ABSTRACT

Title of thesis: SOIL PROPERTIES AND NATIVE PLANT COMMUNITIES IN A KANSAS PRAIRIE

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I hypothesized that the relative proportion of grasses and legumes in native prairie communities are associated with physical and chemical soil properties. In a greenhouse study, I determined species responses to differences in soils *ex situ* by individually growing three grasses, two legumes, and two composites in soils from four sites on a never-plowed prairie at The Land Institute in Saline County, KS. The highest organic matter (OM) soil produced the highest plant dry matter for five of the species. In a field study, I measured 20 soil properties in 24 quadrats (0.5 m^2) with high, low, or no legume cover on the same four sites. After incubation, NH_4 in subsurface soils was lower for high legume cover suggesting higher nitrification. Discriminant multivariate analysis showed the ratio, active C as a percent of total C, and percent OM were the most closely associated surface soil variables with percent legume cover.

SOIL PROPERTIES AND NATIVE PLANT COMMUNITIES IN A KANSAS PRAIRIE

by

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DEDICATION

I dedicate this thesis to my late college professor
and advisor, Tom Dent, who inspired me to venture into the
world of agronomy and sustainable agriculture.

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Chapter 1: Introduction

Problem statement and research justification

The Great Plains region has been one of the greatest resources for grain production in the United States since the 1930's. Its deep, organic matter-rich soils formed during 10,000 years (Paul et al., 1997) of grassland vegetation and became a reservoir of nutrients and organic matter. Since the Homestead Acts of the late 1800's, the eastern half of the U.S., including most of the tallgrass prairie, has been largely converted to either croplands in which annual harvests remove nitrogen and other nutrients from the soil, or pastures with introduced forage species (Barnes and Nelson, 2003). From the 1930's to the 1970's, average yields for corn and wheat in the U.S. more than doubled (USDA, 1945; USDA, 1975), most likely resulting from favorable growing conditions, irrigation, and the development of high yielding varieties adapted to fertilizers and modern farming methods (Oelhaf, 1978). During this same time, fertilizer and lime inputs increased by more than ten fold (ERS, 1969; ERS, 1973). However, while productivity increased, soil nitrogen and carbon losses also increased. The average loss of soil nitrogen across 14 locations in the Great Plains was 39 percent over a 36-year period during the early 1900's (Haas et al., 1957). Out of its total 220 million hectares, over 41 million hectares of the Great Plains lost its topsoil layer by wind erosion between 1934 and 1966 (McKee, 1974). Despite the droughts of the 1930's and 1950's, high yields have still been maintained with the increased use of irrigation. Dryland farming in the northern regions has sustained production without irrigation, because of much less evaporation of water from rainfall and river tributaries from the Missouri River. However, because of higher temperatures in the south, evaporation is much greater and

therefore, irrigation use has enabled even more conversion of grazing lands into croplands. Food production in the past century has increasingly depended on fossil fuels, and hence on fuel imports (McKee, 1974). Clearly, there is a need for alternative systems of agriculture to hold the soil, conserve nonrenewable resources and minimize the use of fertilizers, while still remaining productive.

The native prairie of the Great Plains region, with its mixture of grasses, legumes and other herbaceous perennials may provide a model for an alternative system of agriculture. Perennial grass species such as *Andropogon gerardii* Vitm., dominates the vegetation, keeping the soil covered. These grasses have the majority of their biomass underground and therefore can withstand aboveground natural disturbances, such as fire and grazing. Legumes and nitrogen-fixing bacteria add nitrogen to the soil from the atmosphere while the extensive root system of grasses takes up available nutrients and returns organic forms to the soil through root senescence (Whitehead, 2000).

In contrast, conventional grain farming in the U.S. generally uses herbaceous annuals grown in monoculture. Unless no-till methods are used, this disturbs the soil each growing season and leaves the soil exposed unless covered with cover crops. Since the crop is harvested annually, large amounts of nutrients may be removed from the farming system, requiring added fertilizer. An alternative system, proposed by Jackson (2002) and termed Natural Systems Agriculture (NSA), is being explored by researchers at The Land Institute in Salina, Kansas, to develop agriculture that mimics the prairie ecosystem. One advantage to using this system could be that perennial crops would minimize the amount of soil disturbance required, with planting only once in three to five years. A second advantage would be that perennial N-fixing legumes included with perennial grasses may

minimize dependency on fertilizer inputs. Thirdly, a system with multiple species grown together could potentially increase overall productivity (George et al., 1995; McGinnies and Townsend, 1983; Posler et al., 1993, Tilman, 1996). According to a multi-site field study, carried out across eight European countries, overall plant biomass productivity was positively related to the number of species growing in association (Hector, 1999).

In establishing perennial plants for agriculture, not only must climatic factors like annual temperature and rainfall be considered, but also variations in soil conditions. Physical, chemical, and biological properties of the soil can vary widely even over a few hectares. The structure and texture of soil can influence soil water infiltration (Lowery et al., 1996) and moisture content (Brady and Weil, 1999). The amount of moisture in soil can affect the microbial activity that converts organic forms of nutrients into plant available forms (Rice et al., 1996). Nutrient availability can then influence plant species dominance (Tilman, 1984). Relationships between soil properties and the dominance of certain plant species in a natural prairie environment may aid in tailoring appropriate species mixes for specific soil types in a managed polyculture environment (Soule and Piper, 1992).

In a symbiotic relationship with *Rhizobium* bacteria, legumes fix atmospheric nitrogen and provide themselves and other plants with this most limiting soil nutrient. Since legumes are responsible for most N additions to the prairie ecosystem (West and Nelson, 2003), the balance of legumes with grasses is a critical aspect of sustained productivity. Legumes or other nitrogen-fixing plants provide the most practical alternative to synthetic N fertilizer to replenish the supply of available nitrogen taken up by the non-fixing plants and removed in grain harvests. Therefore, the relationship

between legumes, grasses and soil properties is likely to be important in an agricultural system modeled after the prairie.

Background and literature review

Traditional agriculture, especially in tropical countries, has a long history of using intercropping systems. However, these systems usually involve annual herbaceous or perennial woody plants. Little research has focused in perennial herbaceous polycultures for grain agriculture, especially in a temperate climate. Certainly, rangeland and pasture research considers herbaceous perennials, but only for their use in vegetative growth, not for seed or fruit production. The Land Institute is one of the few places where research is being conducted for the development of using perennial grasses for grain production (Soule and Piper, 1992)

Research on a range of native prairie legumes is needed to provide tools to maintain soil fertility internally in a perennial grain system. Most agricultural research in the U.S. for improving grain production has focused on external inputs. However, managers of forage production have long recognized the importance of legumes in grassland agriculture. Numerous pasture studies suggest legumes, especially clovers (*Trifolium* sp.), grown with pasture grasses improve soil fertility and reduce dependency on N fertilizer (Barnes et al., 1995). Clovers have been extensively studied in their N_2-fixation and forage production responses to added N fertilizer (Ledgard et al., 1996), uptake of labeled N as compared to grasses (Walker et al., 1956), available soil nutrients (Evans, 1977, Jackman, 1972) or other soil properties (Whitehead, 1982). One of the long-term benefits of using legumes is reduced use of N fertilizer, the cost of which is

likely to rise as fossil fuel prices rise with dwindling supplies. The widely grown white clover (*Trifolium repens* L.) grown with tall fescue (*Festuca elatior* L.) has been considered more cost effective than using N fertilizer with tall fescue when fertilizer is at least \$0.44 kg^{-1} and clover stands are maintained for at least three years (Pederson, 1995). In prairie grasslands, some contend that it may not be beneficial to rely on N fertilizer, as it has been shown to increase exotic species over time (Berg, 1995). Lorenz and Rogler (Lorenz and Rogler, 1972) found contrasting results in mixed prairie vegetation. Over an eight-year period, at increasing levels of N, density of western wheatgrass (*Pascopyrum smithii* Rydb.) increased while basal cover of blue grama (Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths) decreased. More research is needed to better understand how the prairie plant community maintains its soil fertility in various environments.

Most grassland research has been on introduced legume species from Europe that have since become well established in the United States (Barnes et al., 1995) and used largely in cool-season grass-legume mixtures. Recently, researchers have investigated the N benefits of using cool-season (i.e. thrive in cool, moist periods of the growing season) legumes with warm-season grasses to extend the seasonal distribution of forage production. In a field experiment, George et al. (1995), used 11 different cool-season legume cultivars inter-seeded into stands of switchgrass (*Panicum virgatum* L.) and compared these with four levels of N treatments in switchgrass alone. For the second year, six legume treatments yielded higher than the 240 kg ha^{-1} N treatment, and all but one legume treatment yielded higher than the 0 kg ha^{-1} N treatment. For the third year, although only three legume treatments yielded higher than the 240 kg ha^{-1} N treatment, all legume-grass combinations, but one, yielded higher than the 0 kg ha^{-1} N treatment,

despite that year's poor growing conditions for legumes. Legumes contributed 84 percent of upper canopy yield in the second year and 56 percent in the third year. George et al. (1995) concluded that after the first year of establishment, cool-season legumes could potentially substitute for N fertilizer and improve seasonal distribution of forage yield.

On the other hand, incompatibility between warm-season grasses and introduced cool-season legumes is an important consideration when optimizing yields or forage quality (Posler et al., 1993). Recent attention has been given to native prairie legumes in their ability to improve forage yield of warm-season grasses. Posler et al. (1993) seeded combinations of native prairie grass species with and without six different native legume species in a field experiment in unfertilized Kansas soil. After four and five years, total yields of grasses with legumes were greater than yields of grasses alone, for five out of the six legume-grass mixtures. McGinnies and Townsend (McGinnies and Townsend, 1983) seeded Russian wildrye (*Psathyrostachys juncea* (Fisch.) Nevski) and crested wheatgrass (*Agropyron desertorum* (Fisch.) Schult.) with sicklepod milkvetch (*Astragalus falcatus* Lam.) and alfalfa (*Medicago sativa* L.) in rows, and after nine years, average forage yields for all grass-legume mixtures were more than that of the grass alone. Dovel et al. (1990) inter-seeded Illinois bundleflower (*Desmanthus illinoensis* (Michs.) MacM.) into stands of kleingrass (*Panicum coloratum* L.). For three successive years after one year of establishment, average yields of kleingrass grown with Illinois bundleflower were less than kleingrass grown alone, but the total yields (grass + legume) were at least 43 percent greater. Although all of these studies showed improvements in

yield or forage quality with certain grass-legume combinations, it was also shown that some legume species do not increase stand productivity.

In addition to finding compatible species, establishing perennial polycultures may require knowledge of the most beneficial proportion of legumes to grasses. In grassland management, it has generally been accepted practice to manage for the legumes rather than the grass. It is recommended that stands of white clover be maintained at proportions of 20 to 40 percent in a grass-clover mixture for optimum productivity (Pederson, 1995). Mallarino and Wedin (1990) broadcast-seeded white clover, red clover (*Trifolium pratense* L.), and birdsfoot trefoil (*Lotus corniculatus* L.) with seeds of tall fescue (*Festuca arundinacea* Schreb.) into plots to obtain dry weight swards with average legume proportions of 30, 50, 60, and 90% dry matter. The best dry matter yields of white clover, in combination with tall fescue, required a proportion of about 50-60%. Optimum proportions of red clover and birdsfoot trefoil were much more variable between years.

Understandably, agricultural research on grasslands is primarily concerned with palatable species for grazing and forage production. Less studied legumes, not palatable for livestock, may still be valuable to the ecosystem. One example is scurfpea (*Psoralea* sp.), which, although is unpalatable for most domestic livestock, is used by wildlife (Holechek et al., 2004), such as plains pocket gophers (*Geomys hursarius*), deer (*Odocoileus virginianus*), and pronghorn (*Antilocarpa americana*) (Stubbendieck and Conard, 1989). These and other legume species may be appropriate in the development of prairie grasslands for managed polyculture systems.

Soil-plant interactions between grasses and legumes represent a mutualistic relationship (Ledgard and Steele, 1992). When soil N is low, legumes have the advantage over grasses as they are able to fix N_2. They compete less for soil N, resulting in more soil N available for grasses. N concentrations in tall fescue herbage have shown positive correlations to white clover proportions in grass-clover mixtures (Mallarino and Wedin, 1990). When soil N is depleted from increased grass growth, as with late winter/early spring growth of perennial ryegrass (*Lolium perenne* L.), for example, legume growth in late spring/summer can be enhanced again by low soil N (Harris, 1987). Wedin and Tilman (1990) studied above and belowground litter quality of five perennial grasses grown in monoculture and estimated their peak mineralization rates for three years. The species varied widely in both their peak mineralization rates and the amounts of nitrate found in the soil during those peaks. Mineralized N levels in soil are highly variable throughout the year and can come from both plants and total organic N in the soil. Plants may affect soil N levels, while the supply of available N in the soil may affect the growth of plants.

Rangeland management data have added much to the knowledge of associations between soil type and plants. Soil survey reports characterize range sites as plant communities composed of certain species associated with a specific type of soil. Although the NRCS Soil Survey indicates the percent of each principal grass species likely to be found in a particular range site, legume species are grouped together with other non-grass species in the percent of “forbs” likely to be found (Palmer et al., 1992). According to the survey, the term “forbs” includes legumes, composites and other non-grass herbaceous species. In rangeland literature, this term is commonly defined as all

non-grass herbaceous species (Holechek et al., 2004) thereby including legumes as forbs. Technically, however, forbs are defined as “forage species, other than grasses, legumes, and woody species” (Barnes et al., 2003) or as "non-legume dicotyledonous species" (Whitehead, 2000), excluding legumes from the definition. Because of their distinctive nitrogen-fixing quality, legumes should be placed in a separate category. If soil survey data on rangeland site characterization included legume species or legumes as a separate group, it could be of more use in polyculture development.

The majority of grassland studies involving plant-soil relationships examine the effects of one or two soil properties, but a few studies consider many properties concurrently. Piper (1995) measured nine soil properties on four areas of contrasting prairie plant communities to characterize the quality of the soil in relation to the plant composition and productivity. Organic matter, total N and K generally were higher at the sites of greater productivity. Brejda et al. (2000) analyzed 20 soil attributes across several major land use areas and determined by discriminant analysis that the "most sensitive indicators of soil quality" were total organic C and total N in the Central High Plains, and total organic C and water stable aggregate content in the Southern High Plains. Similar research on how soil properties vary with prairie plant communities may contribute to developing managed perennial polyculture that will be adapted locally to particular soil conditions.

General research approach

I studied four never-plowed prairie sites with different plant composition and soil properties. The study sites, located at The Land Institute south of Salina, Kansas, lie

within the transition zone between tallgrass and mixed-grass prairie of the Great Plains region. The four sites were characterized previously by Piper (1995). Based on my auger characterization of four pedons and the soil map in the Saline County Soil Survey (Palmer et al., 1992), I confirmed that the four sites were located on three different soil series exhibiting a range of soil properties. I hypothesized that

1. The growth of native plant species in a prairie ecosystem is affected by the differences in soil properties.
2. The relative proportion of grasses and legumes in prairie communities are associated with physical and chemical soil properties.

My objectives were

1. To measure the growth responses of seven native plant species to differences in four prairie soils*ex situ* .
2. To identify soil properties most closely associated with the percent legume cover in native prairie communities.

To test hypothesis #1, I isolated the effect of soil properties on plant growth from the fluctuating influence of rainfall, sunlight, temperature, and topography in a greenhouse study. To meet objective #1, I used soil taken from the aforementioned field sites and grew seven grass, legume, and composite species individually in pots in a randomized complete block design. To quantify the growth response, I measured plant biomass, plant height, and evapotranspiration of each species. I used multi-way analyses of variance to determine the contribution of soils and plant species to differences in plant growth and evapotranspiration in the greenhouse study. Since the plants included species

of grasses, legumes, and composites, I also analyzed for the effect of these three plant groups on plant growth and evapotranspiration.

Recognizing the complexity of plant-soil relationships, I chose not only to focus on the effects of soils on plants, but ultimately on the associations between plants and soil properties. Since relative growth of individual plant species in a controlled environment do not fully reflect the complexity of interactions in the prairie community, I tested hypothesis #2 in a subsequent field study by examining native plant species growing in the same soils at the four selected sites. Grasses and legumes are the two primary plant groups in grasslands managed for forage and differ morphologically in their growth habits and requirements (Nelson and Moser, 1995). I used percent legume cover as a measure of grass-legume balance. In addition, legumes are vital to maintaining soil fertility without added fertilizers. Objective #2 was met by using the four field sites including differing proportions of grass and legume populations. To determine the general composition of the plant communities, I visually assessed the percent plant cover among randomly selected areas within each site, referred to as “quadrats” for the remainder of the manuscript. Quadrats from all sites were then grouped into legume cover categories to characterize three different plant communities as “no”, “low”, and “high” legume cover. To characterize the soil associated with these communities, I considered physical soil properties including soil color, texture, structure, field bulk density, depth of A-horizon, soil moisture content, water infiltration rate, aggregate stability and percent organic matter, and chemical soil properties including total C and N, active C, pH, electric conductivity (EC), extractable P, K^{+}, Mg^{2+}, and Ca^{2+}, and potentially mineralizable C and N.

Multi-way ANOVA were used for determining plant cover differences among soils and associations with soil properties in the field study. I determined sources of variance and differences between soil properties among legume cover category and site (simple pairwise comparison). In addition, I determined correlations between percent legume cover and each soil variable and also found associations between all soil variables and percent legume cover using stepwise multiple regression and discriminant multivariate analysis.

Chapter 2: Plant Growth and Water Use By Seven Prairie Plant Species Grown in Soil from Four Kansas Prairie Sites

Introduction

Plant growth is influenced by soil properties, but in a field environment, soil effects may not be easily distinguished from effects of other factors that also influence plant growth. Topography can cause variations in temperature, sunlight, and soil water supply, which in turn influence plant growth and community species composition (Harmoney, 2001). Slope also has a major impact on rates of soil erosion, which in turn affect soil depth and soil surface properties. Soil properties related to fertility, especially the availability of N and K may affect grasses differently from legumes. Therefore, we hypothesized that the growth of native plant species in a prairie ecosystem is affected by the properties of the surface soils, aside from variations in site factors such as slope and soil depth. Our objective was to measure the growth and water use by native plant species in different prairie soils *ex situ* to isolate the effect of soil properties from other site environmental factors.

A field study by Piper (1995) compared plant composition between four sites of varying topography, soil depth, and soil properties within a 65-hectare, never-plowed prairie area near Salina, Kansas. We conducted a greenhouse study using soils taken from these same four prairie sites used by Piper (1995) and seed of native grasses, legumes, and composites representing three different plant families in the prairie plant community, collected near the sites. Studies indicate that grass species (Wedin and Tilman, 1990) differ from legume species in their productivity (Mallarino and Wedin, 1990) and in their response to available soil nutrients (Ledgard et al., 1996). Our study did not simulate

competition between plant species, but rather kept the species separate to detect any soil by species interactions.

Materials and Methods

Soil preparation

On 21 August 2000, bulk soil samples were collected from the top 15 cm of soil at each of four prairie sites (for site characteristics, see Table 2.1 and chapter 3) on a 65-hectare never-plowed prairie at The Land Institute 4 km SE of Salina, Kansas. These sites were previously delineated and studied for their plant communities by Piper (1995). As no rain had fallen for the previous 24 days, the soil was essentially air-dry at time of sampling. These bulk soils were transported in covered plastic containers to the University of Maryland for use in a greenhouse pot study. In January 2001, the bulk soils were crushed and sieved through a metal screen with 0.95-cm openings, discarding roots and rocks collected on the screen. The bulk soil taken from each site was composited and replicates for each site were taken from this composited soil. From each bulk soil sample, 25 random subsamples (20-30 g each) were collected and composited. The composite sample for each bulk soil sample was analyzed for available P, K^+, Ca^{2+}, and Mg^{2+} using the Mehlich-I extract, percent organic matter by loss on ignition method, and pH (1:1 dH_2O solution) at the University of Maryland Soil Testing Laboratory (Northeast coordinating committee on soil testing. 1995). Percent clay and silt were determined by particle-size analysis by pipette method. The moisture contents of these air-dry soils were determined gravimetrically as 0.02 to 0.03 g g^{-1}. The bulk density of each bulk soil after sieving was determined as dry mass of soil required to fill a 1.0-liter cylinder after

tapping down. The saturation soil moisture content was determined for the four soils by adding water drop-wise until the sample could hold no more and glistened with free water. One-liter plastic pots were filled with 950g of sieved and composited soil and wetted to 65% of saturation water content for one week before sowing seeds. Table 2.1. is a summary of the properties of the four soils used in the greenhouse study. Soils 1 and 4 were both loam textures, but with higher organic matter in soil 1. Soil 2 was a silt loam and soil 3 was a silty clay loam.

Seed germination and greenhouse set-up

We used seed of native plant species wild-collected at The Land Institute. We chose species with seed that was available, viable, and easily germinated for greenhouse conditions. In April 2001, seeds of three prairie grasses, (*Andropogon gerardii* Vitm., *Schizachyrium scoparium*(Michx.) Nash., and *Agropyron* sp.), two legumes (*Baptisia australis* (L.) R. Br. and *Desmanthus illinoensis* (Mishx.) MacM.), and two composites (*Helianthus maximiliani* Schrad. and *Liatris punctata* Hook.) were given appropriate pretreatments (scarification for *Baptisia* and *Desmanthus*, and cold treatment at 3ºC for 15 days for *Andropogon*, *Schizachyrium, Baptisia*, *Helianthus,* and *Liatris*) to stimulate germination and then germinated at 20-24ºC on germination paper soaked with distilled water (Appendix A). Four to five sprouted seeds of the appropriate species were placed in each pot of pre-moistened soil and covered with 50g of soil of the same soil.

Twenty-eight treatment combinations (4 soils x 7 plant species) were placed in a completely randomized block design with blocks used as replicates. Each block was sown and placed on a greenhouse bench on each of four different days within a one-week period to allow sufficient time for harvesting each block in the same sequence at the end

Table 2.1. Selected physical and chemical properties of bulk soil taken from field sites 1, 2, 3, and 4.

Soil	Field texture	Clay[†]	Silt[†]	Lab bulk density[†]	65% saturation moisture[†]	P[‡§]	K^{+}[‡]	Ca^{2+}[‡]	Mg^{2+}[‡]	OM[‡]	pH[‡] in H_20
		-------%-----		g cm^{-3}	g_{H2O} g^{-1} soil	----------mg kg^{-1}----------				%	1:2
1	l	20a	46a	1.1a[¶]	0.27a	14a	333a	1721a	149a	5.7a	6.2b
2	sil	25b	50a	0.9a	0.31ab	26b	311b	1918b	162b	6.4b	6.1b
3	sicl	32c	50a	1.1a	0.33b	33c	125c	4468c	176c	4.3c	7.6a
4	l	21a	44a	1.1a	0.27a	19d	231d	1605a	148a	4.9d	6.1b

[†]Means of two subsamples.
[‡]Means of three subsamples.
[§]Mehlich-I extractant.
[¶]Within columns, means followed by the same letter are not significantly different according to Tukey comparisons (0.05).

of the study. All pots were brought to 65% of water saturation (Table 2.1) and weighed. During the growth of the plants, all pots were periodically returned to this initial weight by adding distilled water to maintain the soil at 65% of water saturation. Pots within each block were re-randomized with respect to location on the bench during each watering to homogenize variation within blocks due to position on the bench. A plastic saucer was placed under each pot to ensure that all added water was accounted for during watering and weighing. After one week, sodium vapor lamps were placed about 1 m above the pots to supplement natural photosynthetically active radiation and to provide a controlled 14-h daylength throughout the plant growth period. After one month of growth, plants were thinned to three per pot.

Measurements and data collection

Soil water potential was estimated from tensiometers readings taken during the last three weeks of plant growth to assist in maintaining water near the optimum level. Tensiometers were placed in four separate pots containing the same soils and each pot containing one plant (*Liatris punctata*, *Helianthus maximiliani*, *Desmanthus illinoensis*, and *Agropyron* sp. placed in soils 1, 2, 3, and 4, respectively). Evapotranspiration was measured on two occasions by watering the pots to their initial weight and then weighing the pots again after allowing the soil to dry out for three days for the first occasion and four days for the second occasion. After 52 days of growth, plant heights were measured (from soil surface to the tip of the tallest leaf) and then plant shoots and roots were harvested, washed, dried at 60° C, and weighed separately for shoot and root dry matter.

Experimental design and statistical analysis

The explanatory variables were soil and species. The response variables were shoot dry matter (DM), root DM, shoot-to-root ratio, total plant DM, relative plant DM, plant height, and evapotranspiration (ET). Total plant DM of species was converted to relative plant DM by calculating the dry matter compared to the pots with the greatest dry matter within a species. Therefore, the pot with the highest dry matter within a species was recorded as 100:

(Dry matter weight / maximum dry matter weight obtained for species) x 100

The PROC MIXED procedure was used for univariate ANOVA to determine soil effect for each response variable. The model included soil, species, soil by species interaction, and block (as random effect) as sources of variation (Appendix B). Differences between means for each soil among all species were determined by pairwise comparisons using Tukey (0.05). When the soil by species interaction was significant, the model only included soil and block (as random effect), and the soil effect on each individual species was determined. The PROC MIXED procedure was also used for univariate ANOVA to determine the effects of soil and plant family (species placed into either grass, legume, or composite families). The model included soil, plant family, soil by plant family interaction, and block (as random effect) as sources of variation. Simple correlations between ET and total plant DM were performed for all soils and for each soil separately. All statistical analyses were conducted using the SAS system (1999-2001).

Results

Soil properties

The soil properties measured on the composite bulk samples that most distinguished the four soils were texture, percent organic matter and levels of extractable K^+. Soils 1 and 4 were both loams but soil 1 was higher in percent organic matter and extractable K^+. Soil 2 was a silt loam and highest in percent organic matter. Soil 3 was a silty clay loam and lowest in percent organic matter and K^+. The higher level of P (Mehlich-I extraction) in soil 3 does not necessarily indicate plant-available P given the calcareous nature and high pH (7.6) of this soil. Soils 1, 2, and 4 had average pH levels 6.1. Levels of extractable Ca^{2+} and Mg^{2+} were the same for both soils 1 and 4, and highest in soil 3.

Plant dry matter

The highest shoot dry matter (DM) averaged among species was harvested from soil 2 and the least from soil 3 (Table 2.2.). Shoot DM did not differ between soils 1 and 4. More average root DM was harvested from soils 1 and 2 than from soil 3 or 4. Plants in soil 3 had a higher average shoot to root ratio than plants in soil 1, but the difference was only significant at the 0.10 level (Table 2.3.). The average total plant DM and the average relative plant DM were highest in soil 2, and lowest in soil 3, but did not differ between soils 1 and 4 (Table 2.4.).

The ANOVA showed a significant soil by species interactions for shoot, root, and total plant DM and relative plant DM, therefore, the main effect of soil will not be discussed for these variables. The simple effects (Table 2.5.) of soil were significant for five individual species: all three grasses (*Agropyron* sp., *Andropogon gerardii*, and

Table 2.2. Shoot and root dry matter (DM) for seven plant species grown in soil from prairie sites 1, 2, 3, and 4. Means of four replications.

	Shoot DM					Root DM				
	Soil 1	Soil 2	Soil 3	Soil 4	Species Mean	Soil 1	Soil 2	Soil 3	Soil 4	Species Mean
	g									
					Grasses					
Ag[†]	0.204bc[‡]	0.445a	0.128b	0.289c	0.266A[§]	0.289a	0.439a	0.068b	0.252ab	0.262AB
Ang	0.398a	0.659b	0.179c	0.379ac	0.404B	0.477a	0.446ab	0.104c	0.257bc	0.321A
Ans	0.310a	0.354a	0.083b	0.197ab	0.236A	0.445a	0.370a	0.050b	0.128b	0.248AB
Grass mean	0.304xX	0.486yX	0.130zX	0.288xX	0.302X	0.404xX	0.418xX	0.074yX	0.212zX	0.277X
					Legumes					
B	0.091ab	0.074ab	0.034a	0.113b	0.078C	0.025a	0.013a	0.013a	0.023a	0.018C
De	0.478a	0.701b	0.301c	0.566ab	0.511D	0.216ab	0.314a	0.089c	0.169bc	0.197B
Legume mean	0.285xX	0.387xX	0.167xX	0.340xX	0.295X	0.121xY	0.163xY	0.051xX	0.096xY	0.108Y
					Composites					
H	0.493a	0.957b	0.335c	0.644d	0.607E	0.263a	0.422c	0.097b	0.225ab	0.252AB
Li	0.060a	0.116a	0.090a	0.055a	0.080F	0.030a	0.066a	0.046a	0.030a	0.043D
Comp mean	0.276xX	0.537xX	0.213xX	0.350xX	0.344X	0.147xY	0.244xY	0.072xX	0.127xXY	0.147Y
Soil mean	0.290a	0.472b	0.164c	0.320a		0.249a	0.296a	0.067b	0.155c	

[†]Ag, *Agropyron* sp.; Ang, *Andropogon gerardii*; Ans, *Schizachyrium scoparius*; B, *Baptisia australis*; De, *Desmanthus illinoensis*; H, *Helianthus maximiliani*; Li, *Liatris punctata*; Comp, composite.

[‡]Within rows, means followed by the same lowercase letter are not significantly different according to Tukey (0.05).

[§]Within columns, means followed by the same capital letter are not significantly different according to Tukey (0.05).

Table 2.3. Shoot-to-root ratio for seven plant species grown in soil from prairie sites 1, 2, 3, and 4. Means of four replications.

	Shoot-to-root Ratio				
	Soil 1	Soil 2	Soil 3	Soil 4	Species Mean
			Grasses		
Ag[†]	0.722a[‡]	1.023ab	1.852b	1.398ab	1.249A[§]
Ang	0.881a	1.591b	1.774b	1.489b	1.434A
Ans	0.837a	0.975a	1.661b	1.483b	1.239A
Grass mean	0.813xX	1.197yX	1.76zX	1.456yzX	1.307X
			Legumes		
B	4.240a	5.695a	7.700a	6.074a	5.927B
De	2.285a	2.300a	3.364ab	3.532b	2.871B
Legume mean	3.264xY	3.998xY	5.532xX	4.803xY	4.399Y
			Composites		
H	1.983a	2.407ab	4.227b	2.938ab	2.889B
Li	2.470a	1.745a	2.281a	3.106a	2.401AB
Composite mean	2.227xY	2.076xX	3.254xX	3.022xXY	2.645Z
Soil mean	1.917a	2.248a	3.266a	2.860a	

[†]For species names see Table 2. 3

[‡]Within rows, means followed by the same lowercase letter are not significantly different according to Tukey (0.05).

[§]Within columns, means followed by the same capital letter are not significantly different according to Tukey (0.05).

Table 2.4. Total dry matter (DM) and relative DM (% of max DM in all soils) for seven plant species grown in soil from prairie sites 1, 2, 3, and 4. Means of four replications.

	Total DM					Relative DM				
	Soil 1	Soil 2	Soil 3	Soil 4	Species mean	Soil 1	Soil 2	Soil 3	Soil 4	Species mean
	g									
					Grasses					
Ag[‡]	0.493ab[†]	0.885c	0.196a	0.541b	0.529A[§]	48.5ab	87.0c	19.3a	53.1b	52.0AB
Ang	0.875ab	1.106a	0.283b	0.636b	0.725BC	65.7ab	83.1a	21.3c	47.8bc	54.5AB
Ans	0.754a	0.724a	0.133b	0.325b	0.484A	74.1a	71.1a	13.1b	31.9b	47.5AB
Grass mean	0.707xyX	0.905yX	0.204zX	0.500xX	0.579X	62.8xyX	80.4yX	17.9zX	44.3xX	51.3X
					Legumes					
B	0.116a	0.087a	0.047a	0.136a	0.096D	48.6a	36.2a	19.5a	56.8a	40.3A
De	0.694a	1.015b	0.390c	0.735a	0.708B	50.4a	73.7b	28.3c	53.4a	51.5AB
Legume mean	0.405xX	0.551xX	0.218xX	0.435xX	0.402X	49.5xXY	55.0xY	23.9yX	55.1xX	45.9X
					Composites					
H	0.756a	1.279b	0.433c	0.869a	0.859C	49.4a	90.1b	28.3c	56.8a	56.1B
Li	0.090a	0.182a	0.136a	0.085a	0.123D	37.8a	76.6a	57.1a	35.6a	51.8AB
Comp[¶] mean	0.423xX	0.781xX	0.284xX	0.477xX	0.491X	43.6xY	83.4yX	42.7xY	46.2xX	54.0X
Soil mean	0.540a	0.768b	0.231c	0.475a		53.5a	74.0b	26.7c	47.9a	

[†]For species names see Table 2. 3.
[‡]Within rows, means followed by the same lowercase letter are not significantly different according to Tukey (0.05).
[§]Within columns, means followed by the same capital letter are not significantly different according to Tukey (0.05).
[¶]Comp, composite.

Table 2.5. Means and significance levels for soil effects of each species on shoot and root dry matter (DM), total DM, relative DM, plant height at time of harvest, and evapotransporation (ET). df = 3, 9

Species	Shoot DM	Root DM	Total DM	Relative DM	Plant Height	ET
	----------g----------				mm	g
Ag[†]	0.266***	0.262**	0.529***	52.0**	275**	145*
Ang	0.404***	0.321**	0.725***	54.5**	265	135**
Ans	0.236**	0.248**	0.484***	47.5**	138	129*
B	0.078	0.018	0.096	40.3	88*	120**
De	0.511***	0.197**	0.708**	51.5***	139**	160***
H	0.607***	0.252***	0.859***	56.1***	148**	176***
Li	0.080	0.043	0.123	51.8	76	120

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.

[†] Ag, *Agropyron* sp.; Ang, *Andropogon gerardii*; Ans, *Schizachyrium scoparius*; B, *Baptisia australis*; De, *Desmanthus illinoensis*; H, *Helianthus maximiliani*; Li, *Liatris punctata*.

Schizachyrium scoparius), one legume (*Desmanthus illinoensis*), and one composite (*Helianthus maximiliani*). No significant simple effect of soil on plant DM was found for the other legume, *Baptisia australis,* and composite, *Liatris punctata*. Analysis of variance showed no soil by species interaction for shoot-to-root ratio, but the soil main effect was only significant at the 0.10 level for this variable.

Plant height, dry matter and water loss

After 52 days of growth, average plant height was highest in soil 2 and lowest in soil 3 (Table 2.6.). Plant heights in soil 1 were not significantly different from plant heights in soil 4. Soil 3 also had the lowest average ET after four days of no watering. Average ET was not different for the other three soils. However, because plant height and ET also showed significant soil by species interactions, the main effects of soil will not be discussed further. The simple effect of soil on plant height was significant for one grass species, *Agropyron* sp., both legumes, *Baptisia australis* and *Desmanthus illinoensis*, and one composite, *Helianthus maximiliani* (Table 2.5.). The simple effect of soil on ET, however, was significant for all species, except *Liatris punctata*.

ET was positively correlated with the accumulation of plant dry matter with r values of 0.63, 0.86, 0.80, and 0.86 for soils 1, 2, 3, and 4, respectively (Figure 2.1.). Soil 3 had the highest ET per gram of plant dry matter, whereas soil 2 had the lowest ET per gram of plant dry matter. Although ET was lowest in soil 3, ET per mg of plant biomass was highest in soil 3, as a result of low plant dry matter (Figure 2.1.). The soil moisture potential among all four soils decreased to an average minimum of -80 ±10 kPa during approximately 169 hrs without watering (Figure 2.2.).

Table 2.6. Plant height at time of harvest and evapotransporation over four-day period (with no added water) for seven plant species grown in soil from prairie sites 1, 2, 3, and 4. Means of four replications.

	Plant Height					Evapotranspiration				
	Soil 1	Soil 2	Soil 3	Soil 4	Species Mean	Soil 1	Soil 2	Soil 3	Soil 4	Species Mean
	----------mm----------					----------g----------				
					Grasses					
Ag[†]	253ab[‡]	349c	207a	290bc	275A[§]	144ab	155a	132b	150ab	145A
Ang	273a	301a	227a	259a	265A	140a	143a	122b	137a	135B
Ans	162a	142a	120a	129a	138B	137a	130ab	117b	133ab	129B
Grass mean	229xX	264xX	185xX	226xX	226X	141xX	142xX	123yX	140xX	136X
					Legumes					
B	97ab	119a	58b	80ab	88C	126a	110b	117ab	128a	120C
De	136ab	161a	111b	148a	139B	162a	170a	142b	167a	160D
Legume mean	117xyY	140xY	84yY	114xyY	114Y	144xX	140xX	129xX	148xX	140X
					Composites					
H	144ab	172c	123a	153bc	148B	177a	187b	158c	182ab	176E
Li	80a	85a	76a	62a	76C	121a	115a	120a	123a	120C
Comp[¶] mean	112xY	128xY	100xY	107xY	112Y	149xX	151xX	139xX	153xX	148X
Soil mean	164a	190b	132c	160a		144a	144a	129b	146a	

[†]Ag, *Agropyron* sp.; Ang, *Andropogon gerardii*; Ans, *Schizachyrium scoparius*; B, *Baptisia australis*; De, *Desmanthus illinoensis*; H, *Helianthus maximiliani*; Li, *Liatris punctata*; Comp, composite.

[‡]Within rows, means followed by the same lowercase letter are not significantly different according to Tukey (0.05).

[§]Within columns, means followed by the same capital letter are not significantly different according to Tukey (0.05).

[¶]Comp, composite.

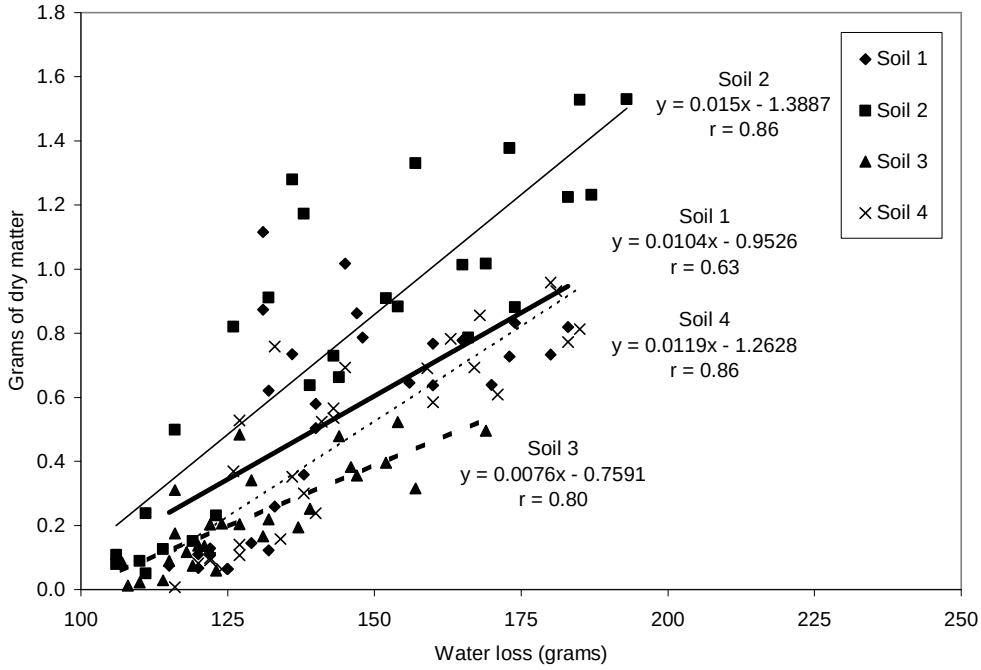

Figure 2.1. Relationship between water loss after four days without watering and plant dry matter at end of 52-day growing period of soils 1, 2, 3, and 4 in the greenhouse.

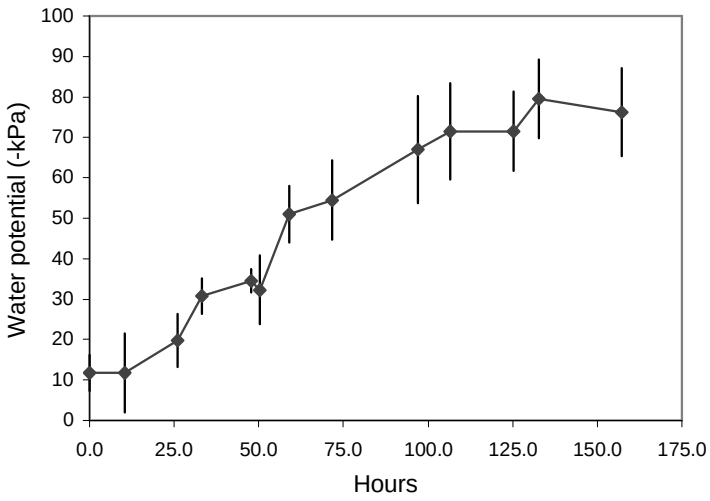

Figure 2.2. Tensiometers soil water potential readings for 169 hours from June 12 to June 19, 2001 at end of 52-day growing period. Mean ±SE of four soils in greenhouse study.

ANOVA by plant family

When tested with ANOVA, the soil by plant family interaction was significant ($P \leq 0.001$) for root DM and relative DM so main effects of soil and plant family for these variables cannot be considered meaningful. For shoot-to-root ratio, neither the soil by plant family interaction nor the soil effect was significant. A significant plant family effect ($P \leq 0.0001$) showed that legumes had the highest average shoot-to-root ratio and grasses the lowest (Table 2.3). In soils 1, 2, and 4, the average shoot-to-root ratio for legumes was more than double that for grasses because of much greater root DM for the grasses (Table 2.2.). In soil 3, the difference between plant families for shoot-to-root ratio was not significant (Table 2.3.).

Soil effects were significant ($P \leq 0.05$) for shoot DM, total DM, plant height, and ET with no soil by plant family interactions. There were no significant main effects of plant family on shoot DM, total DM, and ET. Plant height depended on both soil ($P \leq 0.05$) and plant family ($P \leq 0.0001$). The average height at harvest for all grasses in all soils was greater than the average heights for legumes and composites (Table 2.6.). The average plant height for all plant families was highest in soil 2 and lowest in soil 3, with no differences between soils 1 and 4.

Discussion

Soil effects

No main effects of soil on plant growth and ET can be discussed, because the seven species responded differently to the four soils tested. Simple effects of soil on plant

DM for *Agropyron*, *Andropogon*, *Schizachyrium*, *Desmanthus* and *Helianthus* were all significant (Table 2.5.).

There was a significant soil effect on *Andropogon* and *Schizachyrium* for all variables except plant height. Plant height is probably not a good measure to use in comparing species of such different morphologies, since the species differ widely in leaf area index and biomass. It is not clear from our data why there was a significant soil effect on *Agropyron* sp., a cool-season grass, and not on the other two grass species. However, warm-season grasses are known to generally differ from cool-season grasses in root morphology and early development (Nelson and Moser, 1995). The plants of *Baptisia* and *Liatris* grew very slowly in all the soils during the 52-day growing period, producing much less total plant dry matter than all the other species.

Evapotranspiration and plant dry matter

Soil 2 showed greater efficiency in producing a higher amount of plant dry matter per unit of water. With total DM, soil 2 differed from soils 1 and 4, whereas with ET, there was no difference between soil 2 and soils 1 and 4. The plant growth in soil 2 may be influenced by soil properties in addition to available water. Organic matter content was much higher in soil 2 than in the other soils. Whitehead (1982) also found herbage yields of clover and perennial grass in a greenhouse study were positively correlated with organic matter and water content.

Plant family effects

When species were grouped by plant family, there was a plant family effect on shoot-to-root ratio. Prairie grasses are known to have a root biomass that represents up to 90% of their total plant biomass (Whitehead, 2000). Our results also agree with findings

by Evans in comparing root morphology of grass with clover species (Evans, 1977). Evans compared root morphology of three clovers and five grasses. These grasses had longer, thinner, and finer roots hairs and the root surface area for grass roots was greater than clover roots, although the root surface area per unit of dry weight was similar. Evans (1977) concluded that these differences could be a factor in competitive advantages for grasses in obtaining soil nutrients.

The only variable for which there was both soil and plant family effect was plant height. Grasses clearly dominated in height over the legumes and composites, but were no different from legumes and composites in overall shoot dry matter, most likely because the larger leaf area of legumes and composites compensate for their shorter height relative to grasses. The soil effect on plant height may have been due to differences in organic matter content among these soils. Soil 2 had the highest organic matter content (5.5%) while soil 3 had the lowest organic matter content (3.7%) (Table 2.1.).

Species by soil interactions

Although the three grass species in the greenhouse study had similar total DM, one of the legumes, *Baptisia australis* and one of the composites, *Liatris punctata*, had only 14 percent the average total DM of the other species in their family, *Desmanthus* and *Helianthus* (Table 2.4.). This difference resulted in species by soil interaction and mean values for legumes and composites that were representative of neither species. The total DM of *Baptisia* and *Liatris* also did not differ among soils, whereas for all other species, the total DM weights were significantly different at least between soils 2 and 3. For all other variables measured, *Liatris* did not differ among all four soils, and *Baptisia*

did not differ among all four soils for shoot DM, root DM, shoot-to-root ratio, total DM, and relative DM (Table 2.5.).

We excluded *Baptisia* and *Liatris* and re-analyzed the data using only five plant species, since these two species appeared to be poorly established. This resulted in both soil and species main effects for root DM, shoot-to-root ratio and ET, with no soil by species interaction. Therefore, we concluded that the soil by species interaction for these three variables in the complete ANOVA was caused by *Baptisia australis* and *Liatris punctata*. The relationship among the four soils for root DM and ET of five species was the same as with seven species (Table 2.7.). For shoot-to-root ratio, however, after removing *Baptisia* and *Liatris*, there was a significant soil main effect. Soils 1 and 2 had a lower ratio than soils 3 and 4. The high shoot-to-root ratio in soils 3 and 4 is consistent with the low root DM in these soils. ET, after four days of no watering, was similar for soils 1, 2, and 4, but significantly lower in soil 3. Since the average shoot DM in soil 3 was also the lowest, it is likely that ET was influenced primarily by low shoot DM, which in turn may have been influenced by the soil texture in soil 3. Texture data for these soils indicate that site 3 had 32% clay compared to 20 and 25% clay in sites 1 and 2, respectively. This soil texture difference may explain the lower available water holding capacity of soil 3 since clay soils hold more water too tightly for plants to use and thus provide less available water for plant growth in soil 3.

Grouping the above five species into their plant families in a similar ANOVA to the plant family analysis also resulted in significant (P>0.001) soil effects for root DM and ET with no soil by plant family interaction as in the previous analysis with the five separate species. However, grouping the five species into plant families also resulted in

Table 2.7. Root dry matter (DM), shoot-to-root ratio, and evapotransporation (ET) for five species grown in soils taken from prairie sites 1, 2, 3, and 4. Means of four replications.

	Soil 1	Soil 2	Soil 3	Soil 4
Root DM, g	0.338a[†]	0.398a	0.082b	0.206c
Shoot-to-root ratio	1.342a	1.659a	2.575b	2.168b
ET, g	152a	157a	134b	154a

[†]Within rows, means followed by the same letter are not significantly different according to Tukey (0.05).

significant (P>0.001) soil effects for total DM and relative DM, with no soil by plant family interaction. Since the five species only includes one legume and one composite, the soil effect for total DM and relative DM was improved by grouping the three grasses together.

Conclusions

There was no main effect of soil on plant growth and ET because of species differences among the seven plant species. Some of the plants of *Baptisia* and *Liatris* had extremely low root DM and therefore differed drastically from the other species, probably due to lack of seedling vigor. After removing these two plant species from the data analysis, soil effects were shown for root DM, shoot-to-root ratio, and ET. The differences in shoot-to-root ratio were more evident with just the five species, higher for soils 3 and 4 than for soils 1 and 2.

When we grouped all seven species by family, significant effects of soil were shown for shoot DM, total DM, plant height, and ET, with the highest in soil 2, except in ET, and the lowest in soil 3. Shoot-to-root ratio was no different among soils, but the overall average for plant families differed as follows: legumes>composites>grasses. The differences of shoot-to-root ratio were affected more by morphological differences between plant families than by soil differences. Plant height, on the other hand, was affected by both plant family and soil differences. This may be influenced by morphological differences in plant leaf area, the available water from the soil, and the organic matter content of the soils. Organic matter was highest in soil 2 and lowest in soil 3 (Table 2.1.).

When we removed *Baptisia* and *Liatris* from the plant family analysis, the shoot-to-root ratio did not vary consistently among soils, but the total DM and relative DM resulted in significant soil effects. The soil effect for total DM and relative DM was improved when all three grasses were grouped together in the grass family. Soil 2 showed the highest total and relative DM and soil 3 showed the lowest total and relative DM (Table 2.8.). The only soil property of these soils that showed a similar trend was percent organic matter (Table 2.1). Since the soil properties were measured on bulk composite samples rather than on soil from each greenhouse pot, we cannot determine which soil property directly affected plant growth.

For future greenhouse studies of this nature, we recommend using a greater number of plant species, both warm-season (C_4) and cool-season (C_3), in each plant family. Also, a longer growing period extended beyond the 52 days of our pot experiment may allow slow-growing species to show a greater growth response difference to soil characteristics. For comparison to a field study, we recommend using species that are specific to the field plant communities. Grown in pots both individually and in combination may be useful in comparing species competition. Analysis of the soil from each pot would allow further inferences as to which soil properties affect plant growth.

Table 2.8. Root dry matter (DM), total DM, relative DM, and evapotranspiration (ET) for five plant species grouped in plant families (grasses, legumes, and composites) grown in soils taken from prairie sites 1, 2, 3, and 4. Means of four replications.

	Soil 1	Soil 2	Soil 3	Soil 4
	----------g----------			
Root DM	0.294ab[†]	0.385a	0.087c	0.202b
Total DM	0.719a	1.099b	0.342c	0.701a
Relative DM	54.2a	81.4b	24.8c	51.5a
ET	160a	166a	141b	163a

[†]Within rows, means followed by the same letter are not significantly different according to Tukey (0.05).

Chapter 3: Relationships between Plant Communities and Soil Properties in a Kansas Prairie

Introduction

Plant communities in a native prairie are composed mainly of herbaceous perennials that are naturally supplied with nutrients from within the ecosystem – decaying plant matter, senescing roots, soil organic matter, exchange sites on soil clay surfaces, and fixed nitrogen from the atmosphere (Whitehead, 2000). Perennial grass species dominate the community and contribute much of their productivity as belowground biomass. The high proportion of belowground biomass helps enable the community to withstand extremes of temperature and water, as well as such natural disturbances as fire and grazing. The "natural systems agriculture" being developed by the Land Institute (Jackson, 2002) attempts to incorporate some of this natural resilience into a grain production system that can serve as a more sustainable alternative to the conventional farming systems currently dominating the North American Great Plains region.

Prairie plant communities largely consist of four functional groups: perennial warm-season (C_4) and cold-season (C_3) grasses, N-fixing species (mainly legumes) and forbs, the latter defined as "non-legume dicotyledonous species" (Whitehead, 2000). These groups differ in their shoot and root morphology, and their competitiveness for water, nutrients and light, leading to difference in their frequency in the plant community. Prairie grasses develop a relatively large amount of root biomass with many lateral, fine roots. Thick stands of these grasses can develop in late succession communities in which they often shade out most other plants. Estimates of total root standing biomass of mixed

prairie grasslands range as high as 21,000 kg ha^{-1} from the top 30 cm of soil (Black and Wight, 1979). Belowground plant biomass for *Andropogon gerardii* Vitm. and *Schizachyrium scoparius* (Michx.) Nash. was estimated to be about 12,000 kg ha^{-1} versus only 400-5000 kg ha^{-1} for cold-season grasses, *Agrostis scabra* Willd., *Poa pratensis* L., and *Agropyron repens* (L.) Beauv. (Wedin and Tilman, 1990). The extensive grass root systems can take advantage of available soil nutrients and can supply enough dead plant matter to immobilize and store large quantities of nutrients in the soil organic matter (Whitehead, 2000), as high as 181 kg ha^{-1} of total N and 15.5 kg ha^{-1} of total P according to one estimate (Black and Wight, 1979). Prairie legumes generally have deep taproots, some extending 2 to 3 m into the soil, with relatively few lateral roots (Stevens, 1948). They are often found growing in open areas on nutrient-poor soils (Stubbendieck and Conard, 1989), likely due to their symbiotic relationship with nitrogen-fixing bacteria. Since grasses and legumes differ in their use of soil space, nutrients and water, they may be affected differently by the physical and chemical properties of the soil.

Many studies have shown close correlations between soil N levels and its effect on proportions of grasses to legumes in pastures and grasslands (Fairey, 1991; Harris, 1987; Piper, 1995; Sweeney, 1994; Walker, 1956). Piper (1995) found sites containing a high percent of legume biomass in their plant communities were characterized by relatively low soil N and organic matter levels. When N released by mineralization is limited in the soil, legumes can obtain this essential nutrient from their root nodules, which contain the N-fixing *Rhizobium* bacteria. High levels of soluble mineral N in soils tends to inhibit N fixation by legumes (Walker et al., 1956). Grasses on the other hand, depend mainly on the mineralization of soil organic matter for their N supply. Some

studies (Brophy et al., 1987; Mallarino et al., 1990) have also found evidence of N transfer from legumes to grasses via root decay and mycorrhizal connections (Brady and Weil, 1999). Grasses take up N in both ammonium and nitrate forms, but the latter apparently is more easily taken up. Soil pH may affect the balance of grasses and legumes by its impact on nitrate production via nitrification. Soils higher in pH (> 5) tend to favor the process of nitrification. However, this may be due in part to high levels of exchangeable bases such as Ca^{2+} and Mg^{2+}, which are often found in more alkaline soils (Brady and Weil, 1999).

Plant community composition may be influenced by climate, topography, species competition and compatibility, and soil nutrients and other soil properties. Our study focused on the influence of soil properties. Studies of plant and soil relationships often focus on one or two soil properties that have been known to influence plant growth (Guretzky et al., 2004; Holechek, 1982). However, for ecosystem research, a broader range of soil properties needs to be considered simultaneously. Piper (1995) measured soil texture, pH, percent organic matter, and the plant-available supply of several essential nutrients to characterize the four sites in regards to soil fertility. Other studies as well have considered multiple soil properties. In a greenhouse study, herbage yields of clover and perennial grass were positively correlated (max corr. coeff.=0.62) with % clay, organic matter, water content, and CEC (Whitehead, 1982). In a field study, McVay et al. (1989) measured several physical and chemical soil properties while determining the N benefits of winter legumes grown with grain crops. Aggregate stability and infiltration rates were increased in plots following the legume crops (McVay et al., 1989). In a larger field study, 20 soil attributes among major land resource areas were analyzed by

discriminant analysis to determine how they varied with land use or management practices (Brejda, 2000). Total organic C and total N were the "most sensitive indicators of soil quality" in one region, and total organic C and water stable aggregate content in another region (Brejda et al., 2000).

Our study analyzed prairie soil for its physical and chemical properties present in the field as well as its potential level of microbial activity (in incubated soil). We examined associations between soil properties and plant community composition in four native prairie sites as a follow-up to a greenhouse study that used soil taken from these sites to determine *ex situ* soil effects on growth of seven native prairie plant species (see chapter 2). These native prairie sites, located at The Land Institute southeast of Salina, Kansas, were the focus of an earlier (Piper, 1995) seven-year field study on the composition of prairie plant communities. Because of their importance in prairie ecosystems, we focused our study on grasses and legumes. Since Piper (1995) noted marked differences among the four sites with regard to plant composition and soil properties, we hypothesized that the relative proportion of grasses and legumes in these native prairie communities are associated with physical and chemical soil properties. Our objective was to identify which soil properties are most closely associated with the percent legume cover in native prairie communities.

Materials and Methods

Site selection

Plant composition and soil properties were studied and compared on four 6 m x 15 m plots hereafter termed “sites” in a 65-hectare native prairie tract at The Land

Institute approximately 4 km southeast of Salina, Kansas. The native vegetation in this region is mostly mixed prairie, but borders the western edge of the tallgrass prairie in the Great Plains. These four sites had been earlier delineated and described by Piper (1995) as representing relatively productive (sites 1 and 2) and unproductive (sites 3 and 4) plant communities. Average dry biomass data collected in August of seven consecutive years was 566, 419, 268 and 232 g m^{-2} for sites 1, 2, 3, and 4, respectively (Piper, 1995).

The four study sites (Figure 3.1) are located at the western edge of the Flint Hill uplands. The USDA-NRSC Soil Survey of Saline County (Palmer et al., 1992) mapped the soils on sites 1 and 2 as Longford silt loams (fine, montmorillonitic, mesic Udic Argiustolls), on site 3 as Kipson-Clime complex silt loams (fine, mixed, mesic Udorthentic Haplustolls), and on site 4 as Lancaster-Hedville complex silt loams (fine-loaming to loamy, mixed, mesic Udic Argiustoll and Lithic Haplustolls). All four sites are on well-drained uplands formed on residuum from weathering of shale and limestone at sites 1, 2 and 3 and shale and sandstone at site 4.

Topography, climate, and disturbance

Slope was determined by clinometer readings within each site at each sampling area, hereafter termed “quadrat”, and the slope range for each site was determined by the average of these readings. Site 1 has an east-facing aspect and site 2 has southeast-facing aspect. Both sites 1 and 2 have the least variation in slope. Quadrats within site 1 ranged from 5-10% slope with an average of 7.5% and quadrats in site 2 ranged from 0-6% slope with an average of 2.5%. Site 4 is in close proximity to site 2, but has a south-facing aspect with quadrats ranging from 8-25% slpe (15.8% average). Site 3 has a southwest - facing aspect with quadrats ranging from 27-46% slope (35.2% average). Among these

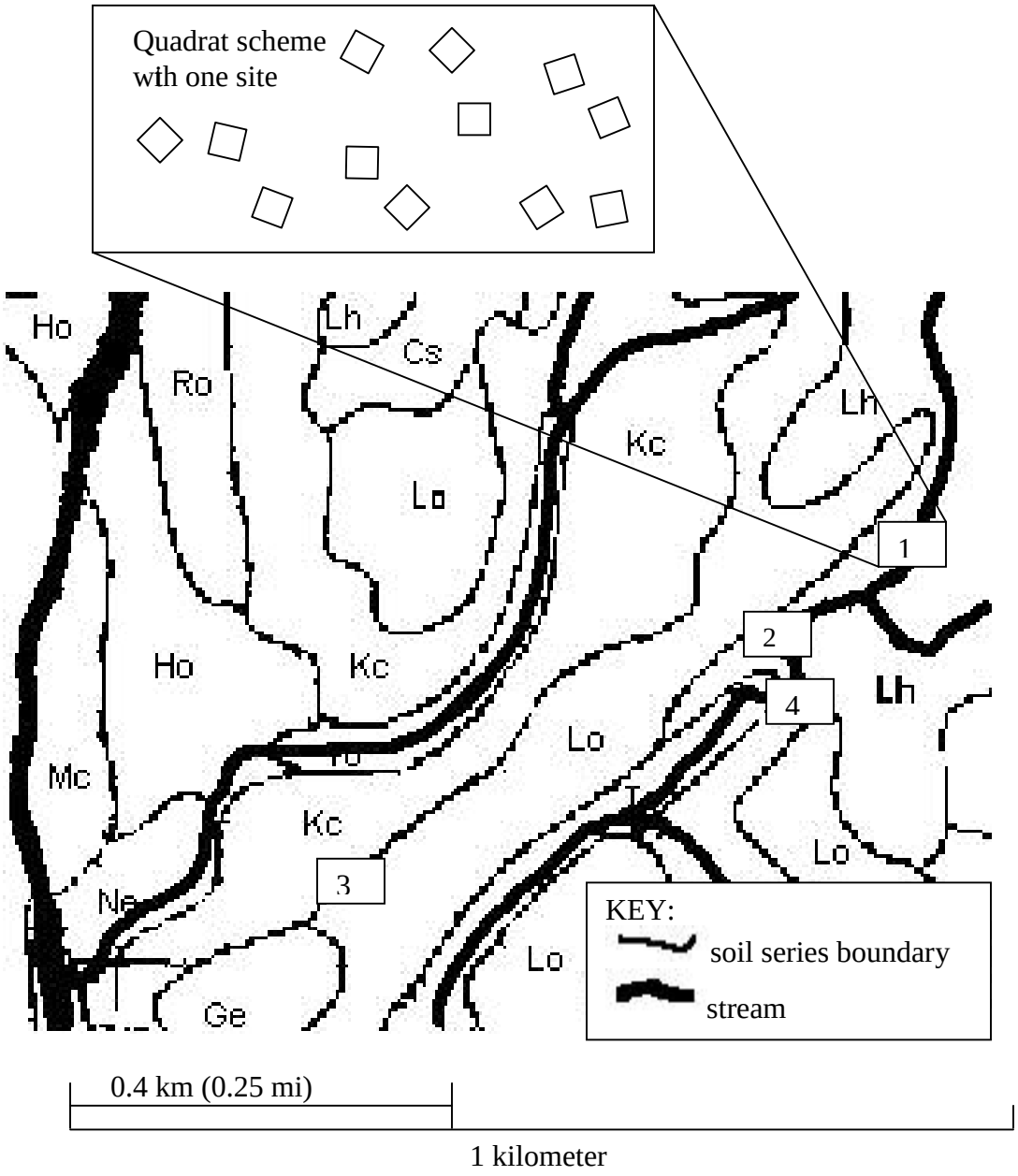

Figure 3.1. Location of four prairie sites, 1, 2, 3, and 4 within soil series (NRCS-USDA Soil Survey of Saline County): Lo – Longford silt loam fine, montmorillonitic, mesic Udic Argiustoll; Kc – Kipson-Clime silt loam fine, mixed, mesic Udorthentic Haplustoll; Lh – Lancaster-Hedville silt loam fine-loaming to loamy, mixed, mesic Udic Argiustoll and Lithic Haplustoll.

four sites, the steeper-sloped sites have a wider range in slopes.

Precipitation data were obtained from a rain gauge approximately 100 m from the nearest study site (personal communication, Bender, M. Sunshine Farm Director at The Land Institute) and monthly average temperature data were obtained for Salina, KS (NOAA, 2003). We collected our field data in July and August of 2000 and 2001. Although the annual precipitation for 2000 was above the 30-year average by 17.9 cm, nearly all of the summer precipitation fell in June and July. The average monthly temperature for August 2000 was also above average, resulting in increased evapotransporation (Appendix C) and dry soil conditions during sampling.

Our fieldwork in 2001 was during the driest part of that summer. Rainfall for July was 3.8 cm below the 30-year monthly average. Although the rainfall in August was 6.58 cm of rainfall, nearly double the monthly 30-year average, only 1.01 cm had fallen by August 17, the last day of our field data collection (Appendix D).

During our field research in the summers of 2000 and 2001, sites 1, 2, and 4 were burned in April of 2000 and 2001 and experienced periodic grazing throughout the growing season by approximately 20 mature Texas longhorn cattle. Site 3 had not been grazed since 1980 (personal communication, Bender, M. Sunshine Farm Director at The Land Institute).

Soil sampling

In August of 2000, a 7.5-cm diameter bucket auger was used to sample to a depth of 75 to 100 cm. Based on one sample per site, a soil profile description was made for each of the four sites. Soil descriptions included approximate depth of horizon boundaries, moist Munsell soil colors, textural class, type of soil structure, presence and

abundance of plant roots, coarse fragments, and any other features noted. Core soil sampling was also taken for preliminary site evaluation (Appendix E).

Soil profile descriptions

Table 3.1. gives general soil profile descriptions for the four prairie sites. The A horizons in sites 1 and 2 extended to 56 and 75 cm, respectively. Sites 3 and 4 had much shallower A horizons, 18 and 25 cm, respectively. Both sites 3 and 4 were on comparatively steeper slopes than sites 1 and 2, and their C horizons were observed within the sampling depths, at 45 cm and 76 cm, respectively. Our field texture data showed sites 1 and 2 generally ranged from silt loam to clay loam, site 3 was silty clay loam throughout its profile, and site 4 ranged from sandy clay loam to silt loam.

The soil structure at all four sites was generally granular to subangular blocky, except in site 3, which was angular blocky to platy below 45 cm. The depth of roots generally followed the depth of A horizons in each of the four sites. Relatively fewer roots were in sites 3 and 4.

These soil profile descriptions were compared to typical pedon descriptions of the mapped soil series (Palmer, 1992) and with soil series descriptions in the Official Soil Descriptions (NRCS, 2000). Profiles of sites 1 and 2 have similar colors throughout their profiles to that of the typical pedon for the Longford series. By texture, site 2 has a deeper mollic epipedon (20 cm thicker) than is typical for Longford. Site 3 is within the Kipson-Clime complex, but exhibits more similarity to Clime than Kipson in its soil colors and its horizons. Site 4 is within the Lancaster-Hedville complex and although it shares some characteristics of both, the depth to lithic contact is most similar to the Lancaster series.

Table 3.1. Selected physical soil properties for four prairie sites.

Depth, cm	HZN[†]	TXT	Color[‡]	Structure	Carbonates/ mottles
			Site 1		
15	A1	l-sil	10YR 3/1	gr	
34	A2	sicl	7.5YR 3/2	gr/sbk	
56	A3	sil	10YR 3/2	gr/sbk	
76	Bt1	cl	7.5YR 4/3	gr/sbk	mottles, reddish
>76	Bt2	cl	7.5YR 4/4	gr/sbk	
			Site 2		
24	A1	sil	7.5YR 3/1	gr	
50	A2	sil	10YR 3/1	gr/sbk	
75	A3	sil	7.5YR 3/2	gr/sbk	mottles, gray
>75	Bt1	sil-cl	7.5YR 4/2	gr/sbk	
			Site 3		
11	A1	sicl	2.5Y 4/2	gr	
18	A2	sicl	2.5Y 3/2	sbk	
30	AB	sicl	2.5Y 5/3	sbk	
45	Bt1	sicl	2.5Y 5/3	abk	mottles
70	BC	sicl	2.5Y 5/3	pl	mottles
>70	C	sicl	2.5Y 5/3	abk-pl	
			Site 4		
25	A	scl	10YR 3/2	sbk-gr	
30	AB	cl	7.5YR 4/2	sbk-gr	
55	Bt1	cl	7.5YR 4/3	sbk-gr	carbonate mass
76	Bt2	sil	7.5YR 4/3	sbk-gr	carbonate mass
>76	CB	sil	10YR 4/3	sbk-gr	carbonate mass

[†]HZN, horizon; TXT, field soil texture by “feel”.
[‡]Munsell designations.

Plant percent cover measurements

In July of 2001, we selected 48 quadrats (12 within each of the four sites) by simple random sampling (Dick, 1996) using a 0.75 x 0.75 m frame of PVC pipe. Within each quadrat, one observer visually estimated the aboveground percent cover of legumes and counted the number and species of legumes present. In addition, we visually estimated the aboveground percent cover of grasses and composites by classifying each quadrat according to the following cover class system as used by Daubenmire (1959): class 1 $\leq$ 5%; class 2 = 6-25%; class 3 = 26-50%; class 4 = 51-75%; class 5 = 76-95% and class 6 = 96-100%. The midpoint of each percent range was then used for subsequent data comparison (Holechek, 2004) with legume percent cover. The range of percent legume cover observed across all quadrats was 0-60%, with 18 quadrats of 0%, 19 quadrats of <10%, and 11 quadrats of 10-60%. Based on these findings, we divided this range into three categories: *no* legume cover (0%), *low* legume cover (between 0 and 10%), and *high* legume cover ($\geq$10%). Then we randomly selected 8 quadrats within each category from which to sample for soil analyses.

Field measurements and soil sampling

Over two consecutive days with no precipitation in August of 2001, we measured water infiltration using a 15 cm diameter cylinder inserted 2 to 3 cm deep into the soil near the center of each quadrat. Vegetation was clipped to the soil surface and loose dead plant matter was removed within each ring. Plastic wrap was used to line the inside of the ring prior to filling the ring with 444 ml of water (a 2.54 cm depth). Two consecutive measurements were taken at each quadrat to estimate the rate of infiltration for both “dry” and “wet” soil (Sarrantonio, 1996).

Between 7 and 17 August 2001 we collected six soil core samples, using a 22.8 mm-diameter closed soil probe, in each of the 24 quadrats to a depth of 40 cm at sites 1, 2, and 4, and 30 cm in site 3 (due to the shallow depth to rock in site 3). Each core was placed horizontally in a 2.54 cm (1-inch) diameter PVC trough (pipe cut lengthwise in half) and then divided into the following depth increments: 0-7.5 cm, 7.5-15 cm, 15-30 cm, and 30-40 cm. For three of the six cores we estimated the depth of the A1 horizon based on color change. We weighed each subcore in the field to calculate the field bulk density. These soil cores were then sealed in plastic bags and kept on ice. The other three soil cores were composited by depth and used to determine field soil water content by drying a 20 g subsample at 65°C overnight and 105°C for two additional hours. The remaining soil from the second three cores was combined by depth increment with the first three cores as a single composite sample for each depth increment and quadrat. All 92 composite samples (24 quadrats x 4 depths, except for site 3 at 3 depths) were air-dried at room temperature, and then sealed in plastic bags until analysis.

Analysis of chemical and physical properties of composite soil samples

Approximately 50g of soil taken from each of the 92 composite samples was sent to the Soil Testing Laboratory at Kansas State University, Manhattan, Kansas and analyzed for available P (Olsen et al., 1954), exchangeable K^+, Ca^{2+}, and Mg^{2+} (N.C.R.P.N., 1988). The coarse fragment (>2 mm) content of each composite sample was determined by weight.

Laboratory preparation and analysis

Subsamples from the 0-7.5 cm and 7.5-15 cm soil samples were weighed and sieved through 2 mm- and 0.5 mm-sieves to determine the percent of whole soil in air dry

aggregates of sizes <0.5 mm, 0.5-2 mm, and >2 mm. Wet aggregate stability of the 0-7.5 cm and 7.5-15 cm samples was estimated by a turbidimetric method (Williams, 1966). From the 0.5-2 mm -sized aggregates previously dry-sieved, 1.00 g from each sample was added to a 50-ml polycarbonate centrifuge tube. Approximately 20 ml of distilled water was slowly added by pipette to the inner side of each tube with minimal disturbance to the soil. Capped tubes were shaken horizontally for one minute at 80 rpm. After four to seven minutes of settling, an aliquot of 3.5 ml was take from the supernatant and transferred to a 1-cm pathlength glass cuvette. Transmittance at 630 nm was determined with a Spectronic 21 spectrophotometer. Transmittance was adjusted to 100.0 with distilled water at start of readings and after every fourth or fifth sample. Each cuvette was tipped over and back twice to ensure homogenous suspension immediately before each reading was taken. For a second reading, the suspension was poured back into the tubes that were then shaken horizontally for two minutes at 160 rpm. After four to seven minutes of settling, a second aliquot of 3.5 ml was taken and transferred to another cuvette and a second transmittance reading was taken at 630 nm. A turbidity ratio, in which the higher the ratio, the stronger the aggregates, was calculated as follows:

Turbidity ratio = 1^{st} aggregate stability reading / 2^{nd} aggregate stability reading

Representative 2-3 g samples from soils of sites 1, 2 and 4 were crushed with an agate mortar and pestle to less than 0.5 mm aggregates. Site 3 soil samples, which were calcareous by HCl effervescence test, were pre-treated with 0.3 M H_3PO_4 (Follett et al., 1997) to eliminate carbonates and then crushed similarly to soils of sites 1, 2, and 4. Between 0.1000 and 0.2000 g of this soil was placed in tin capsules and analyzed for total C, H, and N (Campbell, 1992).

All 92 composite soil samples were further analyzed (in duplicate) for active fraction C using the dilute $KMnO_4$ oxidation method of Weil et al. (2003). Salinity (EC of a 1:2 soil:water suspension), pH_{dH2O} (1:2 soil:distilled water) and pH_{KCl} (1:2 soil:1 *M* KCl,) were also determined.

Soil incubation set-up

Subsamples of soil from the upper two depth increments were incubated at 60% water-filled pore space as recommended by Linn and Doran (1984) and Drinkwater (1996). From a 5.00 g composite sample from each soil sample, we determined the laboratory bulk density (BD) as incubated using a 10-ml graduated cylinder, and then calculated the total pore space (PS), assuming 2.65 g cm^{-3} for particle density (PD). The laboratory gravimetric water (G_w) content of the sample was measured using the same soil subsample, drying at 60°C overnight and 105°C for two hours. These measurements were used to calculate the volumetric water content (V_w), which was then subtracted from the volume of 60% pore space to determine the amount of water needed to fill 60% of the pore space of each soil subsample. The amount of water to add to each sample was calculated as

BD = g soil / ml [1 cm^3 = 1 ml]

PS = 1 – (BD g ml^{-1} / PD g cm^{-3})

Volume of 60 % PS = (volume of soil)(PS)(0.6)

$$G_w \text{ (g g}^{-1}\text{ soil)} = \frac{\text{(air-dry soil wgt – oven-dry soil wgt)}}{\text{oven-dry soil wgt}}$$

$$V_w \text{ (g g}^{-1}\text{)} = \frac{(G_w \text{ g g}^{-1})(\text{BD g cm}^{-3})}{\text{density of water (g cm}^{-3}\text{)}}$$

water to add (ml g^{-1}) = volume of 60% PS - V_w

Short-term incubations for potentially mineralizable C and N typically range from 14-28 days (Drinkwater, 1996). We set up a 16-day incubation as described in Sainju et al. (2002) using 1-L chambers with gas-tight sealed lids to contain 10.0g soil wet to 60% water-filled pore space. Based on a preliminary experiment, we added 3.0 ml of 0.50 *M* NaOH to a plastic vial inside each chamber. A vial of distilled water was placed in each chamber to maintain the soil humidity and therefore the soil water content during the incubation. All 48 chambers were placed in an incubator at 30± 1°C (Drinkwater, 1996). Six "blank" chambers with the NaOH and dH_2O but no soil were also included in the experiment to determine the background absorption of CO_2 in the containers. The temperature was monitored throughout the duration of the experiment.

Measuring mineralizable C

In each container, the beaker of 0.50 *M* NaOH was removed 1, 2, 4, 8 and 16 days after the start of the incubation and replaced with a beaker of fresh 0.50 *M* NaOH on all except day 16. Immediately after removing each NaOH beaker and before titrating, we added at least 3 ml of 0.5 *M* $BaCl_2$ to the NaOH to prevent reversal of CO_2 absorption upon titration. The NaOH was titrated with standardized 0.15 *M* HCl and two drops of phenolphthalein indicator (Rice, 1996) to determine the amount of NaOH neutralized by absorbed CO_2. We summed the CO_2-C measured by the first two titrations to calculate the two-day CO_2-C release. We summed the CO_2-C from all the titrations to calculate the accumulated 16-day CO_2-C released which we refer to as mineralizable C.

Measuring mineralizable N

At the end of the incubation period, we shook each incubated soil sample horizontally for 15 minutes at 100 rpm with 20 ml of 0.1 *M* K_2SO_4 (Weil, 1998) in a 50-

ml polyurethane centrifuge tube. After settling for at least 20 minutes, the supernatant was filtered through VWR #494 filter paper into 20-ml vials. From this filtrate, an aliquot of 0.2 ml was used to determine the extracted nitrate-N by a salicylic acid colorimetric method (modified from Cataldo, 1975). We added first 0.8 ml of 5% salicylic acid/H_2SO_4 solution, and then 19.0 ml of 1.7 N NaOH. After transferring to a cuvette, the absorbance was read with a spectrophotometer set at 410 nm wavelength. Subsequently, we placed 5 ml of the filtrate and 5 ml of dH_2O into a clean 20-ml vial and added 1 ml of ionic strength adjusting solution (5 M NaOH + 0.05 M EDTA + 10% thymolphthalein in ethanol) to measure the NH_4 –N with an ammonia gas sensitive electrode (Orion, 2001) and millivolt meter (Orion Model 940). To obtain measurements of the initial nitrate and ammonium N in the soil samples, we performed the same extraction, filtration and NO_3 and NH_4 analyses on non-incubated soil samples that had been stored dry at room temperature. The difference between N extracted from the incubated soil and N extracted from the non-incubated soil was considered to be the N mineralized during the incubation and is referred to as mineralizable N.

Statistical design and analysis

Using SAS (1999-2001), field and laboratory data was first analyzed by one-way analyses of variance to determine both the effect of soil and the effect of legume category on individual soil properties measured. Pairwise correlations were performed between percent legume cover and soil variables at each depth.

Using SYSTAT (1999), a separate correlation analysis was performed with soil variables from 0-15 cm. Subsequently, we used stepwise multiple linear regression using surface soil properties (except potentially mineralizable C and N) to determine which soil

properties accounted for most of the variation in percent legume cover. We used discriminant multivariate analysis with eight soil variables (field bulk density, C:N ratio, % organic matter, active C as a % of total C, pH_{H2O}, 2-day cumulative CO_2-C, initial mineralizable NO_3 and EC) to determine which soil properties have the most association with percent legume cover.

Results

Cover Class Data

Twelve legume species representing nine genera were observed in 48 quadrats among the four study sites (Table 3.2.). Site 3 had the greatest abundance and diversity of legume species. The three most abundant species (*Dalea purpurea* Vent., *Psoralea argophylla* Pursh, and *Shrankii nuttallii* (D.C.) Standl.) in site 3 also occurred in the most quadrats (at least five) within this site. In site 4, the most abundant legume species (*Lespedeza virginica* (L.) Britt.) occurred in only two quadrats. Site 1 had only two species but considerably more legume plants than both sites 2 and 4, fairly evenly spread among the majority of quadrats. Site 2 had one species, but only one plant.

Cover class by visual assessment for the 24 quadrats selected for soil sampling indicated site 2 had no legumes and sites 1 and 4 had relatively low legume cover (Table 3.3.), predominantly *Amorpha canescens* Pursh (leadplant) at site 1 and *Lespedeza virginica* in site 4 (see Table 3.2.). Site 3 had the highest legume cover. Grass cover dominated all sites, except in site 3 where it was only slightly greater in proportion to legume cover.

Table 3.2. Legume species, their distribution, and grazing pressures within 12 quadrats in each site.

Species	Quadrats/site	Plants/site	Decreaser[†]	Increaser[†]
		Site 3		
Baptisia australis[‡]	4	7	–	X
Dalea multiflora	2	2	X	–
Dalea purpurea	7	21	X	–
Desmanthus illinoensis[‡]	2	4	X	–
Psoralea argophylla	5	23	–	X
Psoralea esculenta	1	1	X[§]	X[¶]
Shrankia nuttallii	7	29	X[#]	–
Lespedeza striata	1	6	X††	–
Total	29	93	6	3
		Site 4		
Lespedeza striata	1	2	–	–
Lespedeza virginica	2	10	X	–
Unidentified clover[§§]	1	2	–	–
Total	4	14	1	0
		Site 1		
Unidentified clover[§§]	9	19	–	–
Amorpha canescens	7	23	X	–
Total	16	42	1	0
		Site 2		
Unidentified vetch	1	1	–	–
Total	1	1	0	0

[†]As reported by Stubbendieck (1989).
[‡]Species grown in greenhouse pot experiment.
[§]Decreases with heavy grazing.
[¶]Increases with light grazing.
[#]Livestock eat new growth before thorns harden.
[††]Decreases slowly.
[§§]Only very small plants found.

Table 3.3. Mean percent cover for legumes, grasses, composites for 24 quadrats across four sites. Values are midpoints of estimated percent cover class.

	Legumes	Grasses	Composites
	----------%----------		
Site 1	5.6a	71.8a	9.6a
Site 2	0.0a	77.5a	38.3b
Site 3	34.0b	43.0a	17.0ab
Site 4	2.7a	56.7a	22.5ab

Within columns, means followed by the same letter are not significantly different according to Tukey (0.05).

Piper (1995) measured plant dry matter for grasses, legumes and composites on the same sites used in the present study during May through August from 1986 to 1992. The mean values of data results (Table 3.4.) indicate little variation of plant proportions over the seven-year study, indicating relatively stable plant communities at these sites. Although we estimated ground cover during one year and Piper measured dry matter for seven years, the relative dominance for the three plant groups was similar at each site. The greatest difference between the data sets is the proportion of composite plant cover in site 2 (about half that of grasses as compared to one-tenth that of grasses in Piper's data) and legumes in site 3.

Soil surface data (Tables 3.5, 3.6.)

In general, the high legume quadrats were on much steeper slopes than the low and no legume quadrats. Most of the quadrats with the highest legume cover and steepest slopes were in site 3, and the steepest sloped quadrat in site 4 was also highest in legume cover. The steepest sloped quadrat in site 1, however, did not correspond to the two quadrats with high legume cover. Legume cover was positively correlated with slope with $R^2 = 0.53$. (Figure 3.2.).

Infiltration measured on pre-wetted soil in the field was slowest in quadrats with low legume cover and fastest in quadrats with high legume cover. However, the average infiltration rates for dry soil were 3 times as great as for wet soil in the high legume quadrats, but only 2.5 times higher in the low and no legume quadrats. In site 3 on average, the second infiltration rate was six times slower than the first infiltration rate (Table 3.6.). The difference for the other three sites was no more than three times slower. The high legume areas had lower aggregate stability than the low legume areas

Table 3.4. Legume, grass, and composite cover and dry matter for four prairie sites and their rank.

	Site															
	1				2				3				4			
	CV[†‡]	DM[§]	CV[†]	DM[§]	CV	DM	CV	DM	CV	DM	CV	DM	CV	DM	CV	DM
	--------%-------		------rank------		-------%-----		-----rank----		-------%-----		-----rank----		-------%-----		-----rank----	
L	5.6	0.2	3	3	0.0	0.0	3	3	34.0	17.1	2	2	2.7	1.2	3	3
G	71.8	87.0	1	1	77.5	87.6	1	1	43.0	59.3	1	1	56.7	75.4	1	1
C	9.6	4.8	2	2	38.3	8.0	2	2	17.0	7.3	3	3	22.5	19.7	2	2

[†]This study.
[‡]CV, cover; DM, dry matter.
[§]From Piper (1995).

Table 3.5. Soil properties by legume cover category for 0-7.5 cm depth (unless otherwise indicated). Means of eight quadrats.

Cover	INFD[†]	INFW	A1HZ	Slope	AGS	CO_2-C[‡]	CO_2-C[§]	CO_2-C[‡¶]	CO_2-C[§¶]	TMIN N	TMIN N[¶]
	-------s/444ml-----		cm	%	ratio	----------g m^{-2}----------					
High	134a[#]	391a	13.8a	27a	0.339a	98.95a	151.14a	61.24a	93.81a	1.09a	2.74a
Low	497a	1188b	18.3a	11b	0.650b	98.30a	150.41a	68.82a	102.32a	0.99a	3.09a
No	342a	840ab	18.4a	11b	0.524ab	88.26a	133.58a	60.35a	89.72a	0.80a	2.75a
Mean	324	806	16.8	16	0.504	95.17	145.04	63.47	95.28	0.96	2.86

[†]INFD, infiltration dry; INFW, infiltration wet; HZ, horizon; AGS, aggregate stability; TMIN, total mineralized.
[‡]Cumulative for 2 d incubation.
[§]Cumulative for 16 d incubation.
[¶]For 7.5-15 cm depth.
[#]Within columns, means followed by the same letter are not significantly different according to Tukey comparisons (0.05).

Table 3.6. Soil properties by site for 0-7.5 cm depth (unless otherwise indicated).

Site	INFD[†]	INFW	A1HZ	Slope	AGS	CO_2-C[‡]	CO_2-C[§]	CO_2-C[‡¶]	CO_2-C[§¶]	TMIN N	TMIN N[¶]
	-----s/444ml----		cm	%	ratio	----------g m^{-2}----------					
1	456a	1193a	19.1a	7a	0.704a	115.18a	173.14a	69.91a	106.81a	1.34a	2.36a
2	292ab	878ab	19.3a	2b	0.612b	107.36ab	160.67ab	66.66a	106.13a	1.40a	2.30a
3	13b	88b	11.2b	35c	0.138c	92.88ab	144.10ab	60.10a	91.09a	0.98a	2.68a
4	405ab	881a	17.2ab	16d	0.516b	76.81b	118.51b	59.27a	85.03a	0.50a	3.53a
Mean	324	806	16.8	16	0.504	95.17	145.04	63.47	95.28	0.96	2.86

[†]INFD, infiltration dry; INFW, infiltration wet; HZ, horizon; AGS, aggregate stability; TMIN, total mineralized.
[‡]Cumulative for 2 d incubation.
[§]Cumulative for 16 d incubation.
[¶]For 7.5-15 cm depth.
[#]Within columns, means followed by the same letter are not significantly different according to Tukey comparisons (0.05).

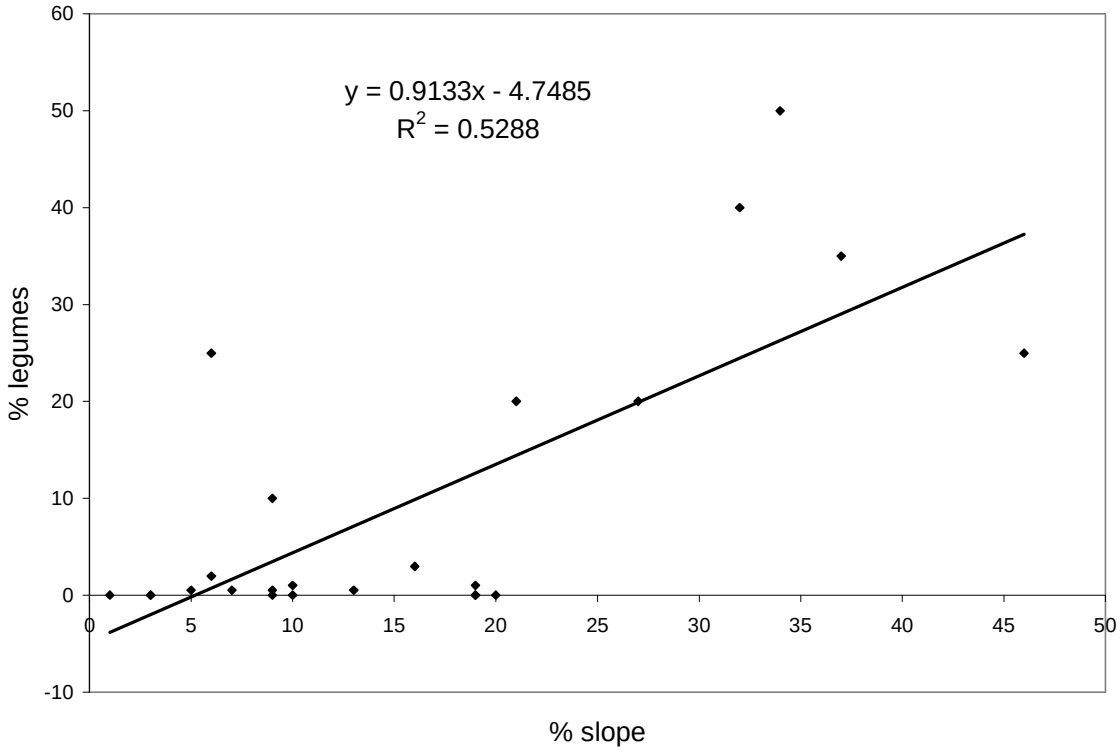

Figure 3.2. Relationship between legume cover and slope of 24 quadrats among four prairie sites.

(mostly in site 1). Sites 2 and 4, which were within about 45 m of each other, had very similar aggregate stability. Both these sites had mostly no legume cover areas. The A1 horizon depth did not differ significantly among legume categories.

Soil core profile data (Tables 3.7, 3.8, 3.9, and 3.10.)

Field bulk densities were significantly higher in the high legume cover quadrats than in the low legume quadrats at the 7.5-30 cm depth. Soil water content (g g^{-1} soil) in the field was highest in the high legume areas for the upper two depths (0-15cm).

Soil depth and legume cover class had no effect on soil P, but soil K^{+} in the 30-40 cm layer was lower in the high legume than in the no-legume quadrats. Levels of extractable Ca^{2+} (g m^{-3}) was significantly higher in the 0-15 cm layers in the high legume quadrats, but there was no difference in soil Ca among legume classes at the 30-40 cm depth. Levels of soil Mg^{2+} were not different in the upper depths, but the no legume quadrats had higher levels of Mg^{2+} in the 30-40 cm layer.

All three legume cover categories had their highest levels of total organic C at the 0-7.5 cm depth with levels decreasing and differing less by depth. The high legume cover areas had the lowest total C (18.54 g kg^{-1}) from 0 to 30 cm, less than half the highest average total organic C (39.28 g kg^{-1}) of low legume cover. The percent organic matter found in these soils followed the same trend as the total organic C. For total N (g kg^{-1}), differences were significant only in the 7.5-15 cm and 15-30 cm depths, with high legume quadrats having the lowest total N. At the 0-7.5 cm depth, the C to N ratios found in these soils ranged from 11.2 to 13.2. The greatest difference in C/N ratio among the legume categories was found in the top two depths (0-15 cm), where ratios in the high legume soils were significantly lower than both no and low legume soils, mostly due to

Table 3.7. Soil properties by legume cover category and soil depth. Mean of eight quadrats.

Depths	Cover	BD[†]	SWC	pH_{H2O}	pH_{KCl}	EC	P[‡]	K^{+}	Ca^{+2}	Mg^{+2}	COF
cm		g cm^{-3}	g g^{-1}			µS m^{-1}	----------g m^{-3}----------				%
0-7.5	High	0.7a[§]	0.10a	7.06a	6.39a	100.8a	0.4a	17.8a	177.8a	25.5a	5.4a
	Low	0.7a	0.06b	6.20b	5.43b	56.0b	0.4a	17.9a	88.4b	16.4a	0.6b
	No	0.6a	0.06b	6.32b	5.45b	63.3b	0.7a	18.4a	90.8b	21.1a	0.5b
	Mean	0.7	0.07	6.53	5.76	73.4	0.5	18.0	119.0	21.0	2.2
7.5-15	High	0.9a	0.09a	7.06a	6.27a	79.3a	0.7a	14.7a	200.0a	29.9a	5.4a
	Low	0.8b	0.07b	6.08b	5.09b	40.8b	0.7a	15.4a	98.9b	19.9a	0.7b
	No	0.8b	0.07b	6.35ab	5.25b	45.8b	0.4a	17.2a	109.0b	29.8a	0.2b
	Mean	0.8	0.08	6.50	5.54	55.3	0.6	15.8	136.0	26.5	2.1
15-30	High	0.9a	0.10a	7.22a	6.31a	64.6a	1.0a	21.0a	445.3a	67.2ab	6.3a
	Low	0.8b	0.08a	6.40a	5.24b	34.0a	0.9a	27.7a	247.8b	51.7a	1.1b
	No	0.8ab	0.09a	6.87a	5.56ab	119.9a	0.8a	29.5a	332.8ab	83.2b	0.2b
	Mean	0.9	0.09	6.83	5.70	72.8	0.9	26.1	341.9	67.4	2.5
30-40	High	0.9a	0.08a	6.89a	5.94a	50.9a	0.8a	10.4a	229.4a	39.4a	8.0a
	Low	0.9a	0.08a	6.83a	5.62a	41.8a	0.7a	14.4ab	204.6a	44.6a	3.0ab
	No	0.9a	0.10a	7.07a	5.78a	143.8a	0.4a	16.8b	309.8a	69.3b	0.1b
	Mean	0.9	0.09	6.94	5.75	84.4	0.6	14.6	251.6	53.5	2.8

[†]BD, field bulk density; SWC, soil water content; EC, electric conductivity; COF, coarse fragments.
[‡]Olsen extracted.
[§]Within columns, means followed by the same letter are not significantly different according to Tukey comparisons (0.05).

Table 3.8. Soil properties by legume cover category and soil depth. Means of eight quadrats.

Depth	Cover	Total C	Total H	Total N	C:N	OM[†]	Active C	AC/TC
cm		----------g kg^{-1}----------			ratio	%	mg kg^{-1}	%
0-7.5	High	18.54a[‡]	10.45a	1.59a	11.2a	3.2a	538.87a	3.54a
	Low	39.28b	4.70b	2.22a	13.2b	5.1b	570.91a	1.97b
	No	27.02ab	4.77b	2.17a	12.3ab	4.7ab	558.27a	2.12b
	Mean	24.95	6.64	1.99	12.3	4.3	556.02	2.54
7.5-15	High	10.69a	9.40a	1.08a	9.4a	1.8a	444.10ab	4.95a
	Low	18.05b	4.21b	1.56b	11.5b	3.1b	550.27a	3.14b
	No	17.21b	4.51b	1.54b	11.1b	3.0b	437.51b	2.60b
	Mean	15.32	6.04	1.39	10.7	2.6	477.29	3.56
15-30	High	7.17a	9.38a	0.79a	8.3a	1.2a	263.97a	4.63a
	Low	12.80b	4.40b	1.24b	10.2a	2.2b	339.07a	2.76b
	No	12.59b	4.93b	1.27b	9.6a	2.2b	308.30a	2.57b
	Mean	10.85	6.23	1.10	9.4	1.9	303.78	3.32
30-40	High	7.82a	6.22a	0.85a	8.3a	1.4a	234.95a	4.11a
	Low	9.87a	4.52a	0.98a	9.9a	1.7a	273.14a	2.91a
	No	9.14a	5.23a	1.01a	8.8a	1.6a	228.51a	2.66a
	Mean	9.17	5.14	0.97	9.2	1.6	247.65	3.05

[†]OM, organic matter; AC/TC, active C to total C.

[‡]Within columns of each depth, means followed by the same letter are not significantly different according to Tukey comparisons (0.05).

Table 3.9. Soil properties by site and soil depth.

Depths	Site	BD[†]	SWC	pH_{H2O}	pH_{KCl}	EC	P[‡]	K^{+}	Ca^{+2}	Mg^{+2}	COF
cm		g cm^{-3}	g g^{-1}			µS m^{-1}	----------g m^{-3}----------				%
0-7.5	1	0.7a[§]	0.07a	6.17a	5.43a	61.1ab	0.3a	17.2a	87.3a	16.4a	0.6a
	2	0.6a	0.08ab	6.23a	5.42a	76.9a	0.7a	21.7a	105.5a	18.7ab	0.5a
	3	0.7a	0.11b	7.59b	6.99b	130.4c	0.5a	18.3a	230.1b	30.8b	8.2b
	4	0.7a	0.06a	6.32a	5.44a	50.0b	0.6a	17.2a	86.3a	19.9a	0.6a
	Mean	0.7	0.07	6.53	5.76	73.4	0.5	18.0	119.0	21.0	2.2
7.5-15	1	0.8a	0.08a	5.99a	5.01a	42.7a	0.4a	15.6a	96.7a	19.6a	0.7a
	2	0.7b	0.08a	6.09a	5.09a	49.8a	0.5a	21.8b	123.5a	23.9a	0.1a
	3	0.9c	0.09a	7.68b	7.05b	104.4b	0.4a	14.7a	257.3b	35.7a	8.5b
	4	0.8ab	0.07a	6.37a	5.25a	39.7a	0.9a	14.5a	103.3a	27.2a	0.2a
	Mean	0.8	0.08	6.50	5.54	55.3	0.6	15.8	136.0	26.5	2.1
15-30	1	0.8a	0.08a	6.09a	4.95a	31.6a	0.4a	20.7a	212.1a	46.3a	1.6b
	2	0.8a	0.11a	6.24a	5.00ab	30.4a	1.2a	37.8b	317.5ab	66.4ab	0.0a
	3	0.9b	0.10a	7.84b	7.12c	85.4a	0.7a	23.2a	571.8c	79.5ab	9.6c
	4	0.8a	0.08a	7.03c	5.74b	112.0a	1.3a	27.9ab	323.4b	77.3b	0.2a
	Mean	0.9	0.09	6.83	5.70	72.8	0.9	26.1	341.9	67.4	2.5
30-40	1	0.9a	0.08a	6.14a	4.92a	31.3a	0.4a	11.3a	163.2a	39.0a	5.6a
	2	0.9a	0.11b	6.32a	4.93a	29.5a	0.3a	20.4b	277.6a	60.9a	0.1a
	3	0.9a	0.06ab	7.84b	7.09b	97.0a	0.1a	11.0ab	319.6a	43.7a	14.0a
	4	0.9a	0.09ab	7.66b	6.52b	142.6a	0.9a	15.6ab	304.2a	63.3a	0.4a
	Mean	0.9	0.09	6.94	5.75	84.4	0.6	14.6	251.6	53.5	2.8

[†]BD, field bulk density; SWC, soil water content; EC, electric conductivity; COF, coarse fragments.
[‡]Olsen extracted.
[§]Within columns of each depth, means followed by the same letter are not significantly different according to Tukey comparisons (0.05).

Table 3.10. Soil properties by site and soil depth.

Depths	Site	Total C	Total H	Total N	C:N	OM[†]	Active C	AC/TC
cm		----------g kg^{-1}----------			ratio	%	mg kg^{-1}	%
0-7.5	1	33.06a[‡]	5.00a	2.49a	13.3a	5.7a	600.10a	1.83a
	2	33.41a	5.30a	2.62a	12.7ab	5.7a	608.49a	1.82a
	3	11.75b	13.91b	1.13b	10.4c	2.0b	518.37a	4.45b
	4	23.15c	4.32a	1.87c	12.4b	4.0c	525.16a	2.28c
	Mean	24.95	6.64	1.99	12.3	4.3	556.02	2.54
7.5-15	1	19.79a	4.27a	1.67a	11.9a	3.4a	533.35a	2.70ab
	2	22.00a	5.06b	1.88a	11.7ab	3.8a	480.17a	2.18a
	3	6.69b	12.59c	0.81b	8.2c	1.2b	419.55a	6.20c
	4	14.40c	14.10a	1.34c	10.7b	2.5c	464.81a	3.23b
	Mean	15.32	6.04	1.39	10.7	2.6	477.29	3.56
15-30	1	14.85a	4.40a	1.37a	10.9a	2.5a	361.87a	2.44a
	2	16.84a	5.51b	1.58a	10.7a	2.9a	383.78a	2.28a
	3	4.11b	12.50c	0.55b	7.3b	0.7b	236.88b	5.80b
	4	9.48c	4.42a	1.04c	8.9c	1.6c	269.13b	2.97a
	Mean	10.85	6.23	1.10	9.4	1.9	303.78	3.32
30-40	1	11.92a	4.53a	1.13ab	10.6a	2.1a	293.80a	2.48a
	2	11.98a	5.84b	1.26b	9.5ac	2.1a	264.35ab	2.21a
	3	3.11b	12.60c	0.52ac	6.0bc	0.5b	203.12ab	6.54b
	4	6.76b	4.56a	0.80c	8.2c	1.2b	211.14b	3.39a
	Mean	9.17	5.14	0.97	9.2	1.6	247.65	3.05

[†]OM, organic matter; AC/TC, active C to total C.

[‡]Within columns of each depth, means followed by the same letter are not significantly different according to Tukey comparisons (0.05).

the low total C. The levels of total H (g kg^{-1}), however, were highest in the high legume cover quadrats for the 0-30 cm depths. For all legume categories, the highest active C was concentrated in the upper 7.5 cm, where the majority of microbial activity occurs. However, the high legume category had the highest active C as a percent of total C because of low levels of total C.

The pH_{H2O} for all legume categories was above 5.0. The high legume quadrats had the highest pH_{H2O} (7.06) in the top two depths. The pH_{KCl} was also highest for the high legume cover quadrats at all depths, except at 30-40 cm where there was no difference among legume classes. EC levels were much higher in the high legume cover quadrats for the upper two depths, but below 15 cm, there were no significant differences.

Incubation data

During a 16-day incubation period, the rate of mineralization for C in all four soils increased sharply in the first 24 hours of incubation (Figures 3.3, 3.4.) and decreased steadily as the incubation period approached the full 384 hours. Potentially mineralizable C was not significantly different among legume categories (Table 3.5.), although the amount of cumulative CO_2-C was higher in soils from site 1 than in soils from site 4 at the 0-7.5 cm depth (Table 3.6.). The greatest difference was observed between the 0-7.5 cm and the 7.5-15 cm depths averaged over all sites (Figure 3.5.). The cumulative mineralizable C after 16 days of incubation reached an average maximum of 149 g CO_2-C m^{-2} soil in soils from 0-7.5 cm, but only 97g CO_2-C m^{-2} soil in soils from 7.5-15 cm.

There was no difference between sites or legume cover for total mineralizable N (nitrate + ammonium) (Table 3.11.). The incubated soils also were no different in total mineralizable N among the four sites for each of the two depths (Table 3.11.) but there

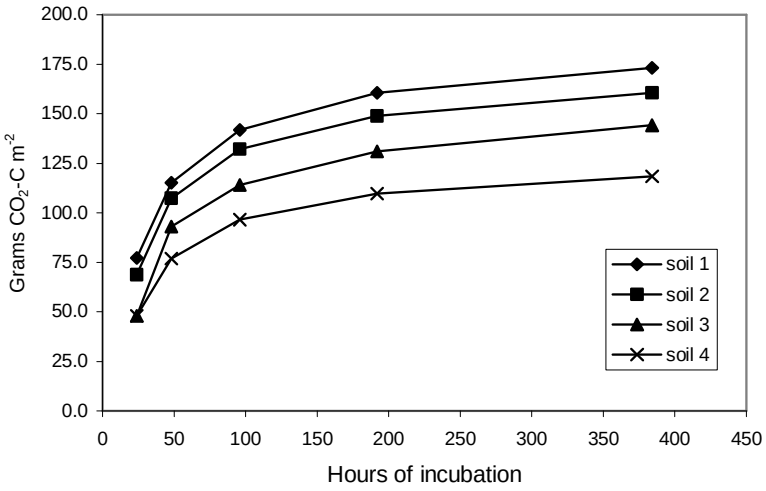

Figure 3.3. Cumulative mineralized C for incubated soils taken from the 0-7.5 cm depth at four native prairie sites.

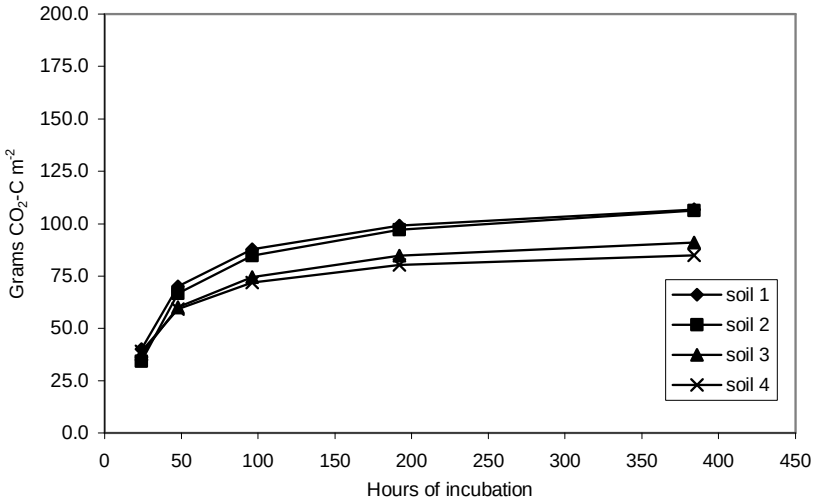

Figure 3.4. Cumulative mineralized C for incubated soils taken from the 7.5-15 cm depth at four native prairie sites.

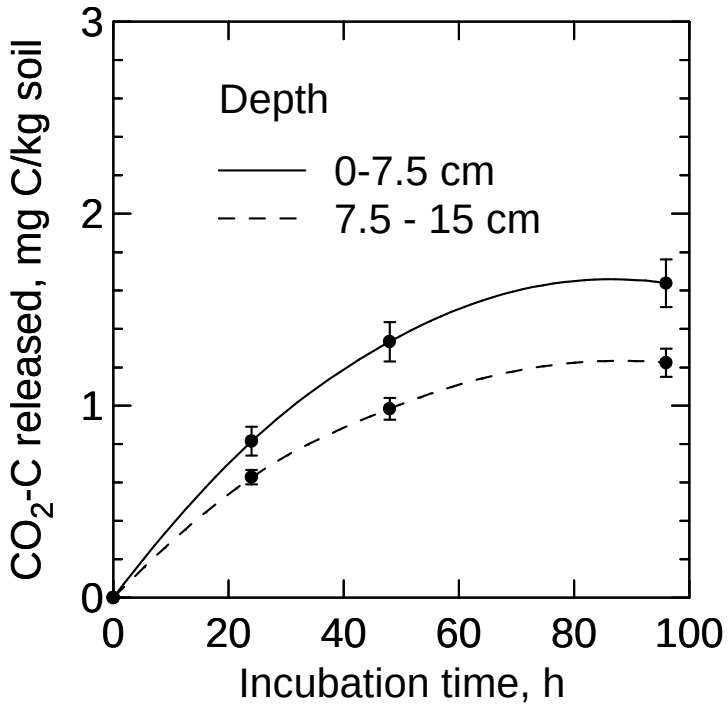

Figure 3.5. Cumulative mineralizable C of incubated soils (first 96 hours) averaged over all sites at two different depths. **significantly different, P<0.001

Table 3.11. Means of mineralized ammonium-N and nitrate-N, and total mineralized N for 16 d incubated soils from four prairie at two different depths (cm).

	NH_4		NO_3		Total mineralized N	
	0-7.5	7.5-15	0-7.5	7.5-15	0-7.5	7.5-15
	----------g m^{-2}----------					
	Site					
1	0.50b†	1.63a	0.85a	0.73a	1.3a	2.4a
2	0.27ab	1.16a	1.13a	1.14a	1.4a	2.3a
3	0.00a	0.13b	1.02a	2.53a	1.0a	2.7a
4	0.05a	0.62c	0.46a	2.91a	0.5a	3.5a
	Legume cover category					
High‡	0.12a†	0.60a	0.96a	2.13a	1.1a	2.7a
Low	0.31a	1.26a	0.67a	1.82a	1.0a	3.1a
No	0.13a	0.78a	0.68a	1.97a	0.8a	2.8a
Mean	0.19	0.88	0.77	1.97	1.0	2.9
±SE	± 0.06	± 0.13	± 0.20	± 0.54	± 0.2	± 0.5

†Within columns, means followed by the same letter are not statistically different according to Tukey comparisons (0.05).
‡Legume cover class of high (10-40%), low (>0, <10%), and no (0%).

were differences in mineralized forms of nitrogen. In the 0-7.5 cm depth, incubated soils of site 1 were higher in mineralized NH_4 than soils of site 3 and 4, whereas mineralized NO_3 was no different among sites. In the 7.5-15 cm depth, incubated soils from sites 1 and 2 had higher mineralized NH_4 than soils from site 3 and 4. Soil from site 3 exhibited the lowest potentially mineralizable NH_4 at the 7.5-15 cm depth. Average values for mineralized NO_3 in soils from site 3 and 4 were higher than soils from site 1 and 2 (at the 7.5-15 cm depth), but these were not significantly different (Table 3.11.).

Soil properties associated with percent legume cover

Pairwise correlations between percent legume cover and 26 soil surface variables (0-7.5 cm), resulted in positive correlation coefficients greater than 0.7 (P<0.0001) for seven soil variables (Table 3.12). Only four of these soil variables were also significantly (P<0.0001) correlated with legume cover at the 7.5-15 cm depth, only two variables at the 15-30 cm depth and none at the 30-40 cm depth. In addition to these soil variables, % coarse fragments was correlated with legume cover at the lower depths (7.5-30 cm) only. Soil variables from 0-15 cm with the highest r^2 values when correlated with legume cover resulted in the following correlation models:

% legume = 7.89 (% activeC/totalC) –14.33 $r^2 = 0.52$

% legume = 16.10 (pH_{H2O}) – 95.08 $r^2 = 0.50$

% legume = -5.41 (C/N ratio) = 71.70 $r^2 = 0.32$

% legume = -4.97 (% organic matter) + 26.99 $r^2 = 0.24$

In a step-wise multiple regression analysis with surface (0-7.5 cm) soil properties (not including potentially mineralizable C and N) and percent legume cover we found that active C to total C explained the most variation and resulted in the highest correlation

Table 3.12. Pearson correlations coefficients for soil variables correlated with percent legume cover. N = 24

Variable[†]	0-7.5[‡]	7.5-15[‡]	15-30[‡]
Total H	0.85677	0.82394	0.78305
AC / TC, %	0.79287	0.80090	0.79336
pH, in KCl	0.78871	0.73489	NS[§]
EC	0.78369	NS	NS
pH, in H_2O	0.76791	NS	NS
Ca^{2+}, extract.	0.74648	0.81443	NS
Slope, %	0.72718	NS	NS
COF, %	NS	0.74754	0.84208

[†]AC/TC, active C to total C; EC, electric conductivity; COF, coarse fragments
[‡]Depth, cm
[§]NS, nonsignificant at less than 0.0001 probability level.

coefficient (r=0.79). Adding % organic matter to the model raised the r value to 0.83 and resulted in the following multiple regression model:

% legume = 61.5 + 18.7 (activeC/totalC) + 5.5 (% organic matter)

None of the other variables correlated sufficiently to significantly improve the r value. We selected eight distinct soil variables (0-7.5 cm) most correlated with legume cover for discriminant multivariate analysis. Table 3.13 lists these variables and their standardized coefficients for factors 1 and 2. Active C % of total C and organic matter were the most important variables in factor 1, which best explained the variation between high legume cover, and low and no legume cover (Figure 3.6.). Carbon to N ratio was the most important variable in factor 2, which best explained the variation between low and no legume cover.

Discussion

Vegetation Cover

Most legume species found in site 3 are species that are reported (Stubbendieck, 1989) to be adversely affected by grazing, however, since there was no grazing on site 3 after around 1980, the presence of these species is not surprising. Leadplant (*Amorpha canescens* Pursh) is among the most favored legume by livestock and therefore its absence is used as an indication for overgrazed areas (Stubbendieck, 1989). Its absence in site 2 and 4 may be due to overgrazing. Site 2 is nearly level (0-6% slope) and has a southeast-facing slope, which is more preferred by cattle because of exposure to cooling southern winds. Although site 4 is steeper (8-25% slope), it is within 50 m of site 2, and also has a south-facing slope. The absence of leadplant in site 3, however, may be due to

Table 3.13. Soil variables and their standardized coefficients.

Soil variables	Factor 1	Factor 2
Bulk density	1.054	0.837
C/N ratio	-1.191	2.044
Organic matter, %	2.093	-0.650
Active C/Total C, %	3.024	1.091
pH, in H_2O	-1.786	-1.077
Cum CO_2-C (2day)	0.376	0.422
Initial min. NO_3	0.597	-0.136
Electric conductivity	-0.439	0.843

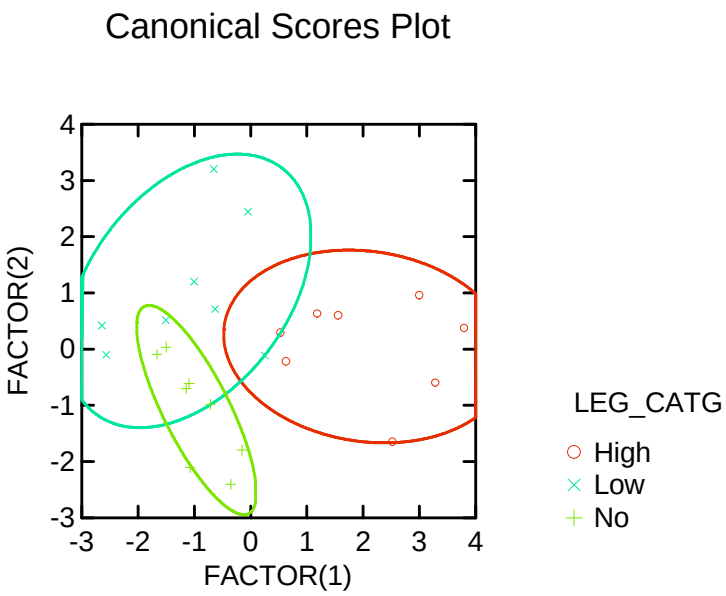

Figure 3.6. Canonical scores plot for legume cover categories of high (10-40%), low (>0, <10%), and no (0%).

other ecological disturbances such as erosion and fire frequency. Hartnett et al. (1996) studied upland and lowland tallgrass prairie sites grazed by bison in the northern Flint Hills of Kansas. They observed that leadplant was completely absent at the lowland sites, regardless of grazing treatment. On upland sites, they observed differences in canopy cover of leadplant on annually burned sites between grazed and ungrazed land, but no difference on 4-year burned sites between grazed and ungrazed land.

Our plant cover measurements for legumes and composites may be higher than Piper's dry matter measurements due to the larger leaf area of these two families of plants. Legumes and composites can cover more ground area with less plant dry matter than that of grasses.

In the field study, it was observed during our plant cover assessment that in some cases the quadrats selected with random sampling did not capture the full range of legume cover in each site. For example, our random sampling did not capture the dense patches of *Amorpha* observed in site 4. Systematic sampling may have been a better method to ensure that the legume cover across the entire site is well represented among the quadrats selected (Dick and Thomas, 1996). Also, it may be more advantageous to increase the size of each of the four sites to include a wider range of legume cover on similar soils. Since three of the sites did not have all three legume cover categories, it was difficult to analyze the data for site and legume cover interaction.

Since the three different legume cover categories (high, low, and no) were not all found in each of the four study sites, some of the legume-soil associations may be related more to a specific site rather than to all areas in a particular legume cover category. Sites 1 and 4 contained quadrats from more than one category, but all the quadrats in site 2 had

no legume cover and all the quadrats in site 3 had high legume cover. Site 2, however, contained only three of the eight no legume cover quadrats in the study, whereas site 3 contained five out of the eight high legume cover quadrats.

Furthermore, the high legume quadrats in site 3 consisted of a variety of legume species, whereas the high legume quadrats in site 1 and 4 consisted of primarily one legume species (Table 3.2.). These different areas of high legume cover may represent different successional stages. Vegetation in site 1 may be classified as a climax stage since it is dominated by deep-rooted grasses with only a few legume and composites species. Site 3 may be considered a mid-successional stage since the high number of legume species suggests a more heterogeneous community (Holechek et al., 2004).

Soil surface properties

The positive correlation between our legume cover and slope data agree with findings by Guretsky et al. (2004) in their study with pasture legumes on a slope gradient (max. 29%) and with different stocking treatments. Legume cover and slope were positively correlated with r^2 values of 0.75, 0.42, and 0.22, for rotational, continuous, and nongrazed treatments, respectively. They attributed high legume cover to less competition from grass on steeper slopes, which are often associated with shallower A-horizons and lower soil organic matter content.

The high infiltration rate (for both “wet” and “dry”) in the high legume cover areas of site 3 was surprising given the lower aggregate stability in these quadrats. This may be due to a number of factors that contribute to soil macropores including dead grass cover, coarse fragments, and soil cracks. The presence of soil macropores at these quadrats could explain initially high infiltration rates as water fills the macropores,

followed by much slower rates with additional wettings, as the water fills soil micropores. Site 3 was the only site from which dead grass shoot matter was present in the sieved material from the bulk soil samples collected in August of 2000 (see chapter 2). When infiltration data was collected in August of 2001, thick layers of dead grass were observed on the soil surface of many of these quadrats. All the high legume quadrats had significantly more coarse fragments in the top 30 cm than the no and low legume quadrats (Table 3.6.). In addition, after 10 days of watering these soils in a greenhouse study (Chapter 2), we observed that the soil where most of these high legume quadrats were located (site 3) developed drying cracks. Soils at all our study sites have shrink-swell potential (Palmer et al., 1992) but possibly more so at site 3 because of more clay exposed at the soil surface. These soils have less stable soil aggregates and steeper slopes (average of 27%), possibly indicating erosion of topsoil layers. Furthermore, composite core samples to 30 cm taken by Piper (1995) were 22, 23, 34, and 25 % clay in sites 1, 2, 3, and 4, respectively. All of these factors could have contributed to the higher infiltration rates at site 3 measured during the dry part of the summer.

Soil core profile

Since all our research sites are on prairie soils that have never been plowed, we would not expect their field bulk densities to vary greatly. All bulk density values were quite low, reflecting the absence of compactive plowing and traffic. The C:N ratios of these soils are typical for Argiustolls in this climatic region, although the C:N ratio of soils in high legume areas was closer to those found in cultivated Argiustolls (Brady, 1999). The average soil water content among sites in the field (max. 0.10 g water g^{-1} soil)

was less than half field capacity (65% saturation). All sites had experienced below average rainfall up until time of soil sampling (see Appendix D).

For all three legume cover categories, the Ca^{2+} was concentrated largely in the lower depths, generally increasing with increasing soil depth, as we would expect with accumulations of calcium carbonates in these semi-humid grassland soils. The higher electrical conductivity (EC) of the high legume cover agrees with the high available Ca and Mg in the uppermost soil layer. Higher levels of H (and lower C:H ratios) in the high legume cover quadrats may indicate more simple compounds in the organic matter with more carboxyl groups whereas in the no and low legume quadrats, low levels of H (and higher C:H ratios) may indicate more humic substances in the organic matter with more complex compounds of double- and triple-bonded C in phenolic groups. This agrees with the higher percent active C to total C of the high legume areas suggesting more easily decomposable organic matter in these soils versus the lower active C to total C of the low and no legume areas with, suggesting less decomposable organic matter.

Incubation data

The greater potentially mineralizable C in surface soils than in subsurface soils is what we would expect since the total C in the 0-7.5 cm depth of non-incubated soils was 9.6 g kg^{-1} higher than in the 7.5-15 cm depth for all sites (Table 3.10.). It is interesting to note that our results show more total mineralized N in soils from 7.5-15 cm than in soils from 0-7.5 cm. This higher mineralization in the lower (7.5-15 cm) depth is contrary to our findings of less potentially mineralizable C at this same depth (Figure 3.5.), unless the lower active C lead to less re-immobilization of mineralized N.

It has generally been accepted that low soil N favors legume growth. The effect of different levels of soil N on legume growth has been examined in numerous studies (Walker et al., 1956, Harris, 1987 and Piper, 1995). Our field data shows total soil N was lower in soils of high legume cover for the 7.5-15 cm and 15-30 cm depths than in soils of low and no legume cover (Table 3.6.). Piper (1995) also found generally lower total N in site 3, where most of the high legume areas are located, but found no differences between NH_4 and NO_3 (1 M KCl-extracted) from air-dried composited soil samples taken at 0-30 cm in June, August and December from sites 1-4 (Piper, 1995). So only the percent of mineralized N to the total N was greater in the soils of high legume cover. Our incubation data showed that the total potentially mineralizable N in soils from all sites and legume cover categories were similar, but the potentially mineralizable NH_4 in the 7.5-15 cm depth was more abundant in incubated soils from sites 1 and 2 than in sites 3 and 4. This may indicate more potentially mineralized N held in the ammonium form of N in sites 1 and 2, and a greater presence of nitrifying bacteria in the soils from site 3 and 4 to convert the ammonium into nitrate. This suggests more potential for nitrification in the low N soils of high legume cover. Since legumes predominated on this steepest and most eroded site, they may have contributed high N residues that resulted in high levels of mineralizable N despite the relatively low total soil organic matter.

Our findings of more mineralized N held in ammonium form in sites 1 and 2, suggests low nitrification occurring at these sites. Although all four of our sites had similar grass cover, sites 1 and 2 had a greater proportion of grasses to legumes. Wedin and Tilman (1990) also found low rates of nitrification in soils with *Andropogon gerardii*, one of the dominant warm-season grasses at our sites. They tested for soil N

mineralization and above and belowground litter quality (C and N) in monocultures of five perennial grasses grown in similar soils. They found that for *Andropogon* peak mineralization rates did not correspond with an increase in NO_3 but were, in fact, low all season.

In the four prairie sites, we had expected that the soils with high legume cover areas (mostly in site 3) would be low in mineralizable N and low in organic matter. Our results show that the soils with high legume cover were no different in mineralizable N than the other legume cover areas. Although they were low in soil organic matter, they were also low in potentially mineralizable NH_4, suggesting high nitrification rate.

Associations between soil series and soil properties

The two soil variables important in the discriminant factor which distinguished high legume cover from low and no legume cover were active C as % of total C and % organic matter. It is interesting to note that in a similar discriminant multivariate analysis on the same eight variables grouped by soil series, these same two variables were also important in the discriminant factor that explained the variation between Clime (site 3), and the other two series (sites 1, 2, and 4) (Table 3.14 and Figure 3.7.). In addition, soil variables in sites 1 and 2, both from the Longford series, were closely related, as we would expect. In fact, the very close grouping of all the Longford series samples from sites 1 and 2 which were about 120 m apart spatially, is quite remarkable considering that none of the soil properties in the discrimination analysis are directly used in classifying the soil series.

Table 3.14. Soil variables and their standardized coefficients.

Soil variables	Factor 1	Factor 2
Bulk density	0.032	0.965
C/N ratio	-0.007	-0.119
Organic matter, %	-0.408	1.284
Active C/Total C, %	-1.140	0.406
pH, in H_2O	-0.060	-0.941
Electric conductivity	-0.329	1.064
Initial min. NO_3	0.085	0.154
Cum CO_2-C (2day)	0.128	0.518

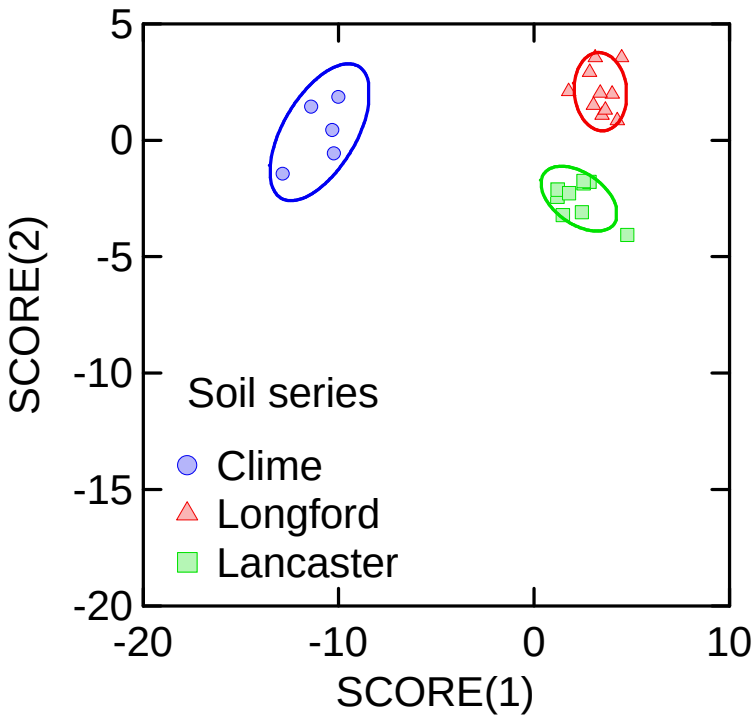

Figure 3.7. Canonical scores plot for three soil series represented at the four prairie sites: site 3 was Clime, sites 1 and 2 were Longford, and site 4 was Lancaster.

Conclusions

We found high legume cover on soils of steeper slopes, higher infiltration rates, and lower aggregate stability than soils with low and no legume cover. For surface soil properties, we found high legume cover on soils of higher Ca, soil water content, total H, active C as % of total C, EC and pH, and % coarse fragments than soils with low and no legume cover. Low legume cover was on soils of higher total C, C:N ratio, and % organic matter than high legume cover. Low and no legume cover were no different for these variables. Mineralizable C and N for incubated soils from all legume cover categories were no different.

In general, for soil variables among these four prairie sites, active C as a % of total C and % organic matter were the most closely associated with % legume cover and best explained the variation between legume cover categories.

Further research is needed among a greater range of plant communities and soil types. Differences in topography should be considered when selecting sites since this factor affects surface soil properties such as active C and soil depth, which in turn effect many other soil properties.

Chapter 4: Overall Conclusions

Greenhouse comparison to field results

Comparisons between the greenhouse study (chapter 2) and the field study (chapter 3) are restricted to general conclusions because of the limited number of species (due to seed availability and viability) used in the greenhouse study. Both legume species (*Desmanthus* and *Baptisia*) in the greenhouse study were found in the field study, but not at all sites where legumes were present. Although I did not collect species data for grasses and composites, we know from Piper's seven-year study that two of the grass species, *Andropogon* and *Schizachyrium*, were dominant grasses at these sites and *Liatris* was present at site 4 (Piper, 1995). *Helianthus* was not found at our sites, but it is native to the area.

Nevertheless, some general comparisons can be made between the greenhouse and the field study. The response variables measured in the greenhouse study that can best be compared to percent plant cover in the field are those concerning aboveground growth: shoot DM and plant height. In our two-way ANOVA for soil and plant family effects, shoot DM showed significant soil effect, although the three plant families did not separate out significantly. For plant height, however, all three plant families responded similarly to soil differences, resulting in both a soil effect and plant family effect. In the field, legume and composite cover differed in the four sites but not similarly. Although grasses did not differ significantly during the one sampling period, the relative differences in average aboveground plant biomass for grasses measured by Piper (1995) (Table 3.4.) across these sites most closely resemble the overall trend in my greenhouse study - highest average shoot DM and plant height in soil 2 and lowest in soil 3 for all

species (Tables 2.2, 2.5.). From this comparison I conclude that the differences in soil from the four sites affected the growth of grasses, even when the factors of slope, aspect, and soil thickness were removed. For legumes and composites, the differences in soil from the four sites were not likely the only factors affecting their growth. In the competition for light and soil nutrients, grasses are more limited by soil nutrients, due to their larger root surface area whereas legumes are more limited by sunlight and can be easily shaded out by grasses. However, I could not observe the effects of plant competition in the greenhouse since the plant species were not grown together in the same pots.

It was noted that the relative differences in % organic matter among the four soils used in the greenhouse was different from those among the four sites, particularly between sites 1 and 2. Organic matter content in sites 1 and 2 were not different in the surface soil layers (Table 3.9), but the bulk soil from site 2 was higher than that from site 1 (Table 2.1.). The bulk soil taken from site 2 may not have been an adequate representation of the soil in that site and therefore may have been from a particularly high organic matter area within site 2.

Recommendations for future research

The majority of time and energy for this research was spent on collecting and analyzing the soil properties. Much less time was spent on assessing the plant communities. Vegetation was assessed for each quadrat by only one observer. Perhaps, I would have come to similar results with more than one observer, but it would have been interesting to compare results. Also, more careful attention to grass species and

composite species would have added to better understanding of the plant communities at the time of soil sampling.

My vegetation measurements for percent cover did not include estimating the percent total groundcover to account for bare soil. Since the percent cover was estimated using a range of percent or cover class, simple addition of the percent cover of each plant family does not necessarily give percent total groundcover.

Vegetation and soil sampling was only taken once throughout the growing season. This provided a "snapshot" view of plant cover and soil properties at one time. However, additional sampling during the early spring and fall may have given a broader view of the seasonal changes occurring in the plant community, such as between cool-season grasses and warm-season grasses, and soil conditions, such as nutrient cycle fluxes.

The extent of soil sampling for this research project would have been best done earlier in the season when the soil moisture was greater. I would have probably had better representation of legume cover in each site, or at least the same number of quadrats in each site for soil analysis.

It is difficult to know how much of an understanding we can gain from removing the many parts of an ecosystem and analyzing them thoroughly. Our intellectual attempts at putting the pieces back together based on research of the parts leaves many questions, one of which is will the pieces fit together the same as when they were in their original place and time? If we want to produce food using the prairie as model, must we understand every part of the model before attempting to use it? One thing is certain, however. If we allow ourselves to see the amazing complexity of the prairie in the midst of turning the soil in our hands, and counting each species, whether we will ever fully

understand each part or not, at least we come away with an appreciation of how well it works when it is a whole.

Appendices

A. Germination treatment of native prairie seeds used in greenhouse study.

Plant type	Scientific name	Common name	Seeds sown	Seeds germinated	Scarified	Cold 3°C 15days	Warm 20-24°C
C_3 grass	*Agropyron* sp.	Wheatgrass	300	48			x
C_4 grass	*Andropogon gerardii*	Big bluestem	200	132		x	
C_3 grass	*Elymus* sp.†	Wildrye	1000	73‡			
C_4 grass	*Schizachyrium scoparius*	Little bluestem	400	66		x	
Legumes	*Amorpha canescens*†	Leadplant	750	6			
	Baptisia australis	Blue wildindigo	200	70	x	x	
	Dalea purpurea†	Purple prairie clover	1000	21‡			
	Desmanthus illinoensis	Illinois bundleflower	80	77	x		
Composites	*Helianthus maximiliani*	Sunflower	200	89		x	
	Liatris punctata	Gayfeather	400	92		x	

†not used in greenhouse experiment due to poor germination
‡presence of mold on some or all seeds.

B. ANOVA effects and degrees of freedom (df) for seven and five plant species (sp) in four composite soils (in four blocks) in greenhouse study.

Source of variation	df	
	7 sp	5 sp
Block	3	3
Soil	3	3
Species	6	4
Soil x species interaction	18	12
Error	81	57
Corrected Total	111	79
Block	3	3
Soil	3	3
Plant family	2	2
Soil x plant family interaction	6	6
Error	97	65
Corrected Total	111	79

C. Maximum, average, and minimum monthly temperatures (Celsius) for the summer months of 2000, 2001 and the 1961-1990 average for Saline County, Kansas.

		2000	2001	30-yr avg
June	Max	30.5	30.5	30.6
	Mean	23.5	23.6	24.0
	Min	16.9	16.8	17.4
July	Max	33.7	36.8	33.7
	Mean	27.2	30.1	27.1
	Min	20.8	23.4	20.5
August	Max	37.7	34.4	33.0
	Mean	30.1	27.4	26.2
	Min	22.5	20.5	19.5

D. Daily precipitation during field study for 2000, 2001, and 1961-1990 average. Data recorded at The Land Institute.

		2000		2001	30-yr avg
Month	Day	cm	Day	cm	cm
June total		9.03		8.66	10.85
July	4	1.00	5	0.69	
	10	0.76	10	Trace	
	17	0.84	23	0.18	
	18	0.94	24	0.43	
	19	0.25	26	1.14	
	20	0.12	27	1.85	
	21	0.64	28	0.46	
	22	2.79			
	28	2.03			
July total		9.37		4.75	8.56
August	14	Trace	10	0.10	
			15	0.33	
			17†	0.58	
			22	0.28‡	
			23	2.44‡	
			24	2.31‡	
			30	Trace‡	
August total		Trace		6.58	3.31
Sept. total		1.22		9.86	3.09
June-Sept total		19.62		29.85	25.81
Annual total		93.57		66.81	75.74

†last day of field sampling
‡data from Salina, KS (NOAA, 2003)

E. Preliminary field soil sampling procedures (summer 2000)

Ten soil core samples (2 cm diameter) were collected at three depth increments (0-20 cm, 20-40 cm, 40-50 cm for sites 1 and 2; 0-10 cm, 10-20 cm, 20-30 cm for sites 3 and 4). For each site and depth, ten cores were composited into a single soil sample for analysis. These 12 composite samples (3 depths x 4 sites) were air-dried, ground and analyzed for soil textural class, pH (1:2 in water), available P, K^{+}, Ca^{2+}, and Mg^{2+}(Mehlich-I extractant), and percent organic matter (loss on ignition) according to the standard methods of the University of Maryland Soil Testing Laboratory (NECCST, 1995).

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