

SEASONAL VARIATION OF KEY SOIL CHARACTERISTICS OF A TALLGRASS
PRAIRIE ALONG A RESTORATION GRADIENT

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BY LAUREN G. UMEK

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Abstract

Current ecological restoration efforts seek to restore a target community, maximize biodiversity or provide habitat for rare species. In practice, restoration ecology is often initiated and sustained without knowledge or reverence to the belowground ecosystem processes, though these processes often subtend the long-term sustainability of aboveground and belowground ecological communities. As such, the ultimate success of restoration may be hindered. An intimate understanding of the impacts of disturbance and subsequent restoration on the ecosystem processes of a prairie can not only contribute to the expanding academic field of restoration ecology, but can also inform practitioners of more ecologically appropriate and effective methods to restore targeted native plant life. This study examines soil chemical and biological properties at three prairies along a restoration gradient in the Skokie Nature Preserve in Lake Forest, Illinois for a single growing season. Striking similarities in most soil characteristics between the restored and the pristine prairie suggest that the restoration of soil function and ecosystem processes may precede plant community establishment. This study demonstrates that the evaluation of soil chemical and biological properties are valuable indicators of ecosystem trajectories and are critical for successful restoration of sustainable ecosystems.

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Table of Contents

Title page	1
Signature page.....	2
Abstract.....	3
Acknowledgements.....	4
Table of Contents.....	5
Introduction/Background	6-15
Materials and Methods.....	16-23
Results.....	24-35
Discussion.....	36-45
References.....	46-49

Introduction

The midwestern tallgrass prairie is a globally rare ecosystem. With less than 0.1% remaining, this habitat is considerably more rare and threatened as an ecosystem than the much publicized tropical rainforest (Manning 1995). Recognizing the loss of this valuable resource, many public and private agencies and organizations have made efforts to purchase and preserve the few remaining tallgrass prairies. In addition to preserving intact systems, efforts are increasingly focused on the purchase and restoration of adjacent and disturbed areas to a pre-disturbed condition.

Currently, the long-term evaluation of conservation effectiveness focuses on biological assemblage and diversity. Such detailed descriptions of observed patterns in both the distribution and abundance of species is a critical organizing concept in ecology. More specifically, these ecological studies examine changes in community composition including the presence (or absence) of species of concern (often rare, threatened or endangered) or of the presence of functional groups over time. A great deal of evaluation also assesses community diversity and its variability through time and with conservation practices.

Effective conservation evaluation however, requires a combination of both species specific approaches and an effective understanding of ecosystem processes. In order to conserve communities, it is necessary to preserve not only the constituents of the community and the structure of these assemblages, but also the ecological large scale and dynamic processes that produce community patterns. Biologists and ecologists have generated several hypotheses relating the production and maintenance of species diversity with ecosystem processes (Pickett et al. 1988, Hobbs and Huenneke 1992, Tilman 1999, Yachi and Loreau 1999, Loreau et al. 2001, Bezemer and van der Putten 2007). Extensions on this “biodiversity ecosystem function

paradigm” have related to biodiversity and to ecosystem stability (Tilman 1996, Hooper and Vitousek 1997, Grime 1998, Setälä and Mikola 1998, Tilman 1999, Wardle et al. 1999, Zak et al. 2003, Bezemer and van der Putten 2007). While the mechanisms linking populations, communities and ecosystems remain unclear, there appears to be a widespread accord that successful restoration of terrestrial systems may be predicated on the recovery of ecosystem function (Ehrenfeld and Toth 1997). Many of these studies cite soil ecology as a central component that links above and belowground ecological interactions and, in turn, ecosystem function (Casper and Jackson 1997, Setälä 2002, Wardle 2002, Smith et al. 2003, Van Der Putten 2003, Wardle et al. 2004). Despite advances in these paradigms, there is no consensus on how the recovery of function should be achieved or how recovery should be measured. To understand the relationship between plant community composition and restoration, a number of factors need to be considered. These include disturbance in general, fire, grazing, physical disturbance, plant-soil interactions, mycorrhizal associations and resource availability.

Disturbance

The most simple model for the maintenance of diversity suggests that species diversity is maintained by the intersection of competitive exclusion and disturbance events that reset the competitive clock (Huston 1994). Huston's model mirrors the prevailing hypothesis relating these ecological processes and biological assemblages, the intermediate disturbance hypothesis. This hypothesis suggests that species diversity should be highest at moderate levels of disturbance (Miller 1982, Petraitis et al. 1989, Grumbine 1994, Collins 2000, Johst and Huth 2005). Most interpretations of this hypothesis explain that high species diversity is maintained through events or interactions that result in selective mortality or random, localized mass

mortality (Petraitis et al. 1989). The intermediate disturbance hypothesis is generally supported for species competing for basal resources by empirical evidence and mathematical modeling (Wootton 1998).

However, disturbance is also known to increase the invasibility of communities, thus posing an important problem for conservation management (Miller 1982, Collins 1987, Petraitis et al. 1989, Collins 1992, Hobbs and Huenneke 1992, Grumbine 1994, Collins et al. 1995, Tilman 1999, Collins 2000, Johst and Huth 2005). As such, the maintenance of locally significant disturbances may be critical for the restoration and preservation of biological diversity in restored habitats. For example, fire suppression, in historically fire-dependent ecosystems, results in significant and detrimental modifications to the biological community (Robertson and Heikens 1994). In general, management of disturbance is required to balance interspecific competition and thus prevent the loss of species of lower competitive abilities for the community (Grumbine 1994). A concern with the term disturbance is that it is often difficult to separate “natural” disturbances that may be integral for establishment and maintenance of ecosystem structure and function and perturbations from anthropogenic disturbances that may or may not disrupt the trajectory of a given system. These anthropogenic disturbances in the tallgrass prairie ecosystems are commonly agricultural production and intensive grazing and are relatively distinct from the ecological disturbances that include fire, grazing and physical disturbance.

Fire

Fire can significantly impact the vegetation structure and ecosystem functioning (Knapp et al. 1998). A considerable amount of research has focused on plant responses to fire in the

tallgrass prairie as it is viewed as an integral natural disturbance that maintains structure and function of these ecosystems (Collins and Wallace 1990). The net vegetative result of fire in the tallgrass prairie ecosystem is an increase in the relative abundance of C₄ grasses and a decrease in the abundance of C₃ grasses and most forbs (Abrams et al, 1986, Bragg and Hulbert 1976). While the reduction of forbs is not typically a desired outcome for most land managers, especially those whose management goals include the maintenance of an aesthetically pleasing landscape, the short-term outcome of a reduction in woody stems and the long term reinstatement of natural disturbance regimes are often viewed as greater benefits than the loss of attractive forbs. In the long term, fire in a tallgrass prairie ecosystem results in an increase in native species richness as well as an increase in both the abundance and diversity of more conservative species. Fire cessation, by contrast, resulted in an increase of richness of alien graminoid and woody species combined with a decline in native grasses and forbs that were prevalent in the burned sites (Bowles et al. 2003). Belowground, the presence of charcoal leads to an increase in soil microbes and an immediate and short term elevation of soil pH, C, N, P, K, Ca, Mg and a decrease in CEC (Egerton-Warburton 2005).

Grazing

The reintroduction of large grazers to the tallgrass prairie is a topic of recent inquiry by the conservation community. Heavy grazing by fenced horses (particularly in wealthy, developing regions of the Midwest) is a common disturbance for tallgrass prairies. Contrary to the previous large grazers of the region, *Bison bison* (American Bison) and *Cervus canadensis* (American Elk), horses and cattle heavily grazed upon a small parcel of land, reducing vegetation to a short lawn of grasses and forbs and significantly compacting the soil. While the impact of intensive grazing by modern mammals (mainly horses) is not well researched, the

implication of heavy grazing in general is an accumulation of N in impacted soils. Grazing conserves N by redistributing mammalian consumed N containing aboveground biomass as labile N in urine and dung. While grazed plants are not N limited, the selective pressure to re-grow photosynthetic shoots following herbivory leaves most plants C limited (Johnson and Matchett 2001). This impact can also be exacerbated if there is potential N enrichment from nearby agricultural sources. As a result of C limitation, root allocation is decreased and plants exhibit increased, though apparently weakened, aboveground growth with growth.

Physical Disturbance

Physical disturbance, in the form of compaction, tillage or erosion generally leads to dramatic reductions in soil biodiversity (Bardgett 2005). The scale of this reduction however can vary by soil type, climate and disturbance degree (Chan 2001). Studies have demonstrated that the conversion of tropical forest to agriculture reduces microbial biomass, termites, microarthropods and nematodes (Bardgett 2005). Physical disturbance have also reduced native earthworm abundance, biomass, and species richness (particularly native species) in other climates (Springett 1992; Fragoso et al. 1997; Dlamini and Haynes 2004). This reduction in soil biodiversity is observed in the temperate prairie at various trophic levels. Collembola diversity, nematode diversity and phenotypic microbial diversity are all reduced in temperate grasslands under the direct or indirect influence of agriculture (Yeates and King 1997, Brand and Dunn 1998, Bardgett et al. 2001). As with other soil biota, studies of arbuscular mycorrhizal fungi also reveal a reduction in diversity and functioning as a result of physical disturbance (Johnson and Wedin 1997, Rillig and Klironomos 2004).

Resource Availability

Resource limitation is a critical ecosystem component that places morphological and evolutionary constraints on plants, ultimately driving plant community composition in virtually all terrestrial and aquatic habitats (Tilman 1988). While tallgrass prairie soils are considered to be extremely fertile, their high organic nutrient content results in soils that are relatively low in inorganic nutrients, ultimately limiting primary production (Owensby et al. 1970). Three resources essentially limit primary production in the tallgrass prairie light, water and nitrogen (Knapp et al 1998). Ecological theory predicts a positive and asymptotic relationship between plant diversity and ecosystem productivity based on the ability of more diverse plant communities to fully use limiting resources (Tilman 1985, Tilman and Wedin 1991, Klironomos et al. 2000). Given infinite resources, each plant would meet its maximum morphological growth rate potential (Tilman 1988). However, existence of resource gradients has been a major driving force for many key ecological and evolutionary processes including genotypic specialization within a species, speciation, and convergence of phylogenetically distinct plants in ecologically similar but geographically distinct habitats (Tilman 1988). Thus, while low resource availability prohibits plants from reaching their productivity potential, the existence of resource limitation, resource dynamics and resource gradients are essential ecological processes that drive plant community composition.

By contrast, excess resource availability or fluctuations in resource availability can hinder the establishment and productivity of a desired plant community and encourage colonization by invasive plant species (Davis et al. 2000, Smith and Knapp 2001, Heneghan et al. 2004).

Nitrogen enrichment, which typically originates from agricultural or atmospheric sources but has been recently shown to occur as a result of colonization by invasive shrubs and other species

with high foliar nitrogen (N) content ((Ehrenfeld et al. 2001, Heneghan et al. 2004, Heneghan et al. 2007). For example, several studies demonstrate that the restoration of native grasslands following years of agricultural fertilizer inputs are inhibited due to elevated soil nutrient levels that favor invasive over native plant species, or reduce the diversity of natives (Blumenthal et al. 2003, Averett et al. 2004). In addition, access to nitrogen in soils often results in a reduction in arbuscular mycorrhizae and other biological properties in tallgrass prairies (Johnson et al. 2003, Lane and BassiriRad 2005). In these instances, successful restoration cannot be achieved without “defertilization” of the soil (Morghan and Seastedt 1999, Averett et al. 2004). The need for site defertilization exemplifies the importance of belowground mechanisms, mediated by soil nutrient availability, in modulating plant competitive interactions.

Plant-Soil Interactions

As the primary source for plant nutrition, soils should be considered an interactive constituent of the plant-soil system (Klironomos 2002). Current plant-soil feedback theory demonstrates that plants can influence soil microbial communities in ways that ultimately influence individual plant performance, competitive interactions, and community structure by altering abundance of belowground plant symbionts and pathogens, biologically important nutrient cyclers and abiotic characteristics (Bever 1994, Bever et al. 1997, van der Putten 1997). Furthermore, these above and belowground interactions are implicated as mechanisms for exotic plant invasion and may become permanently altered following invasion, making native plant reintroduction challenging (Ehrenfeld et al. 2001, Klironomos 2002, Calloway et al. 2004, Reinhart and Callaway 2006). Although the considerations of these relationships will likely aid

restorations, the knowledge of the impacts of these interactions and their subsequent influence on restoration remains understudied.

Mycorrhizae

More than 90% of terrestrial plants have mycorrhizal associations making their role in plant community composition and ecosystem function widespread. Particularly in tallgrass prairie ecosystems, arbuscular mycorrhizal fungi (AMF) abundance and diversity is a significant contributing factor to the maintenance of plant biodiversity and ecosystem functioning (van der Heijden and Klironomos 1998). As an extension of plant root systems, mycorrhizae are capable of extracting supplemental soil nutrients (typically P and to a lesser extent N) and moisture that plant roots are unable to retrieve unassisted. The plant translocates carbohydrates to the fungus that in turn provide the host plant with increased nutrient acquisition, growth, water relations and disease resistance (Allen 1991). This interaction can result in greater fitness and ability for plants to cope with stress. A positive growth response to AMF colonization is particularly apparent with warm-season C₄ grasses and forbs whereas cool season grasses show a lesser effect (Wilson and Hartnett 1998). Drought tolerance is also shown to increase in the presence of AMF symbionts in a number of species and habitats, though this effect can be extremely variable, with two species of the same genus showing different drought tolerance effects on host plants (Allen and Boosalis 1983). However, the degree of this interaction and the dependency or potential benefit to the plant, can vary significantly by plant, plant neighbors and fungal species (Jastrow and Miller 1993, Johnson et al. 1997). In the tallgrass prairie, C₄ plants are more dependent on their arbuscular mycorrhizae for growth and reproduction than their neighboring C₃ plants (Wilson and Hartnett 1998).

Mycorrhizal fungi may also affect plant responses to disturbance. Fire influences both the distribution and abundance of mycorrhizal fungi in tallgrass prairie and the development and function of the symbiosis between the fungi and plants (Knapp et al 1998). For example, fire stimulates active mycorrhizal growth in warm season grasses, potentially explaining the enhanced competitive ability of C_4 grasses and increased productivity following fire (Bentivenga and Hetrick 1991). In addition, tolerance to grazing as determined by regrowth capacity following defoliation in *A. gerardii* was enhanced with mycorrhizal infection (Hetrick et al. 1990). Further examinations reveals that this tolerance is also associated with P availability, suggesting that the mycorrhizal association benefits are numerous and plant-fungus interactions are dependent on soil nutrient levels (Chapin and McNaughton 1989; Schultz et al. 2001; Yoshida and Allen 2001). When soil resources are limited, high AMF species diversity is associated with high plant species diversity and productivity (Dhillon and Gardsjord 2004). However, other studies have demonstrated that, with ample soil nutrient availability, the presence of AMF communities may result in decreased plant diversity (Hartnett and Wilson 1999). As a large portion of the soil biomass, mycorrhizae are capable of competing with plants by immobilizing substantial quantities of N for their own growth (Allen 1991). The small hyphae of mycorrhizae are often prioritized towards microsites containing resources such as water and nitrogen (Egerton-Warburton, Querejeta and Allen, unpublished data). Their large absorptive surface area and secreted enzymes that mobilize N (organic to inorganic) permit efficient extraction and transfer of available N from soils directly to plant roots and is thus a vital component role in the nitrogen cycle (Allen 1991). Although it is clear that nutrient availability may drive the dependence of plants on their mycorrhizal symbionts, the impact of changes to nutrient availability on these relationships remains unclear.

An Integrative Evaluation of Restoration

Investigations into the long-term role of ecosystem processes and their influence on community structure in this study site have determined that several ecosystem factors are correlated with observed aboveground differences along a restoration gradient. This study revealed that soil temperature, light availability, inorganic, available N, total N and total C are all factors contributing to differences in plant communities in two sites differing in their historical land use [and thus restoration state] (Heneghan, Umek and others, unpublished data). This initial study was based upon a single observation of a pristine and a previously disturbed, restored tallgrass prairie at a time late in the growing season every second year beginning in 1999. The present study extends the results of the previous work by examining these long term trends in above and belowground relationships over a broader restoration gradient and temporal scale to examine the following research questions: Do the previously observed patterns in ecosystem properties persist throughout the growing season? Do current restoration practices restore ecosystem function? This project also seeks to guide management practices by asking the following more specific questions: Is aboveground restoration success inhibited by altered belowground conditions? Does resource availability differ along a restoration gradient? Does resource availability correlate with aboveground net primary productivity? What belowground components are most influenced by restoration?

Materials and Methods

Study Location

The study was conducted at the Skokie River Nature Preserve in Lake Forest, IL, a northern suburb of Chicago, IL. The Skokie River Nature Preserve consists of over 120 acres of pristine and restored woodland, savanna and prairie that is managed by the non-profit group Lake Forest Openlands. The three sites selected from this preserve are located just east of the Skokie River and are a part of the same watershed, and are comprised of the same soil type and slope (silty-loam) and only vary in their historical land use (Figure 1, USDA NRCS Web Soil Survey). These three prairies thus exist along a restoration or disturbance gradient. The sites include a restored pasture field (Bennet Meadow), a minimally disturbed prairie (McLaughlin Meadow) and a rare, remnant prairie (Shaw Prairie).

Site History and Current Management

Bennet meadow was heavily grazed by horses from for several decades. Biannual spring fire was reintroduced into the area in 1976 as a restoration technique and continued until more intense management in the form of mechanical and chemical removal of invasive species control and broadcast seeding in 1984. The land use history of McLaughlin meadow is less clear but portions were periodically mowed for hay and other areas were likely farmed for prior in the early 1900s (Christy, personal communication). In 1985, the site was managed as a prairie by biannual spring fires, mechanical and chemical control of invasive species, broadcast seeding (from Shaw) and the introduction of red fescue as a cover crop in areas with heavy brush cover. As an Illinois Nature Preserve, Shaw prairie is considered a high quality, grade “A” prairie. The site was subject to minimal anthropogenic disturbance prior to 1970 because it was viewed by

the land owner as unsuitable for grazing or agricultural production. In 1970, a sewer was installed that bisected the pristine area into a north and south section. The north section remained undisturbed, though an artesian well emerged at the east end of the sewer line resulting in the conversion of the south section of the prairie from a high quality (“A” and “B” grade) prairie to a dense community of cattails. All prairies are currently managed by Lake Forest Openlands with bi-annual fires, and periodic invasive species control in the form of hand applied herbicide for herbaceous plants or hand application of herbicide to cut woody stumps. Bennet was burned prior to sampling (spring 2006), but Shaw and McLaughlin were burned in 2005. This study compares the pristine, north section of Shaw prairie, to the highly disturbed areas of Bennet meadow and moderately disturbed areas of McLaughlin.

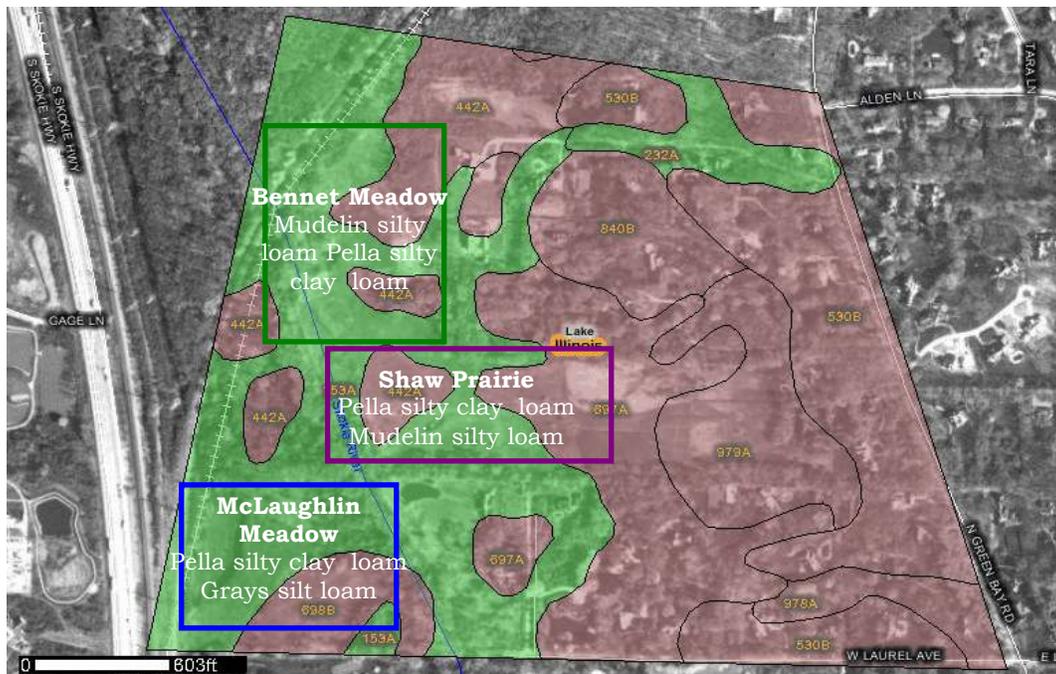


Figure 1: Map of study sites showing soil type from USDA NRCS Web Soil Survey

[\(http://websoilsurvey.nrcs.usda.gov/app/\)](http://websoilsurvey.nrcs.usda.gov/app/)

Study Species

In May 2006, a qualitative vegetation analysis was conducted to determine what plant species were present at each of the study sites. Species selection was then based upon three main criteria: selected species had to be 1) identifiable in May; 2) present in reasonable abundance in all sites, and 3) known mycorrhizal hosts. The pool of eligible species was then narrowed to three species typical of a tallgrass prairie. The final species were *Allium spp.* (including *Allium canadense* L., which was identified and collected from in June and July, and *Allium cernuum* Roth, which was identified and collected from in the remaining months), *Andropogon gerardii* Vitman, and *Silphium terebinthinaceum* Jacq. For ease of interpretation, the study species will be referred to as *Allium*, *Andropogon* and *Silphium* for the remainder of the study.

Both *Alliums* (Liliaceae) are locally frequent in mesic and dry prairies but are rarely the subject of ecological study. *Andropogon* (Poaceae) is a common, dominant C₄ grass in the tallgrass prairie and well adapted to regular fires as indicated by the strong positive correlation of *Andropogon* growth and fire frequency (Knapp et al. 1998). *Silphium* (Asteraceae) is one of the tallest and largest leaved plants in the tallgrass prairie and is considered a characteristic forb of loamy soil prairies. The leaves of this plant are often oriented along a north-south axis, facilitating maximum leaf exposure to sunlight.

Abiotic Soil Analyses

Within each study site (Bennet, McLaughlin and Shaw), and study species (*Allium*., *Silphium*, and *Angropogon*), duplicate cores of the upper 10cm of soil were sampled from beneath three replicate individuals every month throughout the growing season (June-November). In addition, one mycorrhizal hyphae trap was installed under each sampled

individual until the following collection date (see details below). Soil characteristics measured include texture, pH, conductivity, soil moisture, extractable N, available P, total carbon and nitrogen, exchangeable base cations and cation exchange capacity.

Texture

Soil texture is reported as percent sand silt and clay particles and was determined by suspending 15g of soil in 45mL of 3% sodium hexametaphosphate for two hours. Sand was removed from the slurry with a 0.053mm sieve and weighed dry (55°C). The silt was removed from the remaining silt and clay slurry through sedimentation and oven dried (105°C). Clay content was determined as the difference of the dry soil weight and the other two particles.

According to the NRCS Websoil Survey, all sites are silty clay loam, a texture that consists of 0-70% silt, 0-20% sand and 25-40% clay. Texture analysis determined that the soil texture for all three sites is the same but contain a greater quantity of sand particles (82-91%) and minimal silt and clay particles (6.5-8.1% and 2.0-9.5%, respectively) than the survey's reported texture and are classified as either loamy sand or sand. This slight difference in sand % likely reflects local site conditions that are below the sampling scale of the NRCS survey.

Soil Moisture

Soil moisture was measured gravimetrically. Triplicate 25.0g soil samples were weighed and then dried in an oven at 105°C to a constant weight. Soil moisture is reported as % moisture content, calculated as: $[(g \text{ moist soil}) - (g \text{ dry soil})] / (g \text{ dry soil})$.

pH and Conductivity

A 2:1 de-ionized H₂O to soil slurry was stirred with a pH probe following a 30 minute equilibration period. Soil pH was measured electrometrically using a Corning pH meter 430 and conductivity was measured using a Corning checkmate 90 conductivity meter.

Available P

Available phosphorus was determined using Bray 1 extraction method, which is recommended for soils with pH ranges from acidic (<6.0) to slightly alkaline (7.2). This method estimates the relative bioavailability of inorganic ortho-phosphate and uses a combination of HCl and NH₄F to remove easily acid soluble forms of phosphorus. For the slightly acidic to slightly alkaline soils of the Skokie River Nature preserve, AlP and FeP are the primary sources of phosphates and are readily put into solution with the Bray1 extraction method. Phosphates may also be present in soils as MnP, MgP and CaP though in lesser amounts (Elrashidi YEAR). 1.0g of soil was extracted with 10.0mL of Bray1 extractant (0.025M HCl and 0.03M NH₄F) for 5 minutes on a shaker table. The extracts were then filtered gravimetrically using Whatman 42 ashless filter paper. Samples were immediately analyzed for reactive (ortho) phosphate colorimetrically (Hach TNT843 total and reactive phosphorus) on a Hach DR5000 spectrophotometer.

Available N

Available nitrogen was obtained by extracting 4.0g of soil was in 20mL of 2M KCl solution for 24 hours and subsequently filtered gravimetrically before analysis for NO₃-N (cadmium reduction assay) and NH₄-N (salicylate method). Results of colorimetric tests were

read on a spectrophotometer (Hach DR5000), using Hach reagents. These values for NO₃-N and NH₄-N were then added to obtain total available N and converted to µg N/g dry soil.

Total Carbon and Nitrogen

Soil samples were dried for approximately 48 hours at 105°C and then ground in a Spex Certiprep mill for one minute or more to a consistent, fine texture. Triplicate samples were then analyzed for total carbon and nitrogen by combustion using an EA Soil Analyzer at DePaul University. Additional analysis was conducted if reported values gave a relative standard deviation of greater than 3%.

Exchangable Base Cations

100mL of NH₄OAc was added to 10.0g of fresh sieved soil and placed on a shaker table for one hour. The 10mL of the solution was then filtered using a 50mL syringe and a sterile 25mm nylon (45µm) syringe filter. The NH₄OAc was then evaporated and the remaining trace metals were re-suspended in a 5% HNO₃ solution and analyzed for Ca, K, Mg, Na, and Sr using an inductively coupled plasma atomic emission spectrometry (ICP-AES) at Kansas State University. Effective cation exchange capacity (CEC_e) is calculated from measured Ca, Na, and Mg (Ross 1995).

Biological Analyses

Aboveground Net Primary Productivity (ANPP)

Above ground vegetation was clipped and removed from five 0.25 m² quadrats at each site in February 2007. The vegetation was air dried, separated into grasses and forbs, detritus, and coarse woody material and weighed.

Hyphal Productivity

Hyphal productivity was determined using a 2 membrane mycorrhizal fungi hyphae trap (Egerton-Warburton 2005). Traps were composed of two 1.2µm membranes (25mm diameter) on either side of a ~5cm piece mesh (3mm openings). The netting and membranes were then surrounded by a 10cm long piece of fine mesh (1mm openings), sealed on 3 ends with a heat sealer. Hyphae traps were then installed vertically into the soil and collected the following month (approximately 30 days later) starting in June 2006. Careful removal of traps limited destruction of membranes, though some damage did occur during removal. Membranes were then removed from the fabric and mounted onto glass slides with Polyvinyl-Lacto-Glycerol (PVLG) for analysis. Hyphal productivity was determined from scoring 50 microscope fields for hyphae and measured as m² of hyphae produced per day.

Root colonization

Allium., *Andropogon* and *Silphium* roots were removed from soil cores from June and November 2006 collections. Roots were stained with Trypan blue in acidic glycerol using the procedure of Koske and Gemma (1989) with modifications and mounted onto glass slides with

PVLG for analysis. Root colonization was determined from mycorrhizal structure observed over 50 microscope fields. Colonization is reported as percent of root colonized by each fungal structure (hyphae, vesicles, arbuscules and coils).

Statistical analysis was conducted using Microsoft Excel 2003 and JMP 7.0. All parameters were square root transformed prior to analysis as none of the quantified variables met the assumptions for analysis of variance (normally distributed and homoscedastic).

Classification and regression analysis tree (CART) was performed using JMP 7.0. CART is a statistical tool that builds trees for predicting both continuous and categorical variables. This tool allows for the analysis of non-linear, non-parametric data that are not normally distributed and was conducted using non-transformed data. CART was used to determine which continuous variables account for differences between the study sites.

Results

The three sites significantly differed ($p < 0.001$) by moisture, pH, conductivity, nitrate (NO_3), ammonia (NH_4), total available N, total C, total N, C:N, calcium (Ca) and magnesium (Mg). There were not statistical differences by site ($p > 0.05$) for available phosphorus (P), potassium (K), sodium (Na), strontium (Sr) and mycorrhizal root colonization in June and October.

Table 1: Soil parameters that differed significantly by site.

Site	Moisture (%)		pH		Conductivity ($\mu\text{S}/\text{cm}$)	
	Mean	(SE)	Mean	(SE)	Mean	(SE)
Bennet	27.80%	0.90%	7.04	0.08	733	46
McLaughlin	23.80%	0.70%	5.57	0.13	468	23
Shaw	34.00%	0.50%	6.67	0.08	757	40
	NO_3 ($\mu\text{gN}/\text{g soil}$)		NH_4 ($\mu\text{gN}/\text{g soil}$)		Total N (NO_3+NH_4)	
	Mean	(SE)	Mean	(SE)	Mean	(SE)
Bennet	4.51	0.21	4.53	0.27	9.05	0.29
McLaughlin	1.83	0.20	5.64	0.39	7.47	0.46
Shaw	3.40	0.22	7.49	0.41	10.86	0.51
	% Total C		% Total N		C:N	
	Mean	(SE)	Mean	(SE)	Mean	(SE)
Bennet	8.47	0.64	0.03	17.57	1.17	7.04
McLaughlin	3.64	0.10	0.01	14.88	0.25	5.57
Shaw	8.44	0.48	0.04	12.45	0.09	6.67
	Ca (ppm)		Mg (ppm)			
	Mean	(SE)	Mean	(SE)		
Bennet	133.63	4.35	31.37	1.15		
McLaughlin	54.39	4.34	13.77	1.43		
Shaw	135.09	4.60	34.68	1.46		

Inter-annual Variation and Interactions

Seasonal variation across sites was observed in NH_4 , total available N, pH and conductivity ($p < 0.05$). There was a site and month interaction for NO_3 , NH_4 , total available N and conductivity. Only NH_4 and total available N were statistically different under different plant species. NO_3 , NH_4 , total available N and conductivity exhibited a plant and site interaction and only NH_4 and total available N displayed a plant, site and month interaction.

Soil Moisture

Moisture was consistently highest in Shaw soils and lowest at McLaughlin ($p < 0.0001$; Figure 2 & 3). All sites also showed seasonal variation in soil moisture due to variations in rainfall. Soil moisture peaked in September at Bennet and McLaughlin but the highest soil moisture was observed in November at Shaw and was the lowest in June at Bennet, July at McLaughlin and August at Shaw. Overall moisture was highest in Shaw throughout the growing season with the exception of September, when soil moisture at Bennet was equivalent.

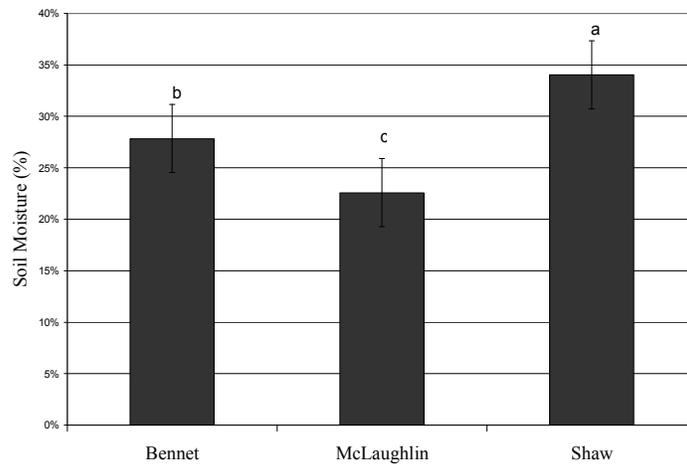


Figure 2: Average soil moisture availability by site throughout growing season.

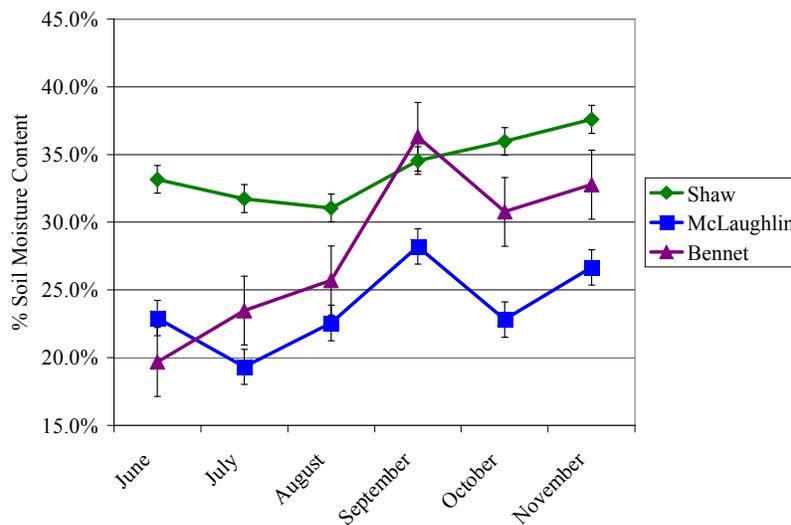


Figure 3: Soil moisture availability at each site for each month.

Available Nitrogen

Soil nitrate (NO_3), ammonia (NH_4) and total available nitrogen ($\text{NO}_3 + \text{NH}_4$) all differed among sites ($p < 0.001$, Figure 4). NO_3 and total available nitrogen also differed within sites throughout the season ($p < 0.001$), but NH_4 did not. There was also a site and month interaction for all available nitrogen measurements, as well as a site and plant interaction. However, there was only a site-month-plant interaction for NO_3 and total available nitrogen. Plant species had no effect on NO_3 but did on NH_4 and total available nitrogen ($p < 0.05$).

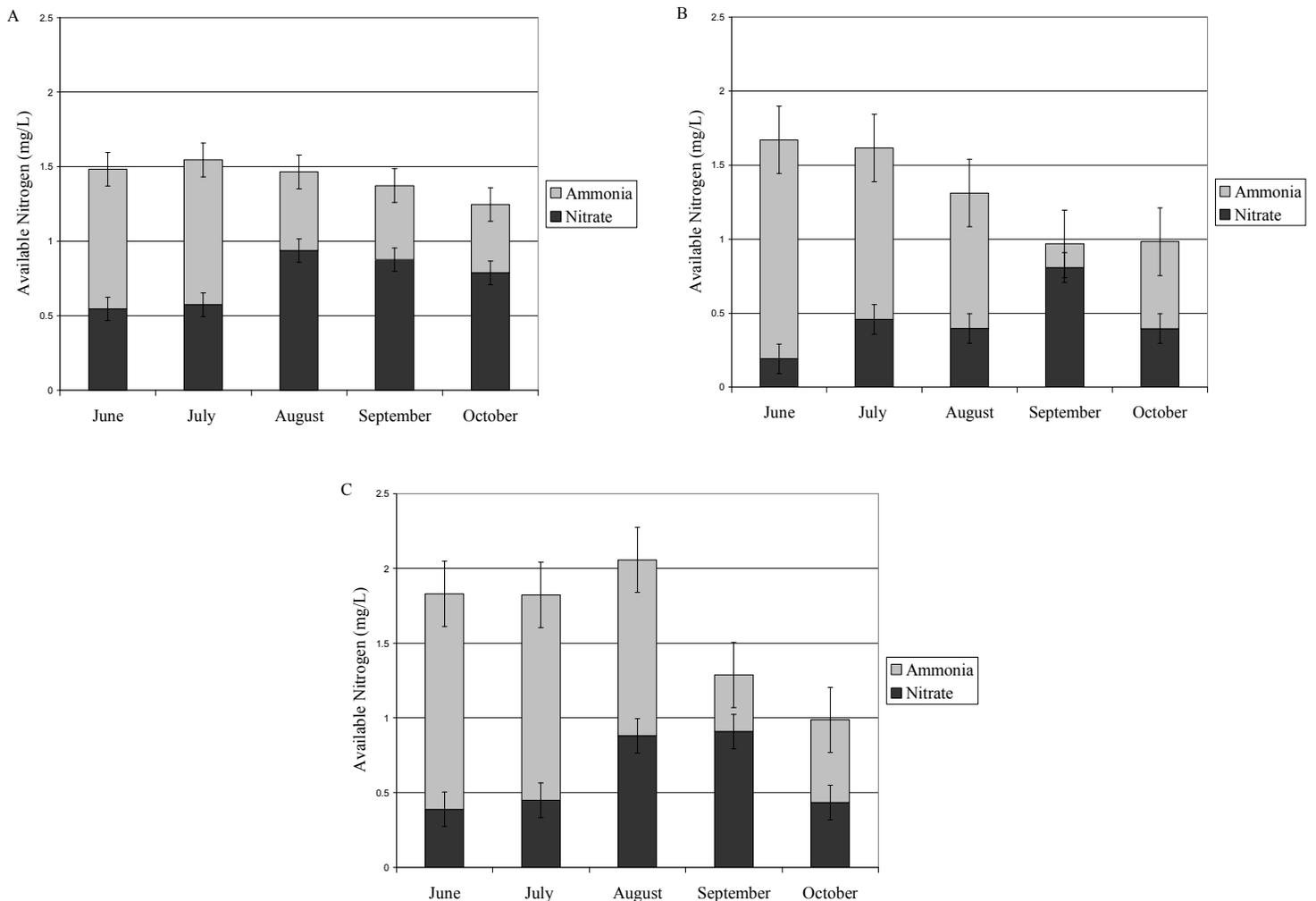


Figure 4: Total available nitrogen by component for Bennet (A), McLaughlin (B) and Shaw (C) through growing season.

Available Phosphorus

Phosphorus availability did not differ significantly across sites ($p=0.83$) or throughout the growing season ($p=0.07$).

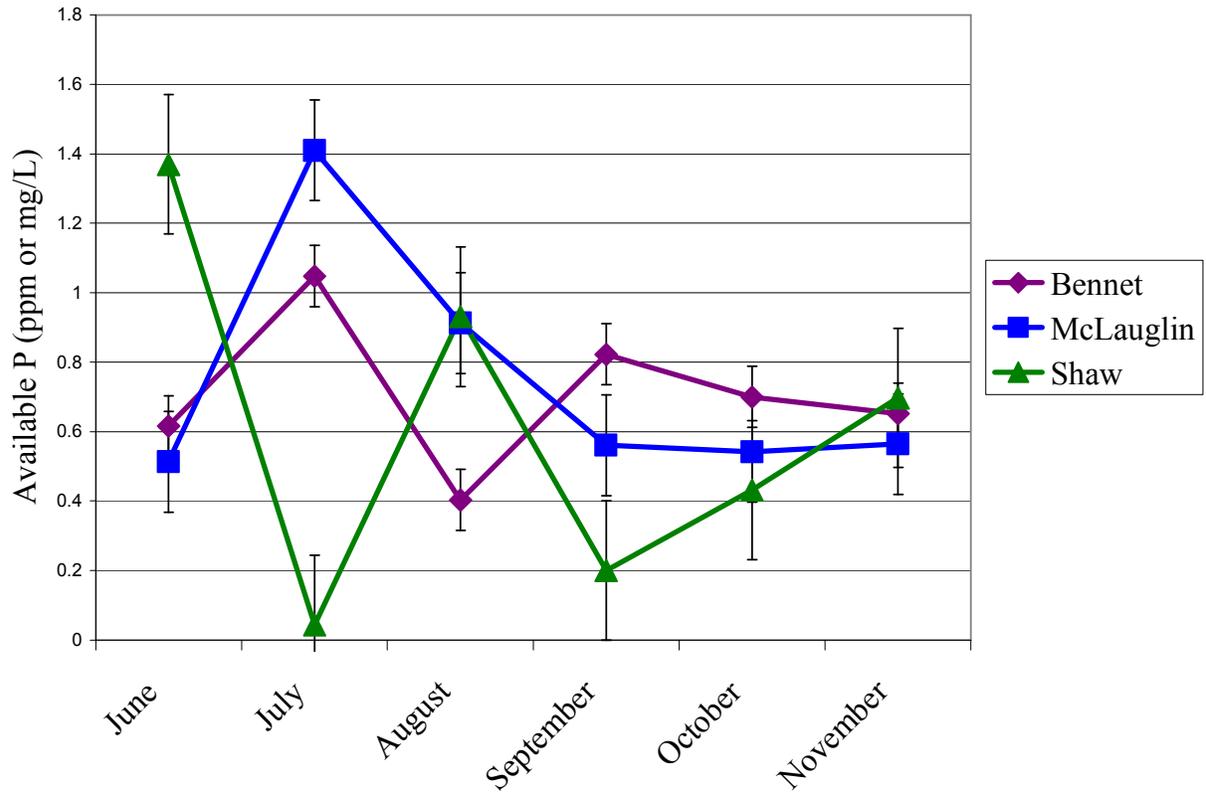


Figure 5: Phosphorus availability for each site for each month

Exchangable Base Cations

Calcium (Ca), magnesium (Mg) and effective cation exchange capacity (CEC_e) were significantly different by site ($p < 0.001$, Figure 6). For these two cations as well as effective cation exchange capacity (CEC_e), McLaughlin had the lowest concentration while Bennet and Shaw were statistically similar. Potassium (K), Sodium (Na) and Strontium (Sr) were not different by site ($p > 0.05$). The only cation that showed a site and month interaction was K ($p = 0.045$). None of the cations measured were statistically different by month ($p > 0.05$).

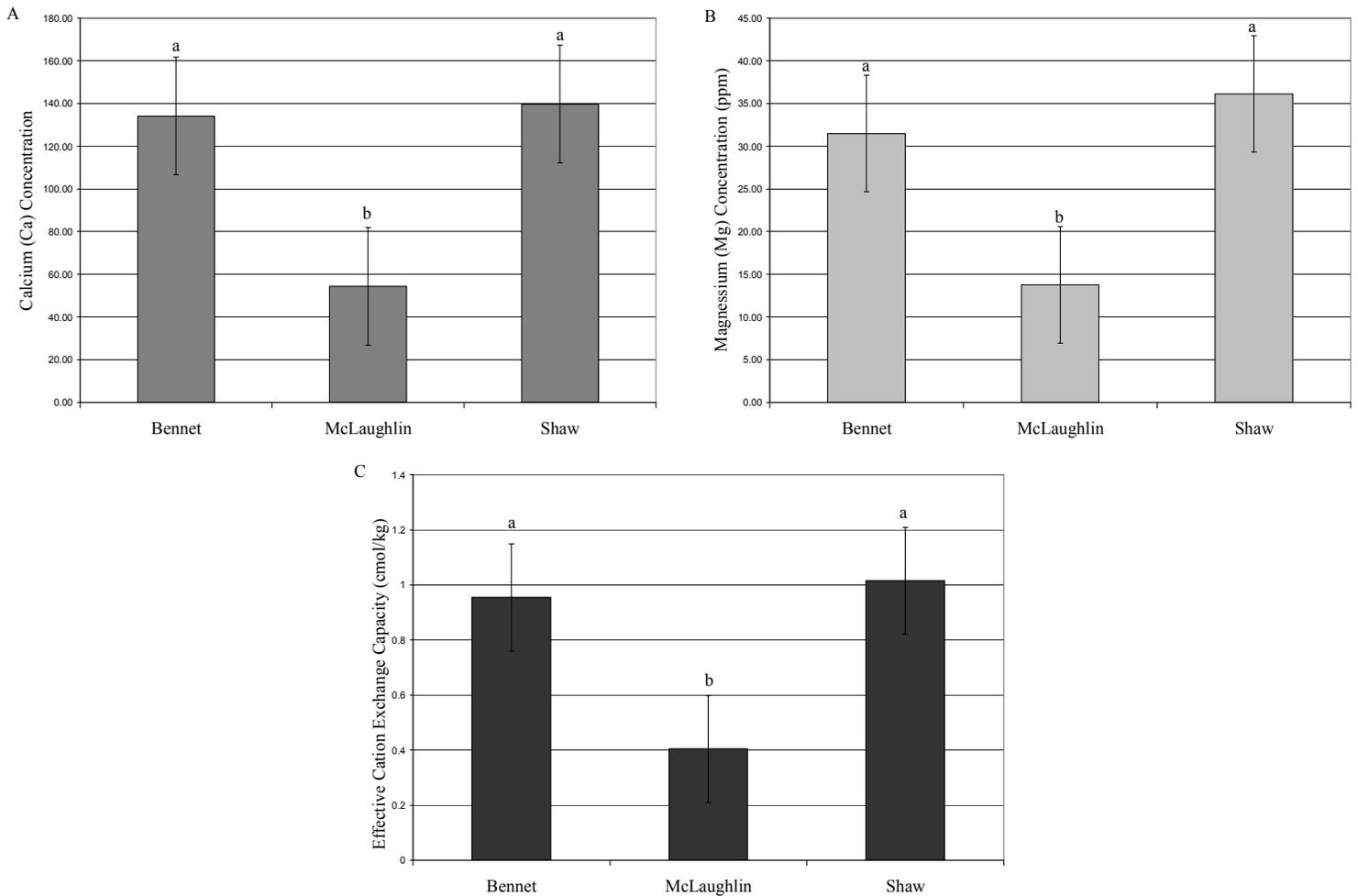


Figure 6: Concentration of Ca (A) and Mg (B) and effective cation exchange capacity (C) by site.

Total Carbon and Nitrogen

Total carbon, nitrogen and C:N is significantly different for all sites ($p < 0.05$, Figure 7).

Bennet has the highest total carbon and Shaw having the highest total nitrogen. McLaughlin has the lowest total carbon and nitrogen. Shaw has the lower though not statistically different total carbon, and the lowest C:N.

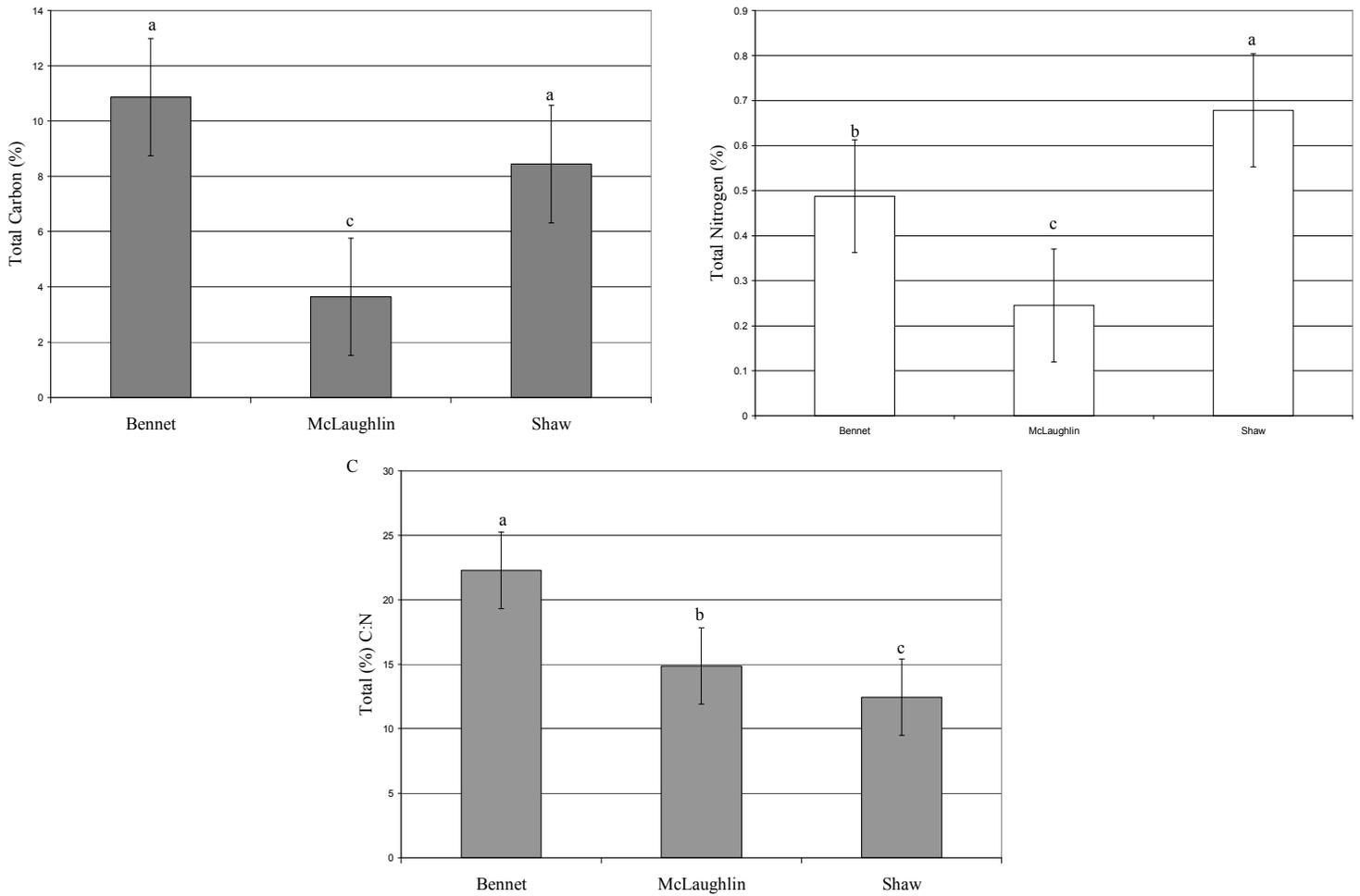


Figure 7: Total carbon (A), total nitrogen (B) and total C:N by site.

pH and Conductivity

pH differed significantly across sites and month ($p < 0.05$). In June, the pH levels in Bennet and Shaw were statistically similar ($p = 0.27$) but higher than McLaughlin ($p < 0.001$); however, in August, the pH of all sites were statistically different ($p < 0.001$, not shown). In Bennet and McLaughlin, the pH value significantly increased from June to August ($p < 0.05$), but did not vary in Shaw ($p = 0.72$; Figure 8). The soil conductivity in June was statistically different in all three sites ($p < 0.05$). In August, Bennet and Shaw conductivity was the same ($p = 0.23$) and higher than McLaughlin ($p < 0.001$).

McLaughlin soils showed consistently lower in both pH and conductivity than the other two sites. Although there is a trend of increased pH and conductivity between June and August in all three sites, this increase was only significant at Bennet ($p < 0.001$). Shaw had the highest conductivity in June, but not August.

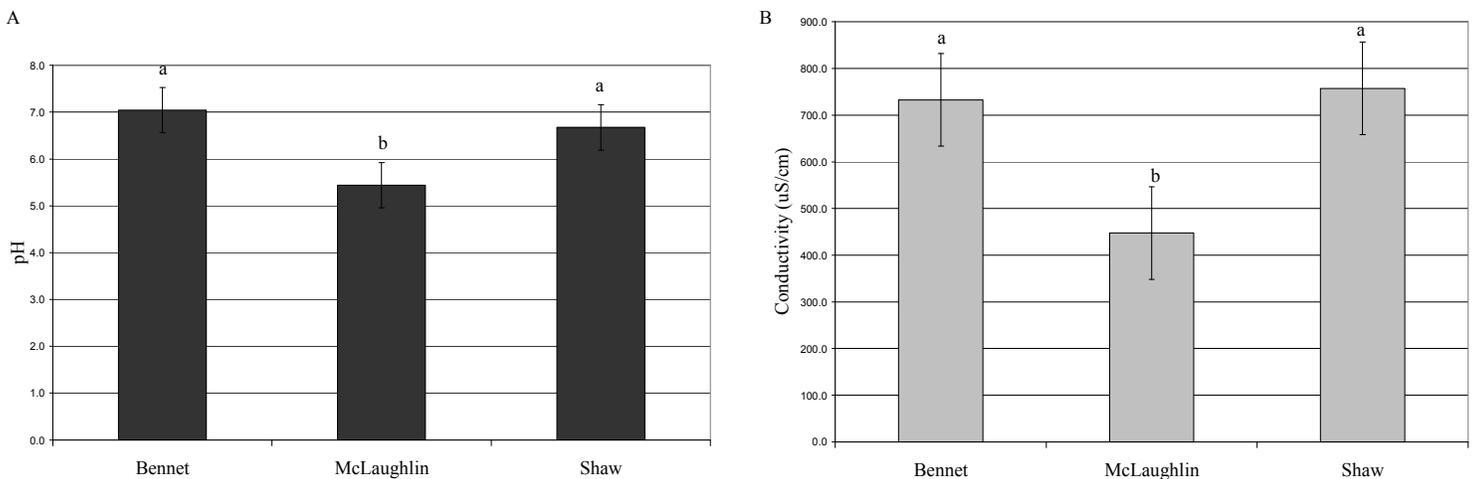


Figure 8: Average soil pH (A) and conductivity (B) by site for June and August.

Aboveground Net Primary Productivity

Aboveground net primary productivity (ANPP) was significantly higher in McLaughlin than Bennet ($p=0.047$) and Shaw (0.051) but ANPP at Bennet and Shaw are not significantly different from each other ($p=0.40$; Figure 9). ANPP did not correlate significantly with net moisture change, average available moisture or any other measured resource.

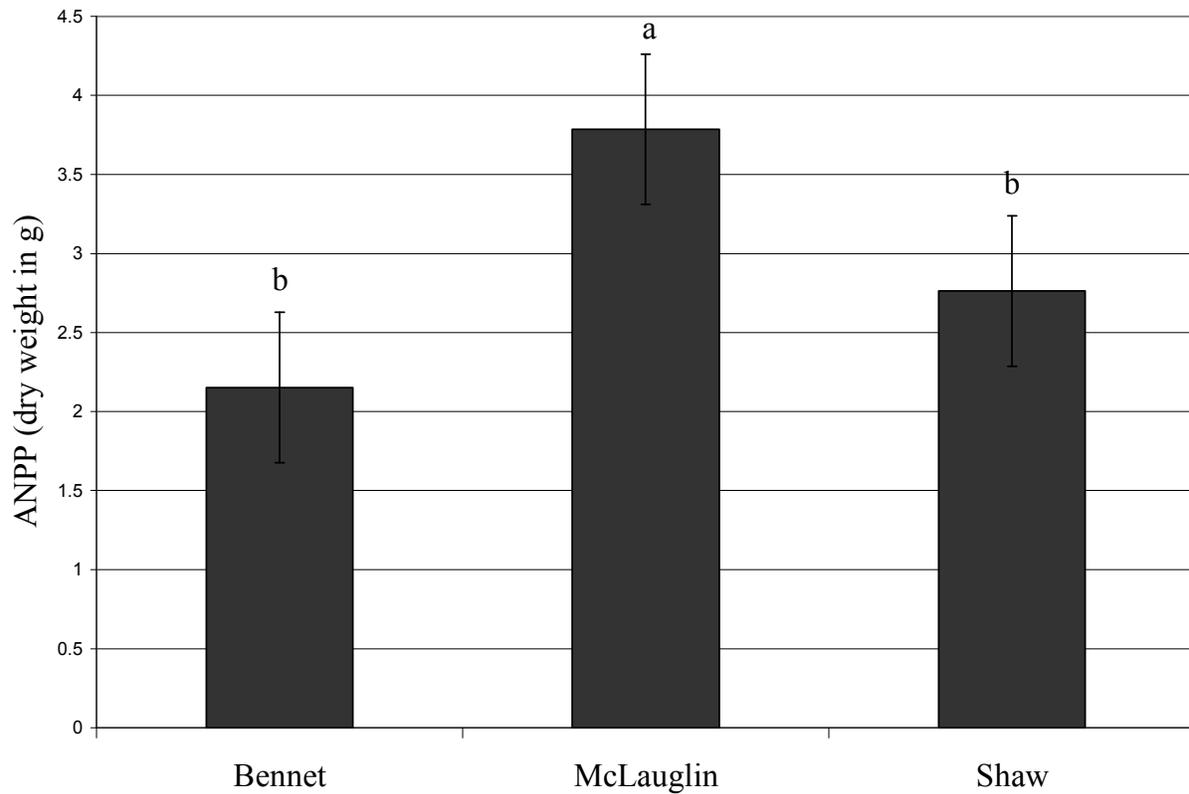


Figure 9: Aboveground net primary productivity at the end of the growing season for each site.

Mycorrhizae Root Colonization

There was no statistical difference in total arbuscular mycorrhizal fungi (AMF) root colonization between sites for either June or October nor was there a significant difference in root colonization between the three species at either month ($p>0.05$, Figure 10).

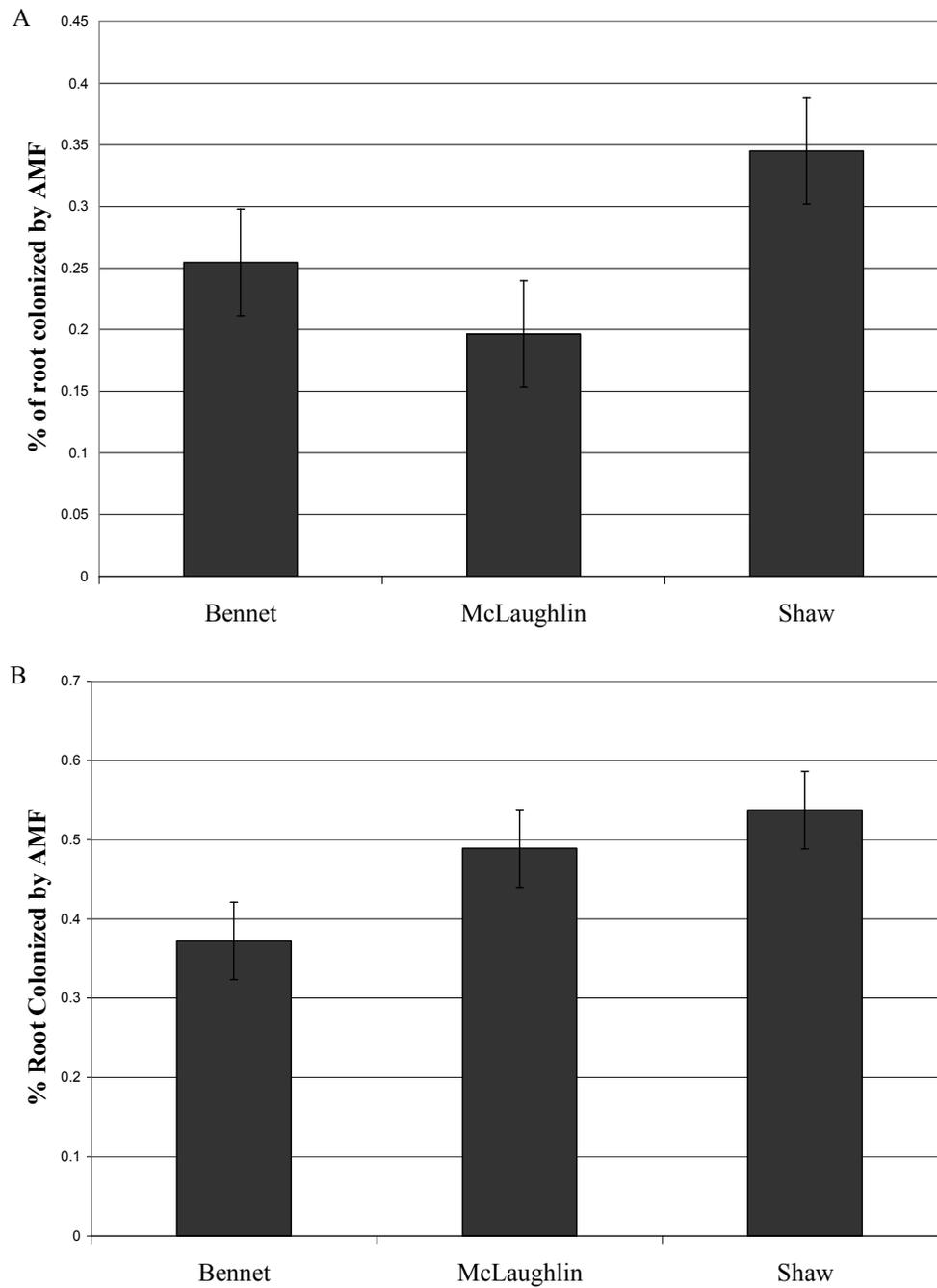


Figure 10: Mycorrhizae root colonization in June (A) and October (B).

AMF Hyphal Productivity

Hyphal productivity was not significantly influenced by site, species nor month ($p > 0.05$,

Figure 11). For all sites, hyphal productivity was highest in July through September.

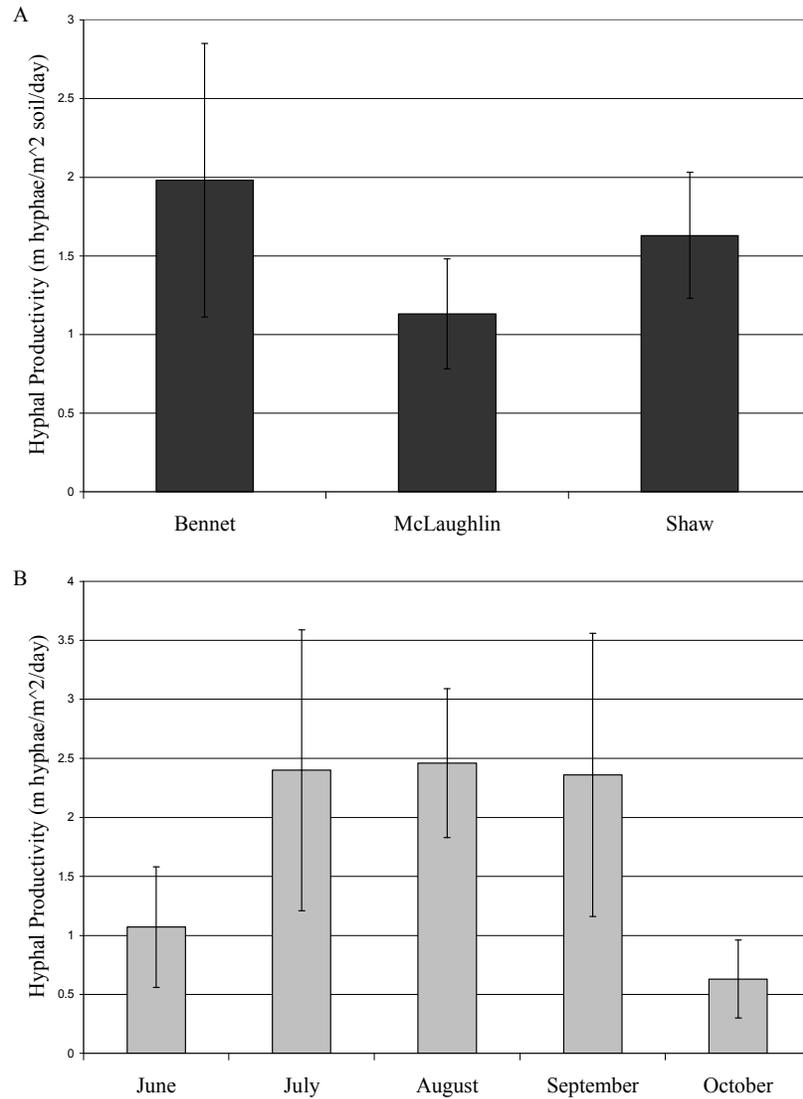


Figure 11: AMF hyphal productivity (m hyphae/m²/day) by site (A) and month (B).

Classification and Regression Tree Analysis

Over 80% ($R^2=0.807$) of the differences between the sites can be determined by soil moisture, available nitrogen and pH. Soil moisture alone accounts for over 30% of the observed variation ($R^2=0.34$) and subsequent partitioning further divides differences between sites by one of these three characteristics. The partition below shows the initial three predicting variables that divide the data by site.

Discussion

Variation by treatment

With the exception of P and AMF root colonization and AMF hyphal productivity, most quantified parameters were significantly influenced by site. This finding shows that most soil properties are significantly influenced by historic land use and restoration status, supporting previous studies showing the relationship between above and belowground processes. However, in most soil characteristics examined in this study (eg. moisture, pH, conductivity, NO₃, total inorganic N, total C and total N, Ca, Mg, mycorrhizal root colonization and hyphal productivity; Table 1), Bennet and Shaw, were more similar to each other than to the third site, McLaughlin. This finding is intriguing as the experimental design exploited the significant land use histories of the Bennet and Shaw to represent the two opposite ends of a restoration gradient.

Further, the patterns of soil resource abundance measured in this study were not consistent with the previous long term studies at Bennet and Shaw. In particular, total N was significantly higher in Bennet than Shaw in 2001 and 2005, indicating that high N content in the disturbed site was a driving force for the lower plant species diversity and the consistent presence of exotic and “weedy” plant species (Heneghan, Umek and others, unpublished data). The discrepancy between this and the previous study could arise from a number of possibilities. It is possible that the similarity in soil characteristics between the two opposite ends of the restoration gradient could suggest the management in Bennet is having a positive effect on the ecosystem properties. More specifically, this study was conducted in the growing season immediately following a spring fire in Bennet, but not in the other two sites. The recent fire is the most likely explanation for the lower total N and higher total C content in Bennet compared to previous years. However, since belowground responses to a fire are visible for at least two

years post-fire and these sites are managed by biannual fires, the ecological responses to fire would persist from the previous year's prescribed burn.

Alternatively, the striking similarities from a belowground perspective could potentially indicate ecosystem processes in Bennet are in fact recovering with management. While this effect is not yet observed in the plant community, it is possible that the plant community is slower at exhibiting a notable response to this restoration. This explanation is in agreement with other similar studies that show that belowground biological components, mycorrhizae in particular, respond to disturbance and management faster than plant communities. For example, this pattern was demonstrated in N enrichment studies in 5 Long Term Ecological Research (LTER) grasslands (Johnson et al. 2003). The similarities between the mycorrhizal root colonization as well as hyphal productivity across these sites suggests that the effects of restoration may have a similar impact, influencing the belowground biological communities well before changes are observed in the plant community. If the latter explanation adequately explains these observed occurrences, the plant community may begin to exhibit positive responses to the apparent successful restoration of ecosystem processes.

Inter-annual and Plant Species Variation

Within each site, available N (notably NH_4), and soil moisture varied throughout the season. These fluctuations are expected in a temperate environment where temperature, precipitation and thus biological activity can vary substantially in any given year. While this study only examined resource availability throughout a single growing season, other studies suggest that variations in biological activity and weather may also result in short-term ecological and resource availability variations.

For all other soil characteristics, inter-annual variation was not significant and therefore they are not likely major contributors to seasonal biological interactions. Future studies of most soil characteristics with the exception of available nitrogen are thus likely well represented by a single sample date.

The lack of variation in most soil characteristics by plant species is explained by the close proximity of each species to its neighbor. Variable and heterogeneous nutrient availability are likely explanations for plant specific distinctions in soil resource availability.

Soil Moisture

Water availability is a strong driver for biological activity in the temperate region. The pronounced difference in soil moisture between the sites has significant implications for both the plant and soil biological communities and their functions. The lower soil moisture at McLaughlin is apparent by casual observation of the plant community. Because the vegetation is dominated by C₄ grasses, primarily large clusters of *Andropogon*, productivity at McLaughlin is relatively high despite its low moisture content. This is consistent with other tallgrass prairie studies that showed that inter-annual soil moisture and precipitation was negatively correlated with grass productivity but positively correlated with forb productivity (Briggs and Knapp 1995).

The overall soil moisture at Shaw has lower inter-annual variation. This is particularly noticeable near of the end of the growing season in September when soil moisture increases McLaughlin and Bennet but remains on a consistent trajectory in Shaw. This suggests that the soils at Shaw are more capable of maintaining a constant moisture level with seasonal precipitation fluctuations and perhaps provide a more reliable source of water for both aboveground and belowground biological activity.

Labile Nutrients

Soil available phosphorus was not significantly influenced by site or month. The high variability in available phosphorus observed in all sites throughout the growing season suggests that, as a resource, P has a patchy distribution but pools are overall similar between sites. Soil heterogeneity is a common phenomenon in many ecosystem studies. This patchiness of resource availability is often associated with uneven distribution of soil biota and plant communities and may serve to maintain biodiversity in many terrestrial ecosystems.

A primary component of inorganic N in temperate soils is NH_4 (as opposed to NO_3), which is readily transported to plants by arbuscular mycorrhizal symbionts (Allen 1991). Ammonium content was significantly impacted by all measured variables (site, plant species, month and interactions among them) which indicated that fluctuations in NH_4 in soils varied depending on restoration state and season. The visible spike in NH_4 in the later summer months of August and September is likely due to its correlation with the peak growth of C_4 grasses. During these comparatively hot and dry months, C_4 grasses thrive and root exudates may enhance soil microbial activity and decrease the proportion of NO_3 available in the soil. The general trend of increased available N in the summer months and a decrease at the end of the growing season is typical for a temperate grassland ecosystem as the later months are periods of vegetative growth cessation and decreased biological activity in the soil. Nitrate content varied only by site and interactions with site, which suggests that this form of N is most likely directly influenced by restoration. The observed variability in plant species is likely due to landscape soil heterogeneity, since most sampled individuals were within close spatial proximity to each other.

Soil exchangeable base cation concentration show similar responses to restoration as pH, conductivity, total C and total N where Bennet and Shaw are similar to each other but both

higher than McLaughlin. The similarity between cations, pH and conductivity is not surprising as these measurements are influenced by each other. Though there is no historical record of cation concentration in either of these sites, the trends observed in this study are parallel to other soil characteristics and may serve as useful references for future studies of these sites. This baseline information will be particularly useful in examining the effects of fire on these trace soil nutrients. Fire induces an increase in soil Ca and Mg but the immediate increase in both K and Na is not detectable in post fire soils as these elements are rapidly lost due to leaching (Likens et al. 1967, Hobbie and Likens 1973, Forgeard and Frenot 1996, Egerton-Warburton 2005). In particular, it would be useful to determine if the similarities between Bennet and Shaw persist in years of different burn cycles, as is observed with total C and total N.

Total Carbon and Nitrogen

The total carbon and nitrogen results from this year's data are significantly different than those from previous studies comparing Shaw and Bennet. In studies conducted in 2001 and 2005, Shaw had a significantly higher C:N ($p < 0.001$) and significantly lower total nitrogen than Bennet, suggesting that the dominance of weedy species at the latter site was due to legacy effects of intensive grazing and heavy herbicide use by land managers. The current observation that Bennet has a significantly lower total N pool than Shaw, while initially surprising, is likely a result of N release during the prescribed burn that occurred in the spring months prior to sampling. Fire is a major pathway of nitrogen loss in ungrazed tallgrass prairie and had been shown to reduce both N mineralization and N availability (Johnson and Matchett 2001). The spring burn at Bennet is also the likely cause of the significantly larger C pool at Bennet.

Aboveground Net Primary Productivity (ANPP)

Patterns in ANPP in tallgrass prairie are a product of spatial and temporal variability in light, water and nutrients; all factors that are driven by topography, fire history and climate (Briggs and Knapp 1995). Ecologists have often correlated biodiversity, productivity and ecosystem stability, suggesting that this relatively simple measure can indicate a great deal about a given system's stability and function (Tilman and Downing 1994, Tilman et al. 1996, Yachi and Loreau 1999, Loreau et al. 2001, Tilman et al. 2001). Previous studies comparing ANPP at Shaw and Bennet over a 6 year period indicated that primary productivity was consistently higher at Shaw than Bennet, supporting the hypotheses relating ecosystem function to aboveground productivity. Moreover, productivity was maintained at Shaw during the drought year (2005) compared to significant decreases in productivity Bennet and another adjacent prairie (Heneghan, Umek and others, unpublished data). The lack of distinction in ANPP between Bennet and Shaw in this study is likely due to a difference in collection methods. Aboveground biomass was collected in this study following the winter season and is therefore not likely an accurate determination of true productivity as detritus is not easily distinguishable from recently produced biomass and recent studies demonstrate that decomposition continues throughout winter (Schadt et al. 2003).

Nevertheless, the high productivity observed at McLaughlin was largely due to *Andropogon*. Since warm season grasses, such as *Andropogon*, are obligate mycotrophs that show large positive growth responses to mycorrhizae and will not prosper in native prairie soils without the symbiosis, while cool season grasses show smaller growth responses with mycorrhizal infection (Hetrich et al. 1988; Hetrich et al. 1992), it was expected that *Andropogon* root colonization would be greater in McLaughlin than the other sites and that colonization on

this species would be greater than other studied plants. The lack of distinction in either of these parameters suggests that perhaps the decreased soil moisture at McLaughlin offers a great enough competitive advantage for the dramatic growth of *A. gerardii* in this site.

Soil Properties Most Influenced by Restoration

Using Categorical and Regression Tree (CART) analysis, the best predictor (or soil characteristic) for site was moisture followed by available nitrogen and pH. This is promising for the application of soil ecology into restoration as it suggests that both current and future restoration projects can be guided by a few simple soil parameters. Therefore, it may be possible for practitioners, using the soil parameters observed at Shaw and ultimately other areas considered high quality prairies as a reference, to set more inclusive restoration goals and have more tools to evaluate restoration success.

The influence of restoration on soil characteristics is apparent in this study. Often restoration practices and the subsequent success [or failure] measured by the presence or absence of a desired plant community. A recent study on prairie restoration in Midwestern tallgrass prairie indicated that the establishment of a native vegetation matrix drives ecosystem processes in the trajectory of the original ecosystem (Baer et al. 2002). However, other studies of atmospheric N deposition show that soil organisms, mycorrhizae in particular, respond more rapidly to disturbances than plants. The similarities in many of the observed soil chemical (pH, conductivity, moisture, available N, total C, total N) and biological properties (mycorrhizal root colonization) suggest a similar rapid belowground response to restoration is occurring. Therefore, I propose that in this case, soil characteristics and thus ecosystem processes are initially influenced by restoration and that these effects will not be observed in the plant

community for several years. Contrary to the previously mentioned study along a restoration gradient, this study demonstrates that restoration immediately sets belowground processes on a trajectory that, with continued management, will ultimately result in a positive plant community response.

Many restorations are deemed “successes” or “failures” based solely on traditional measures of [aboveground] biodiversity. While floral biodiversity can be a valuable indicator of environmental conditions, niche availability and potentially ecosystem functioning, this measurement alone may be artificial and is prone to exploitation. Floral species diversity in a restoration project is often artificial as the manipulation of species composition is often the method by which restoration is carried out and high levels of biodiversity can be maintained through anthropogenic inputs, ie. referring both to manual labor and the reintroduction or removal of certain organisms. Alternatively, a restoration could be labeled a failure where aboveground biodiversity may be low, but below ground organisms and larger scale nutrient cycles are undergoing a gradual recovery. Thus, criteria of vegetational biodiversity alone are no clear indication of restoration success and should only be used as one of a suite of criteria. The goal of restoration should not seek solely to achieve greater plant biodiversity but should seek to increase biodiversity more broadly and do so by restoring the ecosystem processes that support and sustain a high diversity of organisms both above and below ground.

Since the overall goal of natural areas conservation and restoration is the long term preservation of biodiversity, long term success of this project must incorporate or at least consider basic genetic and evolutionary principles for sustainable, long term successful restoration of biodiversity. In fact, failure of some previous restoration sites may be due to the lack of attention to evolutionary processes (Choi 2004). The paucity of literature on the failure

of restoration suggests that the reconstruction of a 'historic' ecosystem appears to be an unlikely goal in the ever-changing and unpredictable future environment. Choi calls for a shift in the restoration paradigm from 'historic' to 'futuristic' (Choi 2004). In other words, a sustainable restoration management plan will: (i) set realistic and dynamic (instead of static) goals for future, instead of past, environment; (ii) allow for multiple trajectories acknowledging the unpredictable nature of ecological communities and ecosystems, (iii) take an ecosystem or landscape approach, instead of ad-hoc gardening, for both function and structure; (iv) evaluate the restoration progress with explicit criteria, based on quantitative inference; and (v) maintain long-term monitoring of restoration outcomes (Choi 2004). While the language Choi (2004) uses is perhaps harsh on current land managers and neglects to recognize the wealth of practical knowledge and experience that managers incorporate into restoration plans, his point remains valid. Without incorporating evolutionary concepts, particularly in light of growing concern of climate change, conservation and restoration plans are destined for a questionable future.

By neglecting soils (thus neglecting ecosystem processes) from the evaluation of restoration success, restorationists are practicing “conservation gardening” (Janzen 1998). While it is true that both conservation gardening and restoration utilize similar techniques and tools, they are primarily different in their ultimate goal. Restoration seeks to restore systems so that they are sustainable – that is, requiring no (or minimal) additional inputs to continue along a successional path.

If the long term goal of conservation is to save a few rare species, we could easily meet this goal by maintaining plant populations in controlled greenhouses. However, if the ultimate goal of conservation is to provide and promote suitable habitats for a variety of rare and common plant and animal species, restoration and conservation must include a soils and belowground

community and ultimately ecosystem perspective. To trivialize this point, one could say, “you can’t grow prairie fringed orchid in a parking lot”. This statement implies the need for a more holistic approach to conservation, particularly in urban settings, if we seek to restore natural areas: we cannot only look at the above ground component.

Restorations can learn from soil ecology and vice versa

Collaborations between researchers and practitioners are ultimately the method by which to answer questions that both parties have. Restorations often do not include soil examination not because the practitioners do not feel it is important; rather, they often recognize that the soil is a critical component for their restoration success, but are unsure of how to know what is “wrong” or how to fix it. Researchers often have these same questions. Therefore, collaborative projects in which researchers and practitioners work together on a restoration design, one that is sufficiently replicated to satisfy the scientist’s goals using methods that are potentially useful to the practitioner, can benefit both parties.

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