversity. Thus, we are challenged to reduce these areas of uncertainty associated with the belowground system while proceeding with management.

6.3 FRAMEWORK

6.3.1 The soil adaptive management cycle

One approach to reducing uncertainty surrounding soil multifunctionality is adaptive management. Adaptive management is designed to reduce uncertainty and winnow amongst competing hypotheses of system response as management proceeds (Allen and Garmestani, 2015). Adaptive management involves generating alternative hypotheses, testing these hypotheses and adjusting management in response to outcomes, and embracing unpredictable events as opportunities to reveal mechanisms and unknown relationships (Williams 2011). Here, we present an adaptive management framework designed to reduce this uncertainty surrounding the soil system –even when soil ecosystem services production is not the explicit management objective.

Adaptive management is appropriate when there is uncertainty regarding response to management, but an ability to manage (i.e., there is "controllability") (Allen et al., 2011). An adaptive management cycle begins with explicit conceptual models of the system at hand, and addresses a management problem with actions that can be tested as alternative hypotheses through monitoring and assessment (Figure 6.2). Knowledge gained through evaluation of monitoring data can be used to improve the next round of adaptive management, through adjustments to the hypotheses tested and management used. Regardless of whether the management goal is enhancing soil ecosystem services production, a straightforward and inexpensive way to improve an adaptive management plan for soils and increase the output of ecosystem services is to integrate the belowground into the conceptual model of the system. This inclusion may reframe the

decision making steps of the adaptive management approach by outlining important soil feedbacks that might otherwise go unmonitored.

For example, after incorporating a soils perspective into his or her conceptual model, a manager may alter management actions and monitoring variables to account for belowground processes and feedbacks. The significance of the monitored soil variables (Table 5.1) to the management problem can then guide the manager's future allocation of monitoring resources. This contrasts with trial and error management, in which management is only adjusted when an error occurs, and lack of error is interpreted as a successful application of management, regardless of the mechanism driving the system's behavior. Adaptive management promotes learning about the system regardless of outcome (Holling 1978), and is thus well suited for the dynamic, non-equilibrium soil system. By promoting the inclusion of soil processes in the adaptive management cycle, managers may improve the output of soil ecosystem services such as food and fiber production, water purification, carbon sequestration, atmospheric and hydrologic regulation, erosion control, and pest and pathogen control (Wall et al., 2004; Wall et al., 2012).

An adaptive management approach that accounts for soil components can reduce overall system uncertainty. However, the soil system operates at multiple scales across space and time –not all of which are commensurate with management. Moderately slow variables that vary over months to decades could be missed by a cursory inclusion of soil components in an adaptive management plan (Table 5.1). Similarly, a snapshot of a rapidly shifting variable from a single point in time may not capture key trends, such as

changing soil microfaunal diversity. In the previous examples of desertification, salinization, and a species invasion, feedbacks between the aboveground and belowground result in non-linear and persistent reductions in ecosystem services. The processes driving these shifts may be detected and avoided using adaptive management. By adding an additional, soil feedback-specific adaptive management cycle to an overall adaptive management program (Figure 6.3), managers can continue to address the fundamental management objective while accounting for soil "means objectives" that could otherwise be overlooked and thus potentially result in a persistent loss of ecosystem services.

Much like adaptive management, the soil adaptive management cycle should be system-specific, and alternative hypotheses should address key uncertainties about system functioning. Many ecosystems have multiple possible alternative, persistent states, and soil feedbacks may not contribute, either ultimately or proximately, to every critical shift among states. The determination of the soil's significance in a given state shift should be made using a priori system indicators monitored during the learning stage of adaptive management (Figure 6.3). These indicators may include increasing bare ground cover, or a change in aboveground plant diversity (particularly a loss of productive native species), both of which are tightly coupled to belowground functioning and biodiversity (Wardle et al., 2004; Bardgett et al., 2014). Because belowground-aboveground linkages create complex feedbacks, simple cause and effect relationships are difficult to ascertain from changes in the aboveground system alone.

6.3.2 The soil adaptive management cycle: application

For example, a one-time measure of bare ground may not indicate a meaningful reduction in belowground functioning, but persistent or otherwise unexplainable bare ground could suggest belowground processes in need of further probing. Setting threshold levels of indicators that, once reached, initiate the soil adaptive management cycle can guide soil management (much like the invasive species triggers used in adaptive management of some protected areas, e.g., van Wilgen and Biggs [2011]). When a soil adaptive management cycle is initiated, alternate hypotheses should be developed and tested to address whether the system uncertainty is arising from feedbacks with the soil system. The specific steps of the structured decision making stage can be adjusted based on the evaluation stage (Figure 6.2, Table 6.1). As uncertainty is reduced or resolved, different outcomes can arise. Uncovering new information about the belowground system may reveal uncertainty in a different process and their importance to the management problem, resulting in another round of the soil adaptive management cycle to test alternative hypotheses, i.e., double loop learning (Lee, 1993).

By identifying alternative hypotheses and indicators based on soil ecosystem services and thresholds to which the system may vulnerable, managers have explicit targets that allow them to proactively decide when to devote additional resources to monitoring and learning about the soil system. Take for example, if a perennial grassland system typically that cross an a priori determined management threshold for bare ground (i.e., % extent, duration, or both). When perennial grasslands experience a broad shift to a desertified state, aboveground-belowground activity may be isolated to spaces occupied by shrubby or xeric plants, and the interspaces barren, making the shift persistent (Peters,

2015). When evaluation of the bare ground monitoring data triggers a soil adaptive management cycle, a conceptual model of the system can guide managers to target system-specific and problem-specific soil variables, such as root biomass, fungal biomass, soil nutrient status, and cation exchange capacity (Table 5.1) in the bare ground versus under vegetation over multiple sampling time points. Monitoring these variables can help explore hypotheses regarding the proximate and ultimate drivers of a system shift that would undermine not only soil ecosystem services but also the fundamental management objective.

Eventually, uncertainty surrounding the soil should be also be resolved in a way that eliminates the need for an additional soil adaptive management loop, either by identifying the soil variable for inclusion in ongoing monitoring, or because new information from the soil system alters the overarching, fundamental adaptive management objective.

There may be no simple management recipe for increasing belowground multifunctionality and avoiding regime shifts, but this approach offers a structured way to proceed with management while constantly seeking to uncover mechanistic relationships. By learning about the system through management, a richer, more complex understanding of the soil system and its mechanistic relationship to system components and external drivers can emerge.

6.4 CONCLUSION

Drivers of global change such as global nitrogen deposition, climate change, and species invasions are creating uncertainty surrounding the future of soil biota and the ecosystem services they underpin. Poor land management that optimizes intensive production of a

narrow suite of ecosystem services may result in non-linear, persistent losses of soil ecosystem services. Thus, in order to preserve the essential benefits soil provides to human society, there is a pressing need to manage ecosystems with diverse, multifunctional belowground systems (Wall et al., 2015) while reducing uncertainty surrounding belowground response to management and global change. By constantly working to reducing this uncertainty, adaptive management can target biodiversity objectives while avoiding critical system thresholds in a dynamic, no-analog future.

6.5 FIGURES

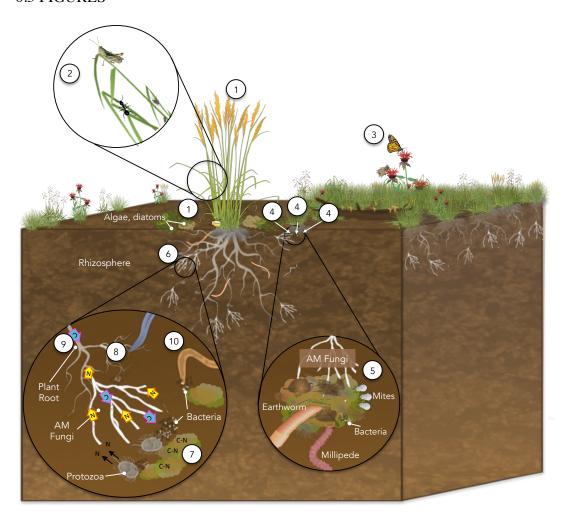


Figure 6.1 A conceptualization of the tightly coupled aboveground-belowground biodiversity and functioning. Primary production (1) is the ultimate source of energy in all ecosystems. Plant materials provide food for a variety of aboveground chewing, sucking, mining (2), and pollinating (3) insects. These plant-insect interactions affect plant chemistry, plant community structure, plant and insect dispersal, and an abundance and diversity of other herbivores and higher trophic levels in the ecosystem (not all shown) (de Deyn and Van Der Putten, 2005). Changes in the quantity and/or quality of litter inputs to the soil (4) can result from aboveground herbivory, and alter the food source for a variety of belowground detritivores (5) (Wardle et al., 2002; de Deyn and van der Putten, 2011). Bacteria, protozoa, and arbuscular mycorrhizal (AM) fungi in the rhizosphere (6) directly influence the mineralization of organic carbon and nitrogen (CeN) stored in humus (7), affecting available nutrients for plants, who may alter fine root turnover (8), and/or release labile carbon (9) to the surrounding soil microbiota in response, stimulating mineralization activity, and indirectly influencing higher trophic levels, such as nematodes that feed on roots and bacteria (10) (Brussaard, 2012). Soil nutrient availability in turn influence plant community structure (Isbell et al., 2013), affecting the quality and quantity of litter inputs back to the soil and thus tightening aboveground-belowground diversity and functional linkages. Vector symbols used in the figure courtesy of Tracey Saxby, Jane Hawkey, and Dieter Tracey of Integration and Application Network of the Center for Environmental Science as University of Maryland.

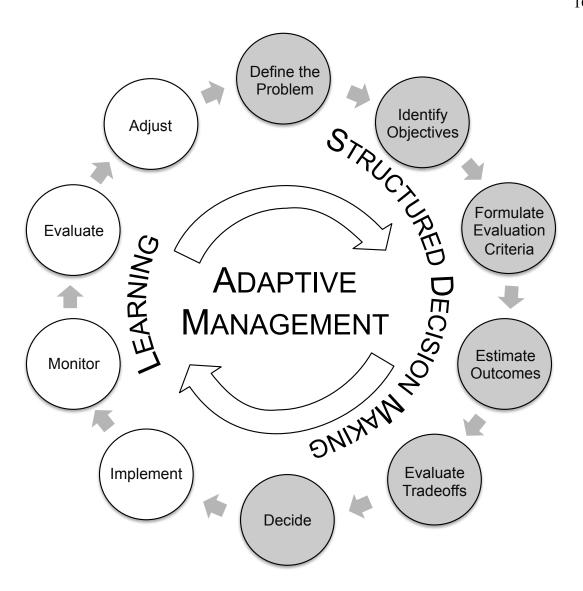


Figure 6.2 The adaptive management cycle [modified from Allen et al. (2011)].

Table 6.1 Testable soil variables, their speeds, and the associated ecosystem system services which they help to maintain. Approximate time scales for each variable include:

Very Slow = millenia, Slow = centuries, Moderately Slow = decades, Moderately Fast = years, or Fast = seasons). The level of estimated training or soil-related expertise required (Low, Medium, or High) and cost estimates for field and laboratory measurements (Low, Medium, or High) are also provided.

Variable	Variable Speed	Associated Ecosystem Services	Expertise	Cost ¹
Texture	Very slow	Landscape diversity, primary productivity, CO ₂ sequestration	Med. to high	Low to med.
Horizon depth	Slow	Erosion control, primary productivity	Med. to high	Med. to high
Compaction/ bulk density	Moderately Fast	Generation of soil structure, runoff control, water-holding capacity, nutrient cycling	Medium	Low to medium
Aggregation	Moderately Fast	Erosion control, landscape diversity/microhabitats, H ₂ O and nutrient transport, CO ₂ sequestration	Med. to high	Low to high
Root biomass	Moderately Fast	Erosion control, maintenance of above/belowground biodiversity, soil structure, CO ₂ sequestration, porosity	Med. to high	Low to high
Nematodes	Moderately fast	Bioturbation, decomposition, soil porosity, biodiversity, nutrient mineralization, CO ₂ sequestration	Med. to high	Low to high
Surface residue	Moderately fast	Topsoil formation, microhabitats, CO ₂ sequestration, soil stability, water-holding capacity	Low to med.	Very low
Fungal biomass	Fast to moderately fast	Biodiversity, primary productivity, CO ₂ sequestration soil structure, nutrient mineralization	Med. to high	High
Salinity	Slow	Primary productivity,	Med. to high	Med. to

_	biodiversity, habitat quality			
Trace nutrients (e.g. iron, manganese)	Slow	Landscape diversity, primary productivity, CO ₂ sequestration	High	Med. to high
Cation exchange capacity (CEC)	Moderately slow	Soil fertility, primary productivity Soil stability, primary	Med. to high	Low to high
Total carbon	Slow to moderately fast	productivity, CO ₂ sequestration, water-holding capacity, biodiversity	High	Med. to high
Nitrogen availability	Slow to fast	Soil fertility, biodiversity, primary productivity, CO ₂ sequestration	Med. to high	Low to high
Total organic matter	Moderately fast	Soil stability, fertility, microhabitats, water cycling, nutrient mineralization	High	Med. to high
Soil pH	Fast	Nutrient cycling, microbial activity, decomposition	Low to med.	Low
Water-holding capacity	Slow	Irrigation, water cycling, nutrient cycling	Med. to high	Low to high
Infiltration	Moderately slow	Runoff control, water cycling, nutrient cycling	Low to med.	Low to med.
Decomposition	Fast	Nutrient cycling, topsoil production, soil stability, fertility, bioremediation	Med. to high	Low to high
Plant defense compounds	Fast	Primary productivity, pathogen control, nutrient cycling	High	High

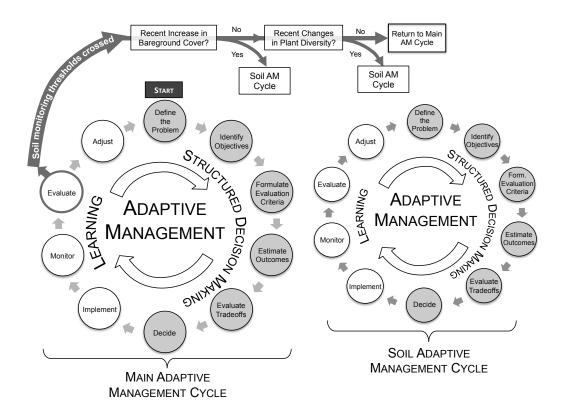


Figure 6.3 An adaptive management framework for reducing uncertainty in the soil system while proceeding with the fundamental management objective.

SYNTHESIS

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ABSTRACT: In Chapters 2, 3, and 4, I reported how four common mid-contract management practices had different effects on soil, plant, and habitat dynamics of a North Central Great Plains Conservation Reserve Program (CRP) grassland. Notable findings include herbicide treatment eliciting higher abundance of nonnative plant species and a belowground shift towards higher carbon and phosphorus requirements, likely due to elevated nitrogen in response to plant death or microbial priming of organic matter. Additionally, I found that interseeding with a high diversity seed mix provided enhanced habitat for multiple taxa and led to increased forb abundance. My statewide survey results show that while landowners identify soil health and habitat as ecosystem services and burning as an effective practice to achieve those ends, they more commonly use herbicide as a management practice. My results supported burning as an effective management strategy for achieving soil and habitat ecosystem services, especially relative to herbicide application. By capitalizing on landowner amenability to burning, influence of agency personnel over management decisions, and high controllability necessary for adaptive management to proceed, my results reveal an opportunity for agencies to assess the effect of herbicide versus burning across the range of past land uses, soil types, and environmental variables that comprise Nebraska's CRP grasslands to achieve multiple, simultaneous ecosystem services.

7.1 DISCUSSION

In Chapters 2, 3, and 4, I discussed how four common mid-contract management practices had different effects on soil, plant, and habitat dynamics of a North Central Great Plains Conservation Reserve Program (CRP) grassland. Notable findings include herbicide treatment eliciting higher abundance of nonnative plant species and a belowground shift towards higher carbon and phosphorus requirements, likely due to elevated nitrogen from lack of plant uptake, root necromass mineralization, and/or microbial priming of organic matter. I also found that interseeding with a high diversity, high forb seed mix provided enhanced habitat for multiple taxa and led to higher forb abundance. These results are especially interesting in light of the statewide CRP enrollee survey I administered, in which respondents identified soil health and habitat as the most desirable ecosystem services, and burning as an effective practice to achieve those ends – even though they more commonly use herbicide as a management practice.

My results support burning as an effective management strategy to achieve simultaneous benefits to soil and habitat, with burning eliciting higher bare ground and slightly higher forb abundance, which are typically considered important for critical life stages of upland game birds, but without concurrent shifts in belowground functioning divergent from that of the control soils. Burning also did not to elicit undesirable aboveground changes such elevated nonnative species abundance. This is likely because the system is adapted to fire disturbance relative to the other types of mid-contract management practices. However, only 26% of landowners are burning on Nebraska CRP lands according to the survey responses, and respondents appear to attribute their decision to instead apply herbicide largely to agency recommendation –rather than to cost or ease of practice. By capitalizing

on landowner amenability to burning and high controllability necessary for adaptive management to proceed, my results provide a rare opportunity for agencies to compare the efficacy of two management practices on ecosystem services identified as important by both landowners and included as overarching objectives of the CRP: soil conservation and habitat provisioning.

Respondents identified nonnative species as the top ecosystem disservice associated with the CRP. The two management practices of herbicide and burning are interesting in comparison to one another in that herbicide is commonly used to control nonnative species and considered at least somewhat effective by landowners in Nebraska, even though my results reveal that it may elicit soil feedbacks that ultimately undermine that management objective. The other, burning, is less commonly used but seen as more effective in the state, and was supported by my results as better supporting respondents' management objectives. Whether my results translate to other contexts that comprise a range of past land uses, soil types, and environmental variables represent the uncertainty needed to enact an adaptive management plan. Specifically, state agencies could design county or even a state level burning versus herbicide experiments on multiple CRP fields to measure various soil and habitat outcomes in response to the two treatments. My own study represents a first round in a structured decision-making and learning loop so that a second round of adaptive management, such as a state-level adaptive management plan, could proceed.

When landowners formulate management decisions, they are faced with multiple explicit and hidden tradeoffs that may inadvertently influence their ultimate management objectives. Surprising feedbacks in response to herbicide in my study reveal the challenge of managing ecosystem service tradeoffs and system complexity even at manageable scales, such as two years over ~200 ha. With increasing scales, to the state, regional, and national level where the CRP operates, more ecosystem services can be generated with fewer tradeoffs, but with decreasing control and increasing uncertainty. Assessing where critical uncertainty can be reduced at each of these scales is essential for ensuring the Conservation Reserve Program lives up to its potential as the largest conservation policy in United States history. My work represents one such effort, by reducing uncertainty in the social and ecological components of a Conservation Reserve Program grassland in the North Central Great Plains.

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9 APPENDIX

Tukey HSD treatment mean comparisons for H3A total soil nitrogen

Treatment Comparisons	diff	lwr	upr	p adj
Control-Burn	-0.12	-0.61	0.37	0.96
Disk-Burn	-0.08	-0.57	0.41	0.99
Herbicide-Burn	0.48	-0.01	0.97	0.06
Interseed-Burn	0.38	-0.15	0.92	0.28
Disk-Control	0.04	-0.45	0.53	1
Herbicide-Control	0.6	0.1	1.1	0.01
Interseed-Control	0.5	-0.03	1.04	80.0
Herbicide-Disk	0.56	0.07	1.06	0.02
Interseed-Disk	0.46	-0.07	1	0.12
Interseed-Herbicide	-0.1	-0.64	0.44	0.99

Tukey HSD treatment mean comparisons for H3A total soil nitrate

Treatment Comparisons	diff	lwr	upr	p adj
Control-Burn	-0.17	-0.56	0.23	0.77
Disk-Burn	-0.1	-0.49	0.3	0.96
Herbicide-Burn	0.35	-0.04	0.75	0.1
Interseed-Burn	0.21	-0.22	0.63	0.66
Disk-Control	0.07	-0.32	0.47	0.99
Herbicide-Control	0.52	0.12	0.92	0
Interseed-Control	0.37	-0.06	0.81	0.12
Herbicide-Disk	0.45	0.05	0.84	0.02
Interseed-Disk	0.3	-0.12	0.73	0.29
Interseed-Herbicide	-0.14	-0.58	0.29	0.88

Tukey HSD treatment mean comparisons for H3A total soil ammonium

Treatment Comparisons	diff	lwr	upr	p adj
Control-Burn	0.03	-0.55	0.61	1
Disk-Burn	0.06	-0.51	0.63	1
Herbicide-Burn	0.19	-0.39	0.76	0.9
Interseed-Burn	0.65	0.03	1.27	0.04
Disk-Control	0.03	-0.55	0.6	1
Herbicide-Control	0.16	-0.43	0.74	0.95
Interseed-Control	0.62	-0.01	1.25	0.06
Herbicide-Disk	0.13	-0.45	0.71	0.97
Interseed-Disk	0.59	-0.03	1.22	0.07
Interseed-Herbicide	0.46	-0.17	1.09	0.25
Interseed-Herbicide	0.46	-0.17	1.09	0.25

Tukey HSD treatment mean comparisons for percent soil carbon

Treatment Comparisons	diff	lwr	upr	p adj
Control-Burn	-0.17	-0.56	0.23	0.77
Disk-Burn	-0.1	-0.49	0.3	0.96
Herbicide-Burn	0.35	-0.04	0.75	0.1
Interseed-Burn	0.21	-0.22	0.63	0.66
Disk-Control	0.07	-0.32	0.47	0.99
Herbicide-Control	0.52	0.12	0.92	0
Interseed-Control	0.37	-0.06	0.81	0.12
Herbicide-Disk	0.45	0.05	0.84	0.02
Interseed-Disk	0.3	-0.12	0.73	0.29
Interseed-Herbicide	-0.14	-0.58	0.29	0.88

Tukey HSD treatment mean comparisons for PLFA biomass

Treatment Comparisons	diff	lwr	upr	p adj
Control-Burn	-74.52	-324.86	175.83	0.92
Disk-Burn	-19.58	-269.93	230.77	1
Herbicide-Burn	118.71	-134.23	371.65	0.69
Interseed-Burn	240.67	-32.93	514.28	0.11
Disk-Control	54.94	-195.41	305.28	0.97
Herbicide-Control	193.23	-59.71	446.17	0.22
Interseed-Control	315.19	41.59	588.8	0.02
Herbicide-Disk	138.29	-114.65	391.23	0.55
Interseed-Disk	260.25	-13.35	533.86	0.07
Interseed-Herbicide	121.96	-154.02	397.95	0.74

Tukey HSD treatment mean comparisons for phosphatase (P) enzyme activity at 35 $^{\circ}$ C.

Treatment Comparisons	diff	lwr	upr	p adj
Control-Burn	0.04	-1.34	1.41	1
Disk-Burn	-0.4	-1.74	0.93	0.9
Herbicide-Burn	1.33	0	2.67	0.05
Interseed-Burn	-0.58	-1.96	0.79	0.73
Disk-Control	-0.44	-1.81	0.94	0.88
Herbicide-Control	1.3	-0.08	2.67	0.07
Interseed-Control	-0.62	-2.04	0.79	0.71
Herbicide-Disk	1.74	0.4	3.07	0.01
Interseed-Disk	-0.18	-1.56	1.19	1
Interseed-Herbicide	-1.92	-3.29	-0.54	0

Tukey HSD treatment mean comparisons for S enzyme activity at 35 °C.

Treatment Comparisons	diff	lwr	upr	p adj
Control-Burn	0.02	-0.02	0.06	0.63
Disk-Burn	-0.03	-0.07	0.01	0.34
Herbicide-Burn	0	-0.05	0.04	1
Interseed-Burn	0	-0.05	0.04	1
Disk-Control	-0.05	-0.09	-0.01	0.02
Herbicide-Control	-0.02	-0.07	0.02	0.49
Interseed-Control	-0.03	-0.07	0.02	0.46
Herbicide-Disk	0.02	-0.02	0.07	0.47
Interseed-Disk	0.02	-0.02	0.07	0.55
Interseed-Herbicide	0	-0.04	0.04	1

Tukey HSD treatment mean comparisons for CB enzyme activity at 35 °C.

Treatment Comparisons	diff	lwr	upr	p adj
Control-Burn	-0.02	-0.25	0.21	1
Disk-Burn	-0.11	-0.33	0.12	0.64
Herbicide-Burn	0.12	-0.11	0.34	0.56
Interseed-Burn	-0.09	-0.32	0.14	0.78
Disk-Control	-0.09	-0.32	0.14	0.8
Herbicide-Control	0.14	-0.1	0.37	0.45
Interseed-Control	-0.07	-0.31	0.16	0.89
Herbicide-Disk	0.23	0	0.45	0.05
Interseed-Disk	0.02	-0.22	0.25	1
Interseed-Herbicide	-0.21	-0.44	0.02	0.09

Tukey HSD treatment mean comparisons for BG Q10

Treatment Comparisons	diff	lwr	upr	p adj
Control-Burn	0.79	-0.71	2.29	0.56
Disk-Burn	1.87	0.42	3.33	0.01
Herbicide-Burn	1.07	-0.38	2.53	0.24
Interseed-Burn	0.59	-0.91	2.09	0.8
Disk-Control	1.08	-0.42	2.58	0.25
Herbicide-Control	0.28	-1.22	1.78	0.98
Interseed-Control	-0.2	-1.75	1.34	1
Herbicide-Disk	-0.8	-2.26	0.65	0.52
Interseed-Disk	-1.29	-2.79	0.21	0.12
Interseed-Herbicide	-0.48	-1.99	1.02	0.89

Tukey HSD treatment mean comparisons for CB Q10

Treatment Comparisons	diff	lwr	upr	p adj
Control-Burn	1.03	-1.18	3.24	0.67
Disk-Burn	1.65	-0.56	3.86	0.22
Herbicide-Burn	2.8	0.59	5.01	0.01
Interseed-Burn	0.8	-1.41	3	0.84
Disk-Control	0.62	-1.65	2.89	0.93
Herbicide-Control	1.77	-0.5	4.04	0.19
Interseed-Control	-0.23	-2.5	2.04	1
Herbicide-Disk	1.15	-1.12	3.42	0.6
Interseed-Disk	-0.85	-3.12	1.42	0.82
Interseed-Herbicide	-2	-4.27	0.27	0.11

Tukey HSD treatment mean comparisons for NAG Q10

diff	lwr	upr	p adj
0.78	-0.64	2.2	0.5
2.35	0.25	4.45	0.02
1.58	0.16	3	0.02
0.32	-0.98	1.63	0.95
1.57	-0.63	3.76	0.25
0.8	-0.75	2.35	0.57
-0.46	-1.91	0.99	0.88
-0.77	-2.97	1.43	0.84
-2.03	-4.15	0.1	0.07
-1.26	-2.71	0.19	0.11
	0.78 2.35 1.58 0.32 1.57 0.8 -0.46 -0.77 -2.03	0.78 -0.64 2.35 0.25 1.58 0.16 0.32 -0.98 1.57 -0.63 0.8 -0.75 -0.46 -1.91 -0.77 -2.97 -2.03 -4.15	0.78 -0.64 2.2 2.35 0.25 4.45 1.58 0.16 3 0.32 -0.98 1.63 1.57 -0.63 3.76 0.8 -0.75 2.35 -0.46 -1.91 0.99 -0.77 -2.97 1.43 -2.03 -4.15 0.1