EFFECTS OF MILITARY TRAINING ON SOIL, VEGETATION, AND THE SMALL MAMMAL COMMUNITY IN A MIXED PRAIRIE

By

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PREFACE

This thesis contains two chapters that describe plant and small mammal ecology as they relate the interaction of soil with military disturbance at Fort Sill, Oklahoma. Each chapter is intended to be submitted to an appropriate peer reviewed journal and is formatted as per the directions to authors for those journals.

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NOMENCLATURE

Plant nomenclature follows the United States Department of Agriculture, Natural Resource Conservation Service. 2004. The PLANTS Database, Version 3.5 (http://plants.usda.gov).

Additional abbreviations:

DCA	Detrended Correspondence Analysis
IDH	Intermediate Disturbance Hypothesis

Small mammal taxonomy

C. hispidus	*Chaetodipus hispidus*
P. leucopus	*Peromyscus leucopus*
P. maniculatus	*Peromyscus maniculatus*
R. fulvescens	*Reithrodontomys fulvescens*
R. montanus	*Reithrodontomys montanus*
S. hispidus	*Sigmodon hispidus*

CHAPTER 1

Effects of Short- and Long-term Disturbance on Vegetation and Soils Resulting from Military Maneuvers in Mixed Prairie

Abstract

Grasslands continue to decrease in area, so loss of grassland species from activities like off-road vehicle use increases the need for models that predict effects of anthropogenic disturbance. I assessed the applicability of the Intermediate Disturbance Hypothesis (IDH) to plant species richness on two soils (Foard and Lawton) in mixed prairie disturbed by military training, using track cover and soil organic carbon as measurements of short-term and long-term disturbance, respectively. Change in species composition across the disturbance gradient also was evaluated temporally. Vegetation and soils were measured in 1-m^2 quadrats at 10 locations varying in disturbance intensities. Data were scaled to three spatial scales (60 m^2, 10 m^2, and 1 m^2) for analysis. Consistent with the IDH, plant species richness peaked at intermediate levels of soil organic carbon at the 10-m^2 and 1-m^2 spatial scales and at intermediate levels of track cover at all three spatial scales on the Foard soil. Species composition changed at locations on the Foard soil but not at locations on the Lawton soil measured by soil organic carbon and track cover. Disturbance increased total plant species richness on the Foard soil. Results suggest that

disturbance up to intermediate levels can be used to maintain biodiversity by enriching the plant species pool.

Introduction

Anthropogenic disturbances such as off-road vehicles use (Webb 1983), land development (Maestas and others 2003), and recreation (Miller and Hobbs 2000, Danley and others 2004) are increasing in scale and frequency, yet response of grasslands to human activities is not as well understood as response of grasslands to historical disturbances (i.e., fire, grazing, burrowing, weather events; Pickett and White 1985, Milchunas and Lauenroth 1993, Engle and Bidwell 2001). Whereas fire, grazing, and weather-driven events historically maintained grasslands (Axelrod 1985, Knapp and others 1999, Collins 2000), human activities may rapidly degrade grasslands. Alternatively, human activities may functionally replace natural disturbances no longer present on the land. Understanding the role of anthropogenic disturbance is increasingly important because of continued rapid loss of grasslands globally (White and others 2000). I define disturbance as an event that results in change in ecosystem or community dynamics, resources, or physical environment (*sensu* White and Pickett 1985).

The Intermediate Disturbance Hypothesis (IDH) was proposed as a conceptual model of the relationship of disturbance intensity and frequency to species richness (Connell 1978). The unimodal-shaped model predicts that the greatest number of species occur at intermediate levels of disturbance while low and high disturbance intensity are predicted to produce lower and similar numbers of species. Several studies have substantiated the IDH using historical disturbances such as fire and grazing (Sousa 1979, Collins and Barber 1985, Collins et al 1995, Vujnovic and others 2002), but the IDH has not been tested extensively under anthropogenic disturbance (i.e., off-road vehicle use). In a meta-analysis, Mackey and Currie (2001) found that the IDH model does not accurately predict richness in anthropogenically disturbed systems; however, IDH model may not be applicable across ecosystems. Milchunas and others (1988) proposed that the IDH model applied to subhumid grasslands with a long evolutionary history of disturbance by grazing; other models are more appropriate for disturbed semiarid grasslands. Collins and Barbar (1985), for example, concluded that fire-return-interval predicted diversity in the tallgrass prairie better than disturbance intensity alone.

Spatial scale also may influence the applicability of the IDH, but no studies have addressed the IDH experimentally across spatial scales (Huston 1994 addresses the concept theoretically). Several studies describe spatial relationships based on alpha and beta diversity (Mackey and Currie 2001, Vujnovic and others 2002, Roxburgh and others 2004) rather than scale relative to area. Examining anthropogenic disturbance at multiple scales may yield further insight into community dynamics and enhance predictive power of models (Turner 1989, Wiens 1989, Pickett and Cadenasso 1995, Fuhlendorf and Smeins 1997). Furthermore, by examining landscapes at multiple scales, the role of variability in edaphic properties relative to species richness can be clarified (Burke and others 1998, Eviner and Chapin 2003).

Grassland plant communities on different soils may vary in their resistance to disturbance. For example, plants growing in saline soils face greater osmotic challenges and may have lower resistance to additional stress (Havlin and others 1999). Soil texture is often variable within a soil series and can play an important role in determining moisture availability and nutrient dynamics (Rowell 1994, Vepraskas 1994). Although soil descriptions are frequently reported in studies, the relationship between soil heterogeneity and diversity is not well recognized in light of anthropologic disturbance.

Species composition and richness are often measured to assess community dynamics following grassland disturbances (Dyksterhaus 1949, Collins and others 1995, Stohlgren and others 2000). An assumption of the IDH model is that under low disturbance intensity late seral communities maintain stability through competition and as disturbance intensity increases early seral plants adapted to quickly colonize newly formed gaps replace late seral species (Denslow 1980, Hobbs and Huenneke 1992). The storage effect and relative nonlinearity are two mechanisms hypothesized to drive community dynamics (Roxburgh and others 2004).

Those characteristics that Milchunas and others (1988) used to formulate diversity models—site productivity, history of disturbance—are likely predictive of change in plant species composition among locations. Arid environments, for example, are less resistant to disturbance, meaning that species composition is more likely to change under further stress than in humid environments (Webb and Wilshire 1983). Plants in arid lands have evolved to maximize use of the limited available resources, community change occurs when the resource pool is altered beyond the capacity of these plants to acquire resources. Although this model likely holds for historical disturbances, models that predict species composition in response to anthropological disturbances have not been developed.

Temporal scale may be as important as spatial scale in interpreting disturbance effects (Delcourt and Delcourt 1988). I propose that certain anthropogenic disturbances (e.g., cultivation and vehicular traffic) differ from natural disturbance in that they may be more intense and over a period of years leading to depletion of soil carbon (Anderson and Coleman 1985, Tiessen and others 1982), an important trait of soil quality (Eviner and Chapin 2004), and therefore greatly alters plant species composition and richness. Models of soil carbon loss are time sensitive and have been well tested in agronomic systems. Models predict 30-50% loss of total soil carbon within 10–40 years of cultivation (Burke and others 1995, Anderson and Coleman 1985); however, organic carbon regenerates very slowly post-cultivation (Potter and others 1999, Schlessinger 1986, Knops and Tilman 2000, Baer and others 2002). Therefore, I hypothesize that the long-term, cumulative effect of disturbance can be inferred by comparing organic soil carbon across a disturbance gradient. For example, soil carbon should be reduced on sites with a long history of severe disturbance. Conversely, tracks or ruts from vehicle passage may reflect only recent disturbance events. Productive sites with long histories of disturbance from grazing may absorb a certain level of current disturbance, obscuring the influence of the longer-term effects of repeated, severe disturbance.

The overall objective of my research was to investigate effects of a gradient of disturbance from military maneuvers in a grassland with a long evolutionary history of disturbance. Competition and succession in focal communities, also necessary processes for a test the IDH, are known to operate in southern mixed grasslands (Collins and Barbar 1985, Engle and others 2000, Fuhlendorf and others 2002, Shea and others 2004, Tunnel and others 2004). I assessed the applicability of the Intermediate Disturbance Hypothesis (IDH) to plant species richness on two soil series in mixed prairie disturbed by military training. I predicted that plant species composition, in contrast, would shift from late seral to early seral species as a function of increasing disturbance. I evaluated track cover and soil organic carbon as potential measurements of short-term and long-term disturbance, respectively, on two soil series and at three spatial scales.

Study Area

The study was conducted at Fort Sill, which is located in Comanche County (34° 38' N, 98° 30' W) in southwestern Oklahoma (Mobley and Brinlee 1967). The region has a subhumid climate with an average annual rainfall of 782 mm. Temperatures range from –16 to 46 °C (mean = 16) (Oklahoma Climatological Survey 2003). Fort Sill, established in 1869 to mediate Native American conflicts, has grown to encompass 38,292 ha (Harris 1991). Although bison (*Bos bison*) and domestic cattle (*Bos taurus*) formally occupied parts of Fort Sill, recent grazing was not a factor in this study. The historical presence of bison, fire, and the military indicates a long history of disturbance (Hagan 1976).

I tested the influence of edaphic features in an anthropogenically disturbed grassland on two soil series, Foard and Lawton, to represent hardland and loamy prairie sites, respectively. Hardland and loamy prairie ecological sites encompass about 18% and 27% of Comanche County, respectively (Natural Resource Conservation Service [NRCS], 2004a). Study locations with Foard soils were characterized by short- and mid-grasses such as blue grama (*Bouteloua gracilis)*, buffalo grass (*Buchloe dactyloides)*, vine-mesquite (*Panicum obtusm)*, sideoats grama (*Bouteloua curtipendula)*, and little bluestem (*Schizachyrium scoparium*). Study locations with Lawton soils were characterized by mid-level and tall grasses such as big bluestem (*Andropogon gerardii*), indian grass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), and switchgrass (*Panicum virgatum*) (Mobley and Brinlee 1967).

Technical series descriptions (NRCS 2001) indicated similarities in the A-horizons of Foard (fine, smectitic, thermic Vertic Natrustoll) and Lawton (fine, mixed, superactive, thermic Typic Argiustoll) soils, but the B-horizons differed. Foard soils typically contain clay pans and a natric component (i.e., increased sodium levels), which influence nutrient cycling including carbon storage capacity, physiological processes of plants, and subsequently species composition (Havlin and others 1999). Salinity can range from 2.0 to 4.0 dS/m at a depth of 23–56 cm. Increased Na levels also accompany more basic pH levels (6.1–8.4, Foard vs. 6.1–7.3, Lawton Loam). Clay content in Foard soils increases with depth resulting in less permeability through the soil column than Lawton soil (Table 1).

Disturbance on the study locations included military vehicle use (tracked and wheeled of various weights), encampments, and land navigation exercises (foot training). Study locations had not been burned for a minimum of four years before sampling. Locations were chosen based on history of recent disturbance to include a range of disturbance intensities as observed by permanent personnel at Fort Sill (J. Kretzer and J. MacIntosh 2003 *personnel communication*). Two locations with Foard soil that had not been used for training in the last 10 years represented an undisturbed condition, and one location had been subjected to soil movement by mechanized earth movers. The range of recent disturbance to locations with Foard soils appeared greater than to locations with Lawton soils.

Methods

I used organic soil carbon and track cover (percentage of sampling unit disturbed by a vehicle) to indicated disturbance intensity. I assumed that organic soil carbon indicates disturbance history over long time periods and track cover effectively represented recent disturbance by military training. Relationships between disturbance and plant communities were assessed by sampling plants in 60 1-m x 1-m quadrats for each of 10 locations (5 locations in each soil Foard and Lawton; 600 total quadrats; Figure 1). Sampling was restricted to >15 m from a roadway and ≥ 50 m between locations.

Sampling for species richness and composition was conducted in spring (12 May–3 June 2003) and autumn (5–22 September 2003). Canopy cover of plant species and cover of vehicle tracks were estimated with a modified cover class system (>0–1%, >1–5%, >5–25%, >25–50%, >50–75%, >75–95%, and >95–100%; Daubenmire 1959); midpoint values for each class were used in analyses. I combined spring and autumn datasets by using the maximum cover value for each species and tracks recorded in either season. The greatest amount of disturbance occurred before spring sampling, so estimates of spring track cover dominated the combined dataset. All analyses discussed here refer to combined data. Vegetation taxonomy follows the National Plants Database (NRCS 2004b), and complete species list is in the Appendix.

I collected soil samples in July 2003 to assess nutrient status and texture. Soil texture can affect water-holding capacity and cation-exchange capacity (Havlin and others 1999). Erosion, compaction, and loss of vegetation cover resulting from disturbance also can affect nutrient availability (Lipiec and Håkansson 2000, Burke and others 1995, Vepraskas 1994, Thurow 1991). Five standard soil cores (1.5 cm x 15 cm) taken in each 1-m^2 quadrat were composited into one sample. Samples were dried overnight at 60° C and ground to pass through a 2-mm sieve. Percent organic soil carbon for each sample was determined using a LECO Truspec dry combustion analyzer (Nelson and Sommers 1996). Cations were analyzed using a Spectro Ciros ICP (Sims 1996). Texture analysis followed standard hydrometer procedures (Gee and Bauder

1996), and salinity values are reported in saturated paste form (United States Department of Agriculture [USDA] 1954).

Data Analysis

Data analysis at multiple scales can often improve interpretations of ecosystem dynamics (Huston 1994, Turner 1989). Therefore, I pooled quadrat-level data to create three spatial scales for analysis (60 m^2, 10 m^2, and 1 m^2). The larger scale (60 m^2) summarized data from all 60 quadrats (1 location) into one sample value. Alternatively, I analyzed data at a 10-m^2 scale in which each block of 10 quadrats represented one sample, and six samples describe one location. Finally, at the 1-m^2 scale, 60 quadrats represented a location (Figure 1).

The relationship between plant species richness and disturbance (i.e., track cover and soil organic carbon) was tested with polynomial regression (PROC GLM; SAS Institute, 2001). I first determined if the regression model differed between soil series by using a dummy variable for soils, and in the absence of a difference, data from the two soils were combined in the regression. The IDH model predicts that the relationship of species richness and disturbance is a polynomial function, so I tested quadratic functions and linear functions as alternative hypotheses. I assumed soil carbon decreased with long-term disturbance intensity whereas track cover increased with recent disturbance. Clay content can influence soil organic carbon (Nichols 1984), but clay did not affect the relationship between disturbance and species richness.

I used a two-step process to assess species composition along a disturbance gradient at three spatial scales. First, plant species composition data were subjected to detrended correspondence analysis (DCA; Hill and Gauch 1980, Peet and others 1988, ter Braak 1987). DCA is an indirect gradient analysis that simultaneously calculates relationships between species and samples (ter Braak and Šmilauer 2002). Species cover data were square-root transformed for DCA to reduce heteroscedasticity among samples (Steel and others 1997). Species and sample plots were used to interpret gradients (ter Braak and Verdonschot 1995, Hill and Gauch 1980). Second, DCA axis-1 sample scores were regressed against disturbance soil organic carbon and track cover in the same manner of that for species richness carbon and track cover. Statistical significance for all procedures is alpha = 0.05.

Results

Consistent with the IDH, plant species richness peaked at intermediate levels of soil organic carbon at the 10-m^2 and 1-m^2 spatial scales and at intermediate levels of track cover at all three spatial scales on the Foard soil (Figure 2). The amplitude in species richness was greatest at the10-m^2 scale on Foard soil. Although unimodal at the 10-m^2 and 1-m^2 spatial scales for soil organic carbon on the Lawton soil, the species richness amplitude was less than that of the Foard soil. The range of track cover and species richness was less on the Lawton soil than the Foard soil. Peak species richness occurred at about 50% loss of soil carbon in both soil series. The undisturbed Foard locations had carbon levels similar to the more heavily disturbed Lawton locations (i.e., between 1.0% and 1.5% carbon at the10-m^2 and 1-m^2 scales). At all spatial scales, species richness peaked at about 1% soil carbon in Foard soils and at about 2.3% in Lawton soils and when track cover was about 40% on Foard soils.

Plant species composition varied directionally on the Foard soil, but we could not detect a directional change in species composition on the Lawton soil (Figure 3). We interpreted the DCA axis-1 as a disturbance gradient, which is represented in Figure 3a in which sample scores from the Foard soil are ordered from left to right from least disturbed to most disturbed. Sample scores differed among soils disturbance intensities at three spatial scales (Figure 3). Compositions of the least disturbed Foard samples were similar to those of most of the Lawton samples (i.e., overlapping envelopes).

The disturbance gradient represented by axis-1 sample scores confirm my interpretation of the environmental gradient in the DCA (Figure 4). The change in plant species composition with decreasing carbon was steep and directional on the Foard soil at all three spatial scales. In contrast, plant species composition changed little with level of soil organic carbon on the Lawton soil even though soil organic carbon varied more on the Lawton soil than on the Foard soil. Plant species composition changed with track cover on the Foard soil but changed little on the Lawton soil.

Locations with less soil carbon and more track cover were also dominated by early seral plant species in contrast to locations with greater soil carbon and less track cover which were dominated by late seral plant species (Chapter 2, Table 2). Species often associated with disturbed sites also were associated with sampling locations known to be the most heavily disturbed. Late seral species were associated with samples on the Lawton soil and undisturbed Foard soil. Species strongly associated with heavy disturbance in samples from the Foard soil were *Bouteloua hirsuta, Hordeum pusillum,* and *Thelesperma filifolium* at the 60-m^2 scale, *Bromus japonicus, T. filifolium,* and *Juncus sp.* at the 10-m^2 scale, and *Amphiachyris dracunculoides, Plantago wrightiana, and T. filifolium* and at the 1-m^2 scale. Samples on the Lawton soil and the undisturbed Foard soil were associated with *Dichanthelium oligantha, Sporobolus compositus, Helianthus maximiliani,* and *Symphyotrichum ericoides* at the 60-m^2 scale, *Dichanthelium oligantha, Schizachryium scoparium, Sporobolus compositus*, and *Symphyotrichum ericoides* at the 10-m^2 scale, and *Dichanthelium oligantha, Sorgastrum nutans, Sporobolus compositus*, and *Symphyotrichum ericoides* at the 1-m^2 scale.

Discussion

Anthropogenic disturbances such as military training, off-road vehicle use, and other recreational activities have the capacity to alter species richness and composition. I used soil organic carbon, a measurement of long-term disturbance intensity, and track cover, a measurement of short-term disturbance intensity as predictors of plant species richness in a subhumid mixed grassland disturbed by military maneuvers. This is the first study to use organic soil carbon as an index of disturbance to test the IDH model. Using soil carbon as an index of disturbance intensity to test the IDH matches the appropriate temporal element of disturbance to perennial plants, which dominate mixed prairie. Studies often decouple the life history characteristics of plant species from the temporal aspects of the disturbance process (Shea and others 2004). Other than my study, the IDH has yet to be tested in response to military maneuvers, and vegetation response to military maneuvers has been studied experimentally only with regard to short-term aspects of disturbance. The greatest length of studies of disturbance on military lands in the Great Plains that I found was about 12 years (Milchunas and others 2000).

My study contributes to an improved understanding of the role of disturbance in Great Plains grasslands by extending the IDH to predict changes in plant species richness with anthropogenic disturbance as opposed to the historical disturbance processes of fire and grazing. The IDH describes a unimodal model that predicts that species richness will be maximized at intermediate levels of disturbance and that increasing disturbance intensity will cause a change in species composition from late to early successional species (Denslow 1988, Hobbs and Huenneke 1992). The model, developed in coral reef systems (Connell 1978), has been tested in grasslands, most often with grazing and fire intensity as disturbance processes (e.g., Collins and Barbar 1985, Martinsen and others 1990, Vujnovic and others 2002). The IDH has been supported in other studies in Great Plains grasslands subject to long evolutionary histories of grazing at a range of precipitation levels (Collins and Barbar 1985, Collins and others 1995, Vujnovic and others 2002, Wilson and Tilman 2002). Thus, the IDH model appears be applicable to ecosystems with long evolutionary histories of disturbance (Milchunas and others 1988, Huston 1994). My results support the IDH model as a means for predicting changes in species richness and composition as a result of military disturbance in grasslands.

The debate over the applicability of the IDH is far from conclusive, and many researchers have either rejected the IDH or restricted its application. In a grassland in New South Wales, Australia, with a relatively short evolutionary history of grazing, the IDH was not supported (McIntyre and Lavorel 1994) because soil disturbance did not affect species richness. Following a meta-analysis across ecosystems and types of disturbance, Mackey and Currie (2001) suggested that the IDH was unlikely to explain richness in systems with anthropogenic disturbance. However, my results suggest that the IDH is appropriate for grasslands disturbed by military maneuvers because these grasslands evolved with periodic soil, grazing, and fire disturbances (Axelrod 1985) that may be similar in process to military disturbance. Use of military vehicles, especially in wet conditions, can move soil and remove biomass (Thurow and others 1993, Grantham and others 2001) similar to the activities of burrowing, wallowing, and grazing by indigenous grassland animals (Collins and Barbar 1985, Knapp and others 1999).

An important criticism is that the intermediate disturbance in most studies is arbitrary and may not reflect operational intermediacy for an ecosystem and the plant community (Huston 1994). My results also contribute to the debate about the IDH hypothesis in that soil carbon sheds light on the theoretical framework explaining the coexistence of species under the IDH model (Shea and others 2004). I avoided the circularity pointed out by Huston (1994) by applying soil organic carbon as an independent variable indicating long-term disturbance. Soil carbon, which responds to disturbance, is independent of the disturbance itself and is continuous in nature. This contrasts with treatment variables such as fire frequency which are derived from the disturbance (Collins and Barbar 1985).

My study also adds insight into the IDH discussion by including spatial scale as an element in the study design. This is especially important because spatial scale may influence the applicability of the IDH, and no grassland studies to this point have addressed the IDH experimentally across spatial scales. When he addressed the concept theoretically, Huston (1999) recognized that spatial scale was an important facet of empirical research because of the importance of spatial variation. A few studies describe spatial relationships in the context of alpha and beta diversity (Mackey and Currie 2001, Vujnovic and others 2002, Roxburgh and others 2004) rather than spatial scale.

Examining anthropogenic disturbance at multiple scales also yields insight into community dynamics and enhances predictive power of ecosystem response to disturbance (Turner 1989, Wiens 1989, Pickett and Cadenasso 1995, Fuhlendorf and Smeins 1997). Furthermore, by examining landscapes at multiple scales, the role of variability in climate and edaphic properties relative to species richness is clarified (Fuhlendorf and Smeins 1997, Burke and others 1998, Eviner and Chapin 2003). For example, restricting analysis to the 60-m^2 scale in my study may have led me to conclude there was no difference between species richness on either soil over either the short-term or long-term (Figure 2).

Although military maneuvers may substitute functionally for historical disturbance processes (e.g., tunneling by prairie dogs, *Cynomys* spp.), it must be recognized that soil carbon and native perennials recover slowly. For example, roughly 25% of soil carbon lost during cultivation can be recovered in 5 to10 years after cultivation ceases (Potter and others 1999, Baer and others 2000, Fuhlendorf and others 2002). Because richness was related unimodally to soil carbon in the mixed prairie at Fort Sill, soil carbon has potential to be a monitoring device for military disturbance of mixed prairies whereby managers could estimate the trainability of an area or the need to defer an area from use. On both soils in this study, species richness was maximized with about 50% loss of soil carbon, but the acceptable amount of loss or gain of soil carbon must be appropriate for the area because capacity for carbon storage varies with soil series, topography, climate, etc. (Burke 1998). Repeated disturbance of a location favored for maneuvers eventually causes loss of vegetation characteristics (dense, perennial grass cover) and soil characteristics (ground cover and soil aggregates) that originally attracted trainers to conduct maneuvers there. Soil carbon may serve the dual purpose for monitoring the suitability of current disturbance levels and for inventorying disturbance carrying capacity especially in situations in which records of number and frequency of users (i.e., person-training days) are not available.

Our results indicate that care must also be taken when interpreting the effect of recent disturbance within mixed prairie because soils may respond differently. For example, response of species richness to track cover on the

Lawton soil was less clear compared with that on the Foard soil, but species richness was maximized at 40% track cover in locations on the Foard soil. This suggests that standard monitoring protocols for military instillations which currently record vehicular disturbance and species richness (Diersing and others 1992) is not equally meaningful for all soils.

Plant species composition was dominated by late seral species at low disturbance and early to mid seral species at greater disturbance, although species richness was equivalent. Therefore, species richness by itself did not completely describe community dynamics. However, assessments of plant species composition in grasslands subjected to variation in disturbance intensity (as number of tank passes) have been inconsistent (Wilson 1988, Prosser and others 2000, Grantham and others 2001, Hirst 2003). In a few studies exotic and annual species replaced native perennial species (Whitecotton and others 2000, Hirst and others 2003). In my study, only one exotic grass was among the 40 most important species, but late seral species were replaced by early seral species with increasing long-term disturbance (i.e., decreasing soil carbon) on the Foard soil.

Plant species composition on Lawton soils varied little, and the range of short-term disturbance was insufficient to test the relationships between short-term disturbance and both richness and plant species composition. The Lawton soil is not sodic as is the Foard soil, which may indicate the Lawton soil has greater resistance to short-term disturbance. Few quadrats in the Lawton soil approached maximum track cover. This might have occurred because new or existing plants may have invaded gaps created by disturbance on Lawton soils over the short-term more rapidly than on Foard soils because of better water infiltration and nutrient availability (Vepraskas 1994, NRCS 2001). Trainers may also have preferred to conduct maneuvers on locations that have the Foard soil because of particular traits (e.g. vegetation height and density, nearness to wooded edges or hills). Although species richness appeared to support the IDH on this soil series, our ability to validate the model for the communities on Lawton soil is limited due to the lack of change in species composition across the disturbance gradient.

These results are meaningful because military disturbance, up to intermediate levels, appears to enrich the plant species pool, especially on the Foard soils. Thus, military disturbance may simulate historical disturbance, such as fire, grazing, and burrowing, which contributed to maintaining habitat heterogeneity and species richness in Great Plains grasslands in North America (Axelrod 1985, Knapp and others 1999, Samson and Knopf 2000, Fuhlendorf and Engle 2001). Fire suppression and extermination of bison, prairie dogs, and other animals have altered some grassland landscapes in ecologically important ways (Owensby 1973,.Knapp and others 1999, Briggs and others 2002, Aner and others 2003). Prairie dogs, for example, are a keystone species that disturb soil, a disturbance process that is not only intense but has been viewed as beneficial to grassland function by creating spatial heterogeneity and maintaining species diversity (Miller and others 1994, Weltzin and others 1997). Lesser prairie chickens (*Tympanuchus pallidicinctus*), for example, might benefit from this kind of disturbance regime because they require multiple types of habitat structure within their home range (Hagen and others 2004).

Although prairie dogs and large ungulates have been extirpated from Fort Sill and many other places in the region, military training may replace the processes of soil movement maintaining biodiversity. While some areas of Fort Sill are subject to frequent fires, which alone can homogenize grasslands (Glenn et al. 1992), other areas are frequently used for tank maneuvers, encampments, etc. These areas varying in disturbance type and frequency complement ones that are infrequently used for exercises (J. Kretzer 2003 *personnel communication*) creating a landscape mosaic of patches in various stages and intensities of disturbance.

Sodic soils are important in terms of land area and exhibit less resistance to disturbance than non-sodic soils, so applying disturbance at a rate where degradation exceeds recovery on these soils is potentially of critical conservation importance from ecological and military training perspectives. For example, large gullies created by human accelerated erosion can impede training missions as well as alter ecological processes. Species composition of communities on Foard soils in this study varied steeply with long-term disturbance, in contrast to Lawton soils that showed little change with long-term disturbance. Consideration of sodic and saline soils, like the Foard soil observed in this study, is pertinent because they cover 6.4 million ha in North America alone, much of that occurring on western rangelands. These soils contain concentrated salts that affect bulk density, water percolation, osmotic potential, and nutrient availability (Szabolcs 1979).

Rates of land degradation from military training often surpass recovery rates (Milchunas and others 2000), emphasizing the need for careful land-use monitoring and evaluation of carrying capacity models. Indeed, providing adequate training facilities for troops is of national importance; however, if carrying capacity limits are ignored, degraded training ranges may actually inhibit training missions. At the same time, maintaining multiple soil and vegetation states using military maneuvers may support biodiversity (Fuhlendorf and Engle 2001) and satisfy federal land conservation mandates (Goodman 1996). Although the IDH may be an important management tool, maintenance of a landscape mosaic with patches in a variety of stages of recovery from disturbance may be better than attempting to maintain maximum diversity across a landscape. Using the IDH model in conjunction with long- and short-term disturbance variables may assist managers to find a balance between positive ecological disturbance and degradation in mixed prairies.

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Literature Cited

Anderson, D. W., and D. C. Coleman. 1985. The dynamics of organic matter in grassland soils. *Journal of Soil and Water Conservation* 40:211–216.

Aner, G. P., S. Archer, R. F. Highes, R. J. Ansley, and C. A. Wessman. 2003. Net changes in regional woody vegetation cover and carbon storage in Texas Drylands, 1937–1999. *Global Change Biology* 9:316-335.

Axelrod, D. I. 1985. Rise of the grassland biome, Central North America. *The Botanical Review* 51:163–201.

Baer, S. G., C. W. Rice, and J. M. Blair. 2000. Assessment of soil quality in fields with short and long term enrollment in the CRP. *Journal of Soil and Water Conservation* 55:142–146.

Baer, S. G., D. J. Kitchen, J. M. Blair, and C. W. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. *Ecological Applications* 12:1688–1701.

Briggs, J. M., G. A. Hoch, and L. C. Johnson. 2002. Assessing the rate, mechanisms and consequences of conversion of tallgrass prairie to Juniperus virginiana forest. *Ecosystems* 5:578–586.

Burke, I. C., W. K. Lauenroth, and D. P. Coffin. 1995. Soil organic matter recovery in semiarid grasslands: implications for the conservation reserve program. *Ecological Applications* 5:793–801.

Burke, I. C., W. K. Lauenroth, M. A. Vinton, P. B. Hook, R. H. Kelly, H. E. Epstein, M. R. Aguiar, M. D. Robles, M. O. Aguilera, K. L. Murphy, and R. A. Gill. 1998. Plant-Soil interactions in temperate grasslands. *Biogeochemistry* 42:121–143.

Collins, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *The American Naturalist* 155:312–325.

Collins, S. L., and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. *Vegetation* 64:87–94.

Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology* 76:486–492.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.

Danley, R. F., K. L. Murphy, and E. M. Madden. 2004. Species diversity and habitat of grassland passerines during grazing of a prescribe-burned, mixed-grass prairie. *Western North American Naturalist* 64:72–77.

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. *Northwest Science* 33:43–64.

Delcourt, H. R., and P. A. Delcourt. 1988. Quaternary landscape ecology: relevant scales in space and time. *Quaternary Science Review* 2:23–44.

Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46:18–21.

Diersing, V. E., R. B. Shaw, and D. J. Tazik. 1992. US Army Land Condition-Trend Analysis (LCTA) Program. *Environmental Management* 16:405–414.

Dyksterhuis, E. J. 1949. Condition and management of rangeland based on quantitative ecology. *Journal of Range Management* 2:104–115.

Engle, D. M., M. W. Palmer, J. S. Crockett, R. L. Mitchell, and R. Stevens. 2000. Influence of late season fire on early successional vegetation of an Oklahoma prairie. *Journal of Vegetation Science* 11:135–144.

Engle, D. M., and T. G. Bidwell. 2001. The response of central North American prairies to seasonal fire. *Journal of Range Management.* 54:2–10.

Eviner, V. T., and F. S. Chapin, III. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology and Evolution Systematics* 34:455–485.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* 51:625–632.

Fuhlendorf, S. D., H. Zhang, T. R. Tunnell, D. M. Engle, and A. F. Cross. 2002. Effects of grazing on restoration of Southern mixed prairie soils. *Restoration Ecology* 10:401–407.

Fuhlendorf, S. D., and F. E. Smeins. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. *Journal of Vegetation Science* 8:819–828.

Gee, G. W., and J. W. Bauder. 1996. Particle Size Analysis. Pages 377–411 *in* D. L. Sparks et al. (eds.) Methods of Soil Analysis. Part 3, Chemical Methods. Soil Science. Society of America, Inc. Madison, WI.

Glenn, S. M., S. L. Collins, and D. J. Gibson. 1992. Disturbances in tallgrass prairie: local and regional effects on community heterogeneity. *Landscape Ecology* 7:243–251.

Goodman, S. W. 1996. Ecosystem management at the Department of Defense. *Ecological Applications* 6:706–707.

Grantham, W. P., E. F. Redente, C. F. Bagley, and M. W. Paschke. 2001. Tracked vehicle impacts to vegetation structure and soil erodibility. *Journal of Range Management.* 54:711–716.

Hagen, C. A., B. E. Jamison, K. M. Giesen, T. Z Riley. 2004. Guidelines for managing lesser prairie-chicken populations and their habitats. *Wildlife Society Bulletin* 32:69–82.

Hagan, W. T. 1976. United States-Comanche Relations: The reservation years., Yale University Press, New Haven.

Harris, K. D. 1991. LCTA data summary/progress report, Fort Sill Oklahoma. Lawton, Oklahoma, US Army Corps of Engineering Research Laboratory. Pages 5–13.

Havlin, J. L., J. D. Beaton, S. L. Tisdale, and W. L. Nelson. 1999. Soil fertility and fertilizers: an introduction to nutrient management Upper Saddle River, New Jersey, Prentice Hall.

Hill, M. O., and H. G. Gauch, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47–58.

Hirst, R. A., R. F. Pywell, R. H. Marrs, and P. D. Putwain. 2003. The resistance of a chalk grassland to disturbance. *Journal of Applied Ecology* 40:368–379.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: Implications for conservation. *Conservation biology* 6:324–337.

Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.

Huston, M. A. 1994. Biological diversity. Cambridge University Press, Great Britain.

Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86:393–401.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, and L. C. Johnson. 1999. The keystone role of bison in North American tallgrass prairie. *Bioscience* 49:39–50.

Knops, J. M. H., and D. Tillman. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology* 81:88–98.

Lipiec, J., and I. Håkansson. 2000. Influences of degree of compactness and matric water tension on some important plant growth factors. *Soil & Tillage Research* 53:87–94.

Mackey, R. L., and D. J. Currie. 2001. The diversity-disturbance relationship: Is it generally strong and peaked? *Ecology* 82:3479–3492.

Martinsen, G. D., J. H. Cushman, and T. G. Whitham. 1990. Impact of pocket gopher distrubance on plant species diversity in a shortgrass prairie community. *Oecologia* 83:132–138.

McIntyre, S., and S. Lavorel. 1994. Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. *Conservation biology* 8:521–531.

Maestas, J. D., R. L. Knight, and W. C. Gilgert. 2003. Biodiversity across a rural land use-gradient. *Conservation biology* 17:1425–1434.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63:327–366.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132:87–106.

Milchunas, D. G., K. A. Schultz, and R. B. Shaw. 2000. Plant community structure in relation to long-term disturbance by mechanized military maneuvers in a semiarid region. *Environmental Management* 25:525–539.

Miller, B. K., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. *Conservation Biology* 8:677–681.

Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. *Landscape and Urban Planning* 50:227–236.

Mobley, H. L., and R. C. Brinlee. 1967. Soil survey, Comanche County, Oklahoma. U.S. Government Printing Office, Washington D.C.

Natural Resource Conservation Service. 2001. Official soil series descriptions. Soil Survey Division, United States Department of Agriculture. http://ortho.ftw.nrcs.usda.gov/osd/.

Natural Resource Conservation Service. 2004a. National soil information system. National Soil Survey Center, United State Department of Agriculture, Lincoln, Nebraska. http://nasis.nrcs.usda.gov.

Natural Resources Conservation Service. 2004b. The PLANTS database, version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon, and organic matter. In D.L. Sparks (ed.) Methods of Soil Analysis. Part 3. Chemical Methods. SSSA:5. Soil Science Society of America, Madison, WI.

Nichols, J. D. 1984. Relation of organic carbon to soil properties and climate in the Southern Great Plains. *Journal of the Soil Science Society of America* 48:1382–1384.

Oklahoma Climatological Survey. 2003. Mesonet data. Oklahoma Climatolocal Survey, University of Oklahoma, Norman, Oklahoma. http://www.ocs.ou.edu.

Owensby, C. E., K. R. Blan, B. J. Eaton, O. G. Russ. 1973. Evaluation of eastern redcedar infestations in the northern Flint Hills. Journal of Range Management 26:256–260.

Peet, R. K., R. G. Knox, J. S. Case, and R. B. Allen. 1988. Putting things in order: the advantages of detrended correspondence analysis. *American Naturalist* 131:924–934.

Pickett, S. T. A., and M. L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* 269:331–334.

Pickett, S. T. A and P. S. White (eds.) 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Inc., Orlando.

Potter, K. N., H. A. Torbert, H. B. Johnson, and C. R. Tischler. 1999. Carbon storage after long-term grass establishment on degraded soils. *Soil Science* 164:718–725.

Prosser, C. W., K. K. Sedivec, and W. T. Barker. 2000. Tracked vehicle effects on vegetation and soil characteristics. *Journal of Range Management.* 53:666–670.

Rowell, D. L. 1994. The determination of the density of soil particles. Soil Science: Methods and applications. England, Longman Scientific & Technical, England.

Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85:359–371.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. *Bioscience* 44:418–414.

SAS Institute Inc. 2002. SAS/STAT user's guide. Version 9.01. SAS Institute Inc., Cary NC, USA.

Schlesinger, W. H. 1986. Changes in soil carbon storage and associated properties with disturbance and recovery. 194–220 in Trabalka, J. R. and D. E. Reichle. The changing carbon cycle: a global analysis. Springer-Verlag, New York.

Shea, K., S. H. Roxburgh, and E. S. J. Rauschert. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* 7:491–508.

Sims, J. T. 1996. Lime requirement. Pages 491–515. D. L. Sparks (ed.) *in* Methods of soil analysis, Part 3. Chemical Methods. Society of America, and Agronomic Society of America, Madison, WI.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225–1239.

Steel, R. G. D., J. H. Torrie, and D. A. Dickey. 1997. Principles and procedures of statistics a biometrical approach. 3rd edition. McGraw-Hill, Massachusetts.

Stohlgren, T. J., A. J. Owne, and M. Lee. 2000. Monitoring shifts in plant diversity in response to climate change: a method for landscapes. *Biodiversity and Conservation* 9:65–86.

Szabolcs, I. 1979. Review of research on salt-affected soils. Natural resources research: 15. UNESCO, Paris.

ter Braak, C. J. F. 1987. Ordination. Pages 91–173 *in* Jongman, R. H., C. J. F. ter Braak and O. F. R. van Tongeren, (eds.). Data Analysis in Community Ecology. Pudoc, Wageningen, The Netherlands.

ter Braak, C. J. F., & P. Šmilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: Software for canonical community Ordination (version 4.5). Microcomputer Power (Ithaca, NY, USA).

ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57:255–289.

Thurow, T. L. 1991. Hydrology and erosion. Pages 141–144 *in* R. K. Heitschmidt, and J. W. Stuth. Grazing management: an ecological perspective Timber Press, Portland, Oregon.

Thurow, T. L., S. D. Warren, and D. H. Carlson. 1993. Effects of tracked vehicles on characteristics of a Central Texas Rangeland. *Transactions of the American Society of Agricultural Engineers* 36:1645–1650.

Tiessen, H., J. W. B. Stewart, and J. R. Bettany. 1982. Cultivation effects on the amounts and concentration of carbon, nitrogen, and phosphorus in grassland soils. *Agronomy Journal* 74:831–835.

Tunnell, S. J., D. M. Engle, and E. E. Jorgensen. 2004. Old-field grassland successional dynamics following cessation of chronic disturbance. *Journal of Vegetation Science* 15:431–436.

Turner, M. G. 1989. Landscape ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171–197.

United States Department of Agriculture. 1954. Diagnosis and improvement of saline and alkali soils. Agriculture Handbook no. 60. United States Department of Agriculture, Salinity Laboratory, Riverside, California.

Vepraskas, M. J. 1994. Plant response mechanisms to soil compaction. Pages 263–287 in Wilkinson, R. E. (ed.) Plant-Environment Interactions. Marcel Dekker, Inc., New York.

Vujnovic, K., R. W. Wein, and M. R. T. Dale. 2002. Predicting plant species diversity in response to disturbance magnitude in grassland remnants of central Alberta. *Canadian Journal of Botany* 80:504–511.

Webb, R. H. 1983. Compaction of desert soils by off-road vehicles. Pages 51–76 *in* R. H. Webb, and H. G. Wilshire (eds.). Environmental effects of off-road vehicles: impacts and management in arid regions. Springer-Verlag, New York.

Webb, R. H. and H. G. Wilshire (eds.). 1983. Environmental effects of off-road vehicles: impacts and management in arid regions. Springer-Verlag, New York.

Weltzin, J. F., S. Archer, and R. K. Heitschmidt. 1997. Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology* 78:751–763.

White, R., S. Murray, and M. Rohwder. 2000. Pilot analysis of global ecosystems: grassland ecosystems. World Resources Institute, Washington D.C.

White, P. S. and S. T. A. Pickett. 1985. Natural Disturbance and patch dynamics: an introduction. Pages 3–13 *in* S. T. A. Pickett and P. S. White (eds.), The ecology of natural disturbance and patch dynamics. Academic Press, Inc., Orlando.

Whitecotton, R. C. A., M. B. David, R. G. Darmody, and D. L. Price. 2000. Impact of foot traffic from military training on soil and vegetation properties. *Environmental Management* 26:697–706.

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.

Wilson, S. D. 1988. The effects of military tank traffic on prairie: A management tool. *Environmental Management* 12:397–403.

Wilson, S. D., and D. Tilman. 2002. Quadratic variation in old-field species richness along gradients of disturbance and nitrogen. *Ecology* 83:492–504.

Table 1. Mean (standard deviation) of surface properties (0-15 cm) for two grassland soils at Fort Sill, Oklahoma (n=300).

	Particle size (%)					
	Clay	Sand	Carbon (%)	SAR	pH	Electrical conductivity (dS/m)
Foard	21 (6)	59 (9)	1.0 (0.4)	6.0 (12.0)	6.8 (0.6)	1.5 (4.0)
Lawton	23 (8)	47 (11)	2.0 (0.7)	0.5 (0.3)	6.5 (0.3)	0.7 (0.3)

Table 2. Plant and soil characteristics, ($\bar{X}$ ± SD) of sampling locations[1] (F-Foard, L-Lawton), longevity[2], life form[3], seral stage[4].

Soil series-Location	Plant richness	Bare ground	Carbon	Track cover	Plant DCA axis 1 sample score	Location Successional stage	Dominant plants[5]
			(%)				
F-1	61	3 ± 9	1.6 ± 0.2	3 ± 9.9	0.87	Late	*Sporobolus compositus* (P,G,M-L), *Schizachyrium scoparium* (P,G,L), *Dichanthelium oligosanthes* (P,G,M-L)
F-2	42	6 ± 7	1.5 ± 0.1	0.5 ± 2.7	0.59	Mid-late	*Schizachyrium scoparium* (P,G,L), *Dichanthelium oligosanthes* (P,G,M-L), *Sporobolus compositus* (P,G,M-L)
F-3	65	27 ± 14	0.9 ± 0.2	36 ± 30.4	1.46	Mid	*Amsonia ciliata* (P,F,E), *Schizachyrium scoparium*, (P,G,L), *Mimosa nuttallii* (P,L,L-E)
F-4	43	85 ± 22	0.5 ± 0.1	98 ± 0.0	2.70	Early	*Plantago patagonica* (A,F,E-M), *Bromus japonicus* (A,G,E), *Hordeum pusillum* (A,G,E)
F-5	66	26 ± 16	0.8 ± 0.1	35 ± 28.0	1.64	Mid-late	*Schizachyrium scoparium* (P,G,L), *Sorghastrum nutans* (P,G,L), *Ambrosia psilostachya* (A,F,M-L)
L-1	53	11 ± 6	1.2 ± 0.1	10 ± 17.4	0.43	Late	*Schizachyrium scoparium* (P,G,L), *Andropogon gerardii* (P,G,L), *Dichanthelium oligosanthes* (P,G,M-L)
L-2	60	8 ± 9	1.2 ± 0.2	11 ± 21.7	0.62	Mid	*Schizachyrium scoparium* (P,G,L), *Dichanthelium oligosanthes* (P,G,M-L), *Psoralidium tenuiflorum* (P,L,M-L)
L-3	71	11 ± 10	2.9 ± 0.4	17 ± 23.9	0.0	Early-mid	*Sporobolus compositus* (P,G,M-L), *Bromus japonicus* (A,G,E), *Schizachyrium scoparium* (P,G,L)
L-4	70	7 ± 8	2.4 ± 0.4	17 ± 25.6	0.26	Late	*Schizachyrium scoparium* (P,G,L), *Sporobolus compositus* (P,G,M-L), *Helianthus maximiliani* (P,F,L)
L-5	65	10 ± 9	2.2 ± 0.2	20 ± 20.0	0.36	Mid	*Sporobolus compositus* (P,G,M-L), *Bromus japonicus* (A,G,E), *Symphyotrichum ericoides* (P,F,L-E)

1 Values given at the $60m^2$ scale for 10 locations at Fort Sill Oklahoma.
2 A-annual, P-perennial.
3 F-forb, G-grass, L-legume.
4 L-late, M-mid, E-early
5 Three most dominant plants (as determined by importance values) listed in order of importance.

Figure legends

Figure 1. Sampling design applied to each of 10 study areas. Vegetation and soil sampling was done on a 1 x 1-m quadrat basis and scaled up to 10 m^2 and 60 m^2.

Figure 2. Total species richness as a function of organic soil carbon and track cover at three spatial scales (60 m^2, 10 m^2, and 1 m^2). Organic soil carbon and track cover represent disturbance intensity at two time intervals, long-term and recent, respectively. Greater carbon levels are associated with lower disturbance intensity, while greater track cover is associated with greater disturbance intensity. Solid regression lines refer to Foard samples and dashed lines refer to Lawton samples. Fitted polynomials presented for ($P \le 0.05$) regressions at 60 m^2 (a. there was no difference between soil series, $P = 0.27$, b. Foard, $y = 0.76x - 0.009x^2 + 49.74$, $r^2 = 0.74$, $P = 0.03$; Lawton, $P = 0.28$), 10 m^2 (c. Foard, $y = 89.55x - 39.94x^2 - 14.79$, $r^2 = 0.37$, $P < 0.01$; Lawton, $y = 35.90x - 7.58x^2 - 3.20$, $r^2 = 0.46$, $P = 0.02$, d. Foard, $y = 0.47x - 0.006x^2 + 25.88$, $r^2 = 0.52$, $P < 0.01$; Lawton, $P = 0.20$), and 1 m^2 (e. Foard, $y = 38.83x - 16.24x^2 - 6.90$, $r^2 = 0.56$, $P < 0.01$; Lawton, $y = 14.58x - 2.96x^2 + 2.14$, $r^2 = 0.22$, $P < 0.01$. f. Foard, $y = 0.18x - 0.002x^2 + 13.45$, $r^2 = 0.41$, $P < 0.01$; Lawton, $y = 0.05x + 16.93$, $r^2 = 0.06$, $P < 0.01$).

Figure 3. Plots of sample scores produced by detrended correspondence analysis (DCA) at three spatial scales, 60 m^2 (a. eigenvalues for axis 1 and 2 are

0.380 and 0.137 with total inertia of 1.61; axis 1 and 2 account for 23.5% and 8.5% of the variance in species data, respectively), 10 m^2 (b. eigenvalues for axis 1 and 2 are 0.421 and 0.241 with total inertia of 3.63; axis 1 and 2 account for 11.6% and 6.6% of the variance in species data), and 1 m^2 (c. eigenvalues for axis 1 and 2 are 0.527 and 0.368 with total inertia of 9.03; axis 1 and 2 account for 5.8% and 4.1% of the variance in species data). The distribution of Axis 1 scores appears to be influenced by a gradient of increasing disturbance intensity.

Figure 4. Axis 1 DCA sample scores regressed against soil carbon and track cover at three spatial scales (60 m^2, 10 m^2, and 1 m^2). Greater axis sample scores indicate increasing dissimilarity in species composition. Fitted polynomials presented for ($P \leq 0.05$) regressions at 60 m^2 (a. Foard, $y = -1.66x + 3.19$, $r^2 = 0.85$, $P < 0.01$, Lawton, $P = 0.13$, b. Foard, $y = 0.02x + 0.74$, $r^2 = 0.98$, $P < 0.01$; Lawton, $P = 0.21$), 10 m^2 (c. Foard $y = -7.17x + 2.39x^2 + 5.87$, $r^2 = 0.87$, $P < 0.01$; Lawton, $y = 1.54x - 0.39x^2 - 1.02$, $r^2 = 0.38$, $P = 0.02$. d. Foard, $y = 0.03x + 0.54$, $r^2 = 0.91$, $P < 0.01$; Lawton, $P = 0.06$), and 1 m^2 (e. Foard $y = -4.75x + 1.43x^2 + 6.96$, $r^2 = 0.34$, $P < 0.01$; Lawton, $y = -1.67x - 0.33x^2 + 1.26$, $r^2 = 0.30$, $P < 0.01$. f. Foard, $y = 0.02x + 3.19$, $r^2 = 0.29$, $P < 0.01$; Lawton, $y = 0.01x + 3.01$, $r^2 = 0.08$, $P = 0.01$).

Figure 1.

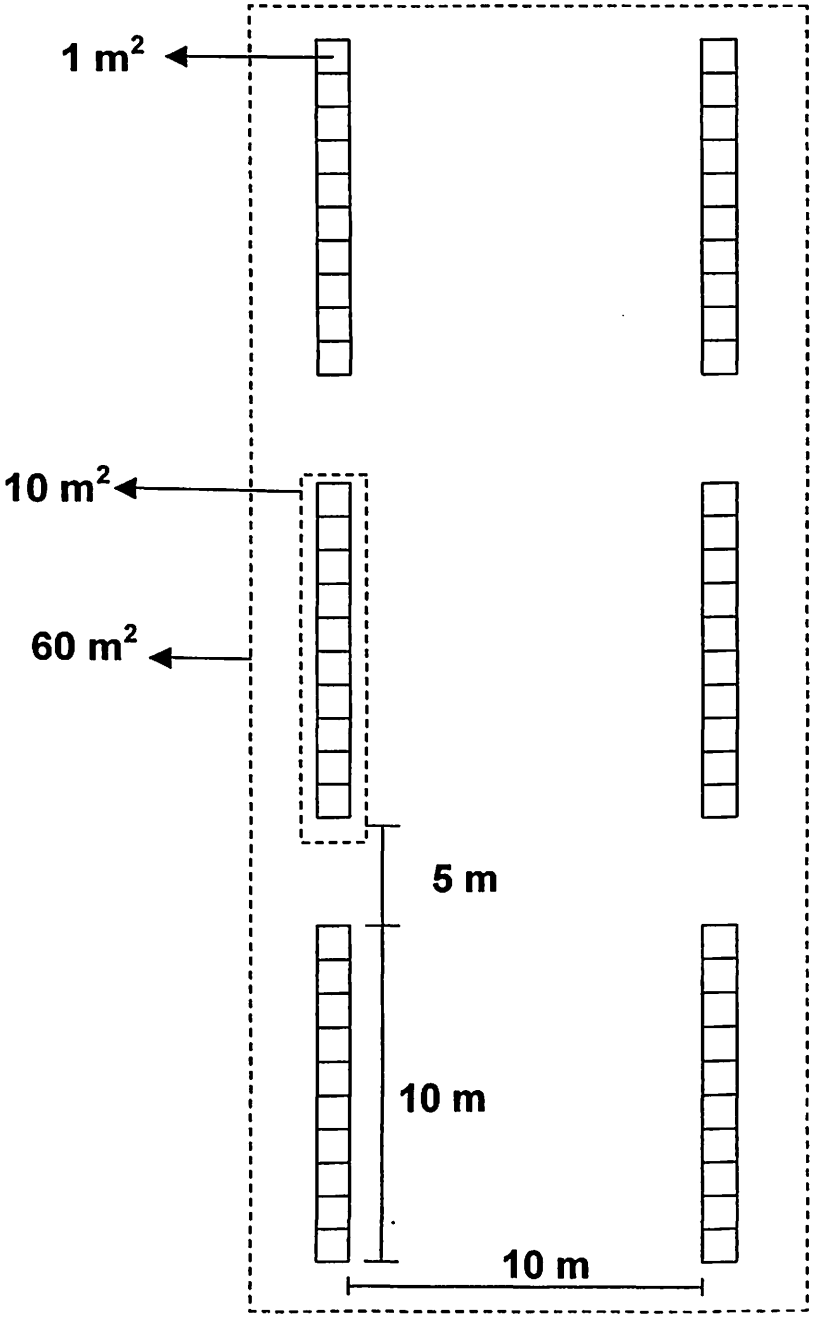
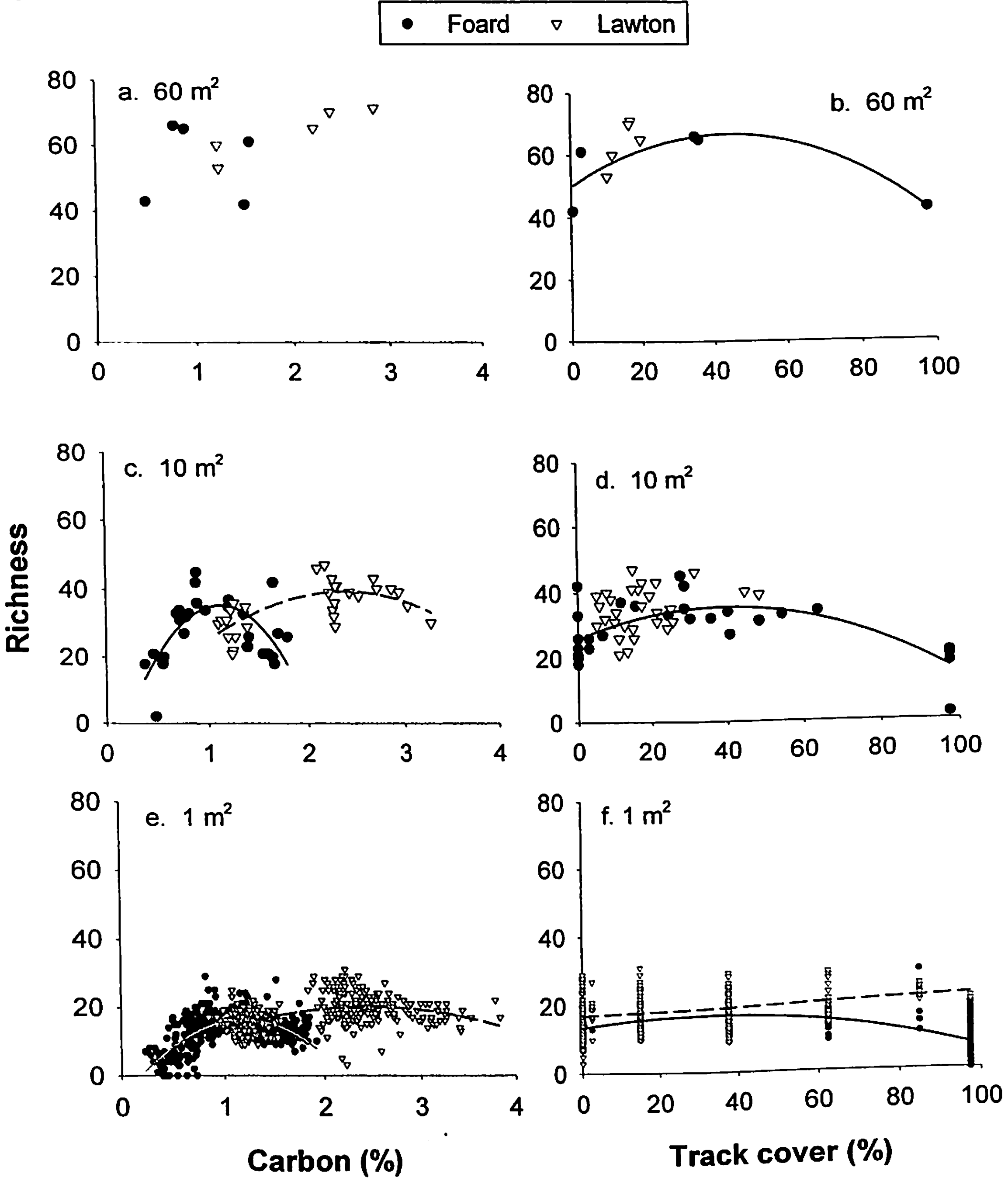


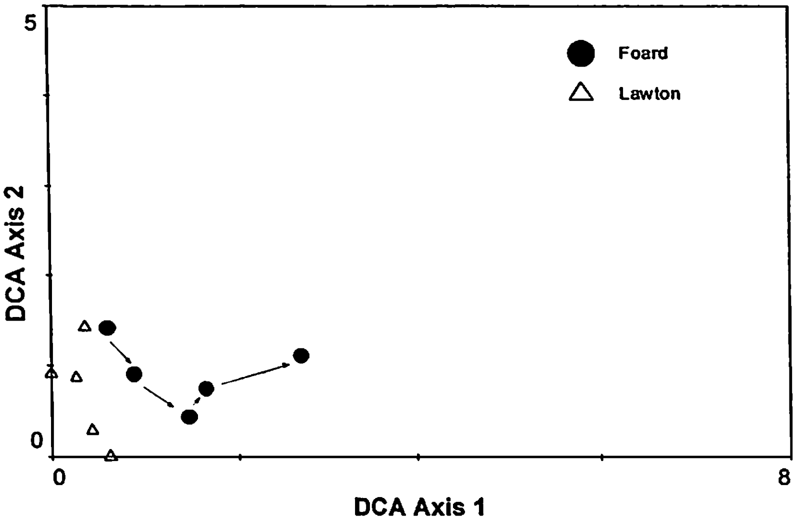
Figure 2.



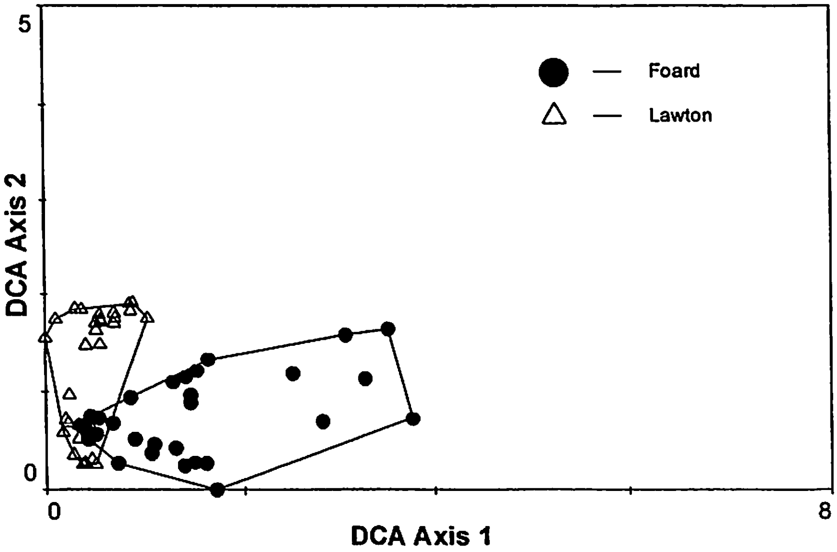
● Foard
▽ Lawton
a. 60 m^2
b. 60 m^2
c. 10 m^2
d. 10 m^2
e. 1 m^2
f. 1 m^2
Richness
0
20
40
60
80
0
1
2
3
4
0
20
40
60
80
100
Carbon (%)
Track cover (%)

Figure 3.

a. 60 m^2



b. 10 m^2



c. 1 m^2

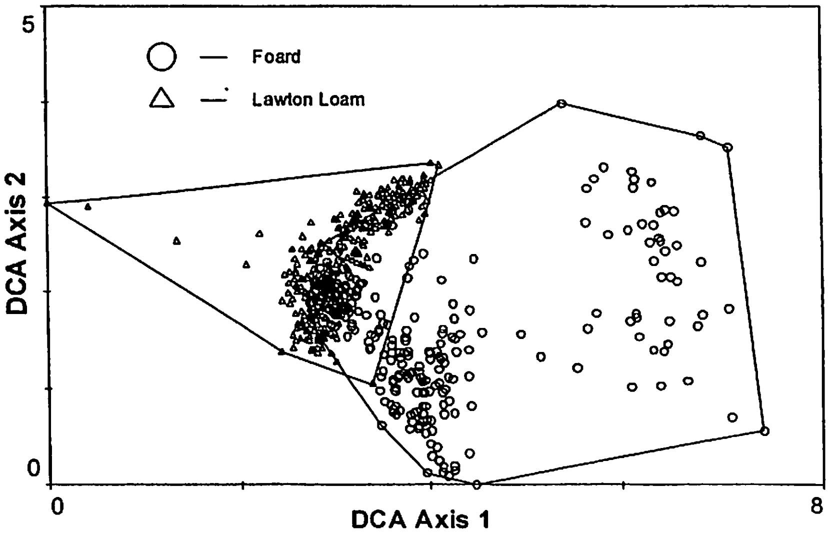
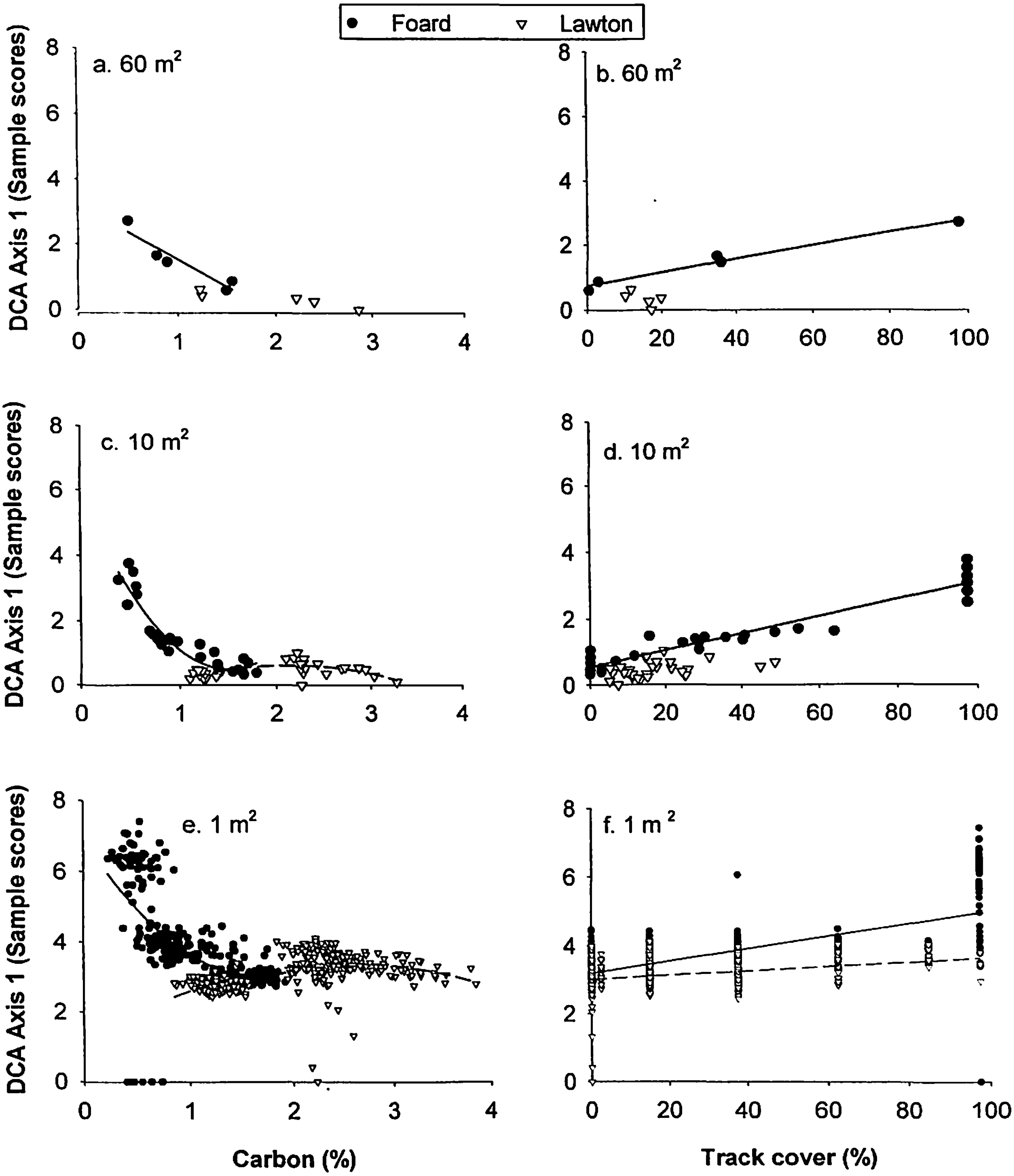


Figure 4.


● Foard
▽ Lawton
a. 60 m²
b. 60 m²
c. 10 m²
d. 10 m²
e. 1 m²
f. 1 m²
DCA Axis 1 (Sample scores)
DCA Axis 1 (Sample scores)
DCA Axis 1 (Sample scores)
0
2
4
6
8
0
1
2
3
4
0
20
40
60
80
100
Carbon (%)
Track cover (%)

CHAPTER 2

Small mammal response to long- and short-term disturbance in a mixed prairie: a different footprint

Abstract

I investigated the roles of plant communities and soils in determining species richness and composition of small mammals in a mixed prairie disturbed by military maneuvers. I compared communities on 2 soil series, Foard and Lawton, across a gradient of disturbance intensity. Small mammal richness varied little between soil series as expected, but species composition differed. Seven species were captured across the study area. Individual species abundances were a function of both long-term (organic soil carbon) and short-term (cover of vehicle tracks) disturbance intensities, but the footprint of responses differed between disturbance variables. *S. hispidus* and *P. maniculatus* were abundant across the study area; *S. hispidus* was most abundant at lightly disturbed Lawton locations; and *P. maniculatus* was most abundant at heavily disturbed Foard locations. *C. hispidus* and *R. fulvescens* were only captured on disturbed Foard or lightly disturbed Lawton soils, respectively. The difference in plant species composition across study areas was reflected in small mammal preferences for particular habitat conditions including disturbance intensity. Small mammals may useful as biological

indicators of ecosystem change because they were easily measured and responded predictably to disturbance.

INTRODUCTION

Responses of grassland small mammal communities to human activities such as off-road vehicle use (Goran 1983, Severinghaus et al. 1980) and habitat conversion (Johnson et al. 2002, Silva 2001) in many ways parallel responses of small mammals to natural disturbance such as fire and grazing (Grant et al. 1982, Kaufman and Kaufman 1997, Kaufman et al. 1990). Small mammal communities often respond rapidly to changes in habitat structure (Abramsky, 1978, Kaufman et al. 1983, Kincaide et al. 1983) and plant composition (Kaufman et al. 1983), and they occupy key positions in food webs (Kaufman et al. 1998) making them informative biological indicators of change (Dale and Beyeler 2001). Observing species with specific habitat requirements (characteristic indicator species) and those having more broadly defined habitats (detector indicator species) provides a better understanding of habitat status over time (Kaufman et al. 2000, McGeoch et al. 2002).

Some small mammal species are very adaptable as evidenced by research in cultivated lands of the tallgrass prairie region (de la Peña et al. 2003, Kaufman and Kaufman 1990, Kaufman et al. 2000). For example, *Peromyscus maniculatus* is a ubiquitous species but increases in abundance in areas disturbed by grazing and fire (Clark 1989, Kaufman et al. 1983, Matlack et al. 2001). Conversely, *Reithrodontomys fulvescens* declines after a disturbance such as fire (Kaufman et al. 1983).

Although many small mammals clearly respond to structural habitat characteristics such as litter and plant density (Abramsky, 1978, Kaufman et al. 1983, Kincaide et al. 1983), the study of small mammal ecology is incomplete without consideration of soil, and vegetation (Grant and French 1980). For example, topographic gradients influenced habitat structure and therefore impacted small mammal communities in tallgrass prairie (Clark et al. 1989). Ecologists infrequently considered the role of below ground processes on small mammal populations (Gibson et al. 1990), albeit they recognize effects of habitat fragmentation and heterogeneity on population dynamics (Barrett and Peles 1999).

Soils have various capacities to produce vegetation, and those capacities can be altered by disturbance (Chapter 1). We define disturbance as an event that results in change in ecosystem or community dynamics, resources, or physical environment (*sensu* White and Pickett 1985). Grassland plant communities on different soils may vary in their resistance to disturbance, which also impacts other organisms (Dodd et al. 2002, Ludwig and Tongway 1995, Michunas et al. 1999). For example, plants growing in saline soils or arid environments face greater osmotic challenges and may have lower resistance to additional stress (Havlin et al. 1999). Soil texture is often a heterogeneous soil property and plays an important role in determining moisture availability and nutrient dynamics necessary for plant survival such as carbon (Rowell 1994, Vepraskas 1994). Altered nutrient dynamics may impact vegetation structural characteristics such as litter and plant height (Burke 1998), which influences animal communities (Abramsky, 1978, Kaufman et al. 1983, Kincaide et al. 1983).

Temporal scale of small mammal responses to disturbance in grasslands may be important because of annual population fluctuations (Kaufman et al. 1983). Some anthropogenic disturbances differ from natural disturbance because intense anthropogenic activities (e.g., cultivation) over a period of years has the potential to exhaust soil carbon (Anderson and Coleman 1985, Tiessen et al. 1982), an important trait of soil quality (Eviner and Chapin 2003). Loss of soil carbon alters plant species composition, plant species richness (Chapter 1), and presumably small mammal community dynamics.

Soil carbon indicates cumulative long-term disturbance intensity because it is lost at predictable rates with agricultural disturbance (Anderson and Coleman 1985, Burke et al. 1995) and is not derived from the disturbance. Models predict 30–50% loss of total soil carbon within 10–40 years of cultivation (Anderson and Coleman 1985, Burke et al. 1995); however, organic carbon regenerates very slowly post-cultivation (Baer et al. 2002, Knops and Tilman 2000, Potter et al. 1999, Schlessinger 1986). Therefore, the long-term cumulative effect of disturbance can be inferred by comparing organic soil carbon across a disturbance gradient. Small mammals may react differently to short-term disturbance events (e.g., fire) than to continued long-term disturbance. In contrast, the general response pattern of small mammals to disturbance from military maneuvers may be similar to that of grazing and fire (Kaufman et al. 2000).

My objective was to assess the interaction of soil characteristics and anthropogenic disturbance to vegetation and small mammal communities in a mixed prairie. Specifically, I asked 1) if long-term disturbance influenced small mammal species richness, species composition, and abundances of individual species in a manner similar to short-term disturbance and 2) if small mammal communities and individual species were influenced by plant species richness and species composition and if responses differed between soil types. I evaluated these questions through trapping of small mammals coupled with vegetation and soil sampling of study locations varying in histories of disturbance on 2 soil series in a southern mixed prairie.

MATERIALS AND METHODS

Study area.—The study was conducted at Fort Sill, located in Comanche County (34° 38' N, 98° 30' W) in southwestern Oklahoma. Fort Sill, established in 1869 to mediate Native American conflicts, has grown to encompass 38,292 ha used for artillery training by the United States Army (Hagen 1976). The area has a subhumid climate with an average annual rainfall of 782 mm (593 mm in 2003). Temperatures range from –16 to 46 °C (2003 average temperature equaled the annual mean of 16 °C; Oklahoma Climatological Survey 2003).

Sampling locations were divided between soil series, Foard and Lawton, present throughout the southern Great Plains. Foard soils, representative of the Hardland ecological site, and Lawton soils, representative of the Loamy Prairie ecological site, encompass about 18% and 27% of Comanche County, respectively (Natural Resource Conservation Service [NRCS] 2004a). I tested the influence of edaphic features in an anthropogenically disturbed grassland using 2 soil series. Foard locations were characterized by short and mid-level grasses such as blue grama (*Bouteloua gracilis)*, buffalo grass (*Buchloe dactyloides)*, vine-mesquite (*Panicum obtusm)*, sideoats grama (*Bouteloua curtipendula)*, and little bluestem (*Schizachyrium scoparium*). Lawton locations were characterized by mid-level and tall grasses such as big bluestem (*Andropogon gerardii*), indian grass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), and switch grass (*Panicum virgatum*— Mobley and Brinlee 1967; Table 1).

Technical series descriptions (NRCS 2001) indicated similarities in the A-horizons of Foard and Lawton Loam soils, but the B-horizons differed. Foard soils contain clay pans and a natric component (i.e., increased sodium levels), which influenced physiological processes of plants and subsequently species composition (Hopkins et. al. 1991; Table 1). Salinity can range from 2.0 to 4.0 dS/m at a depth of 23–56 cm. Increased Na levels also accompany more basic pH levels (6.1–8.4, Foard vs. 6.1–7.3, Lawton Loam). Study locations were demarcated ≥15 m from a roadway and 50 m from each other.

Disturbances on study locations included military vehicle use (tracked and wheeled of various weights), encampments, and land-navigation exercises (e.g., foot training). Locations were chosen based on history of short-term disturbance to include a range of disturbance intensities as observed by permanent personnel at Fort Sill (J. Kretzer and J. MacIntosh *pers. comm.*). Two locations with Foard soil that had not been used for training in the last 10 years represented an undisturbed condition, in contrast to 1 location that had been subjected to soil movement by mechanized earth movers. The range of short-term disturbance at locations with Foard soil appeared greater than at locations with Lawton soil. Although bison (*Bos bison*) and domestic cattle (*Bos taurus*) previously occupied parts of Fort Sill, short-term grazing by large herbivores was not a factor in this study. Focal areas had not been burned for a minimum of 4 years prior to this study.

Trapping.—I established permanent 3 x 5 trapping grids in 10 locations (Fig. 1) to sample the small mammal community. Two Sherman live traps (7.6 x 8.9 x 22.9 cm) baited with oatmeal were placed within 0.5 m of each other at each of the 15 stations that were separated by 10 m (Fig. 1). Cotton was added to traps for nesting material when temperatures were expected to fall below 10°C during the night. Traps were set at sunset and checked each morning for 4 consecutive nights during the new moon in May, June, August, and September 2003 (4,800 total trap nights). After identification, animals were toe clipped for future recognition (Animal Care and Use Committee 1998; Oklahoma State University Animal Care and Use Protocol G-0312), and voucher specimens were deposited in the Oklahoma State University Collection of Vertebrates. Capture data from all 4 sessions were combined for analyses.

Vegetation.—Relationships between disturbance and plant communities were assessed by sampling plants in 60 1-m x 1-m quadrats for each of 10 locations (5 locations/soil series, 600 total quadrats; Fig. 1). Vegetation sampling took place in May–June and September–October 2003 to obtain accurate estimates of species richness. Species composition, bare ground, and track-cover measurements followed a modified Daubenmire (1959) cover class system (>0–1%, >1–5%, >5–25%, >25–50%, >50–75%, >75–95%, and >95–100%); midpoints for each class were used in analyses.

Measurements of vegetation structure included plant height (cm), angle of obstruction (degrees; Harrell and Fuhlendorf 2002), and litter depth (cm). The tallest living plant in each quadrat was used to index height. Angle of obstruction measurements, 4/quadrat (i.e., one in each cardinal direction), were averaged within each location. Litter depth was measured 5 times/quadrat (i.e., 300 measurements/study location); readings were taken in the corners and center of the quadrat to the nearest cm. I combined spring and autumn datasets and used the maximum value for measurements of species, track-cover, and vegetation structure recorded in either season to more accurately reflect total species richness and composition of sampling locations. The greatest amount of disturbance occurred before spring sampling, so spring track-cover estimates dominated the combined dataset. Vegetation taxonomy followed the National Plants Database (NRCS 2004).

Soil.—I collected soil samples in July 2003 to assess differences in soil nutrients and texture between Foard and Lawton soils along the disturbance gradient. Five standard soil cores (1.5 cm x 15 cm) taken in each quadrat were composited into 1 sample. Samples were dried overnight at 60° C and ground to pass through a 2-mm sieve. Percent organic soil carbon for each sample was determined using a LECO Truspec dry combustion analyzer (Nelson and Sommers 1996). Cations were analyzed using a Spectro Ciros ICP (Sims 1996). Texture analysis followed standard hydrometer procedures described by Gee and Bauder (1986), and salinity values were reported in saturated paste form (United States Department of Agriculture 1954).

Data analysis.— Anthropogenic disturbance was assessed as a consequence of long-term (organic soil carbon) and short-term (track-cover) disturbance. Vegetation richness and composition were pooled over 60 1-m^2 quadrats to match the scale of small mammal observations at each location. I was unable to control the disturbance regime on sampling locations in this study so I used organic soil carbon and track-cover (percentage of sampling unit disturbed by a vehicle) to index disturbance intensity. Soil carbon decreased with disturbance intensity while track-cover increased.

Regression analysis was applied to test for relationships among vegetation, small mammal, and disturbance variables (PROC GLM; SAS Institute Inc. 2001). The relationship between species richness and disturbance (i.e., track-cover and soil organic carbon) was tested with polynomial regression (PROC GLM; SAS Institute, 2001). I first determined if the regression model differed between soil series by using a dummy variable for soil, and in the absence of a difference, data from the 2 soils were combined in the regression.

I used detrended correspondence analyses (DCA) to test whether plants and animal communities were organized along environmental gradients (Hill and Gauch 1980, Peet et al. 1988, ter Braak 1987). DCA is an indirect gradient analysis that simultaneously calculates relationships between species and samples (ter Braak and Šmilauer 2002). Plant species cover data were square root transformed for DCA to reduce heteroscedasticity among samples. Species and sample biplots were used to interpret gradients (Hill and Gauch 1980, ter Braak and Verdonschot 1995). DCA sample scores represented the similarity of species composition in a sample relative to other samples. For example, a group of species with a sample score of 1.0 had different species composition than a sample with a score of 3.0. I used DCA sample scores of small mammals and plants to test the relationship of species composition and disturbance. Importance values (IV = relative frequency + relative cover * 100) were calculated for all plant species and summed across all 10 locations. Importance values were not used in DCA analyses. Statistical significance for all procedures was alpha = 0.05.

RESULTS

Two temporal measurements of soil disturbance, track-cover and organic soil carbon, exhibited a positive relationship at locations on Foard soil indicating that responses of small mammals and plants to disturbance may be the product of both short-and long-term disturbance (Fig. 2). Mean soil organic carbon was 0.5–1.6% on Foard soil and 2.2–2.9% on Lawton soil. There was no relationship between track-cover and soil organic carbon on Lawton soil suggesting that responses to disturbance may be limited to long-term disturbance on this soil (Fig. 2). Mean track-cover was 0.5–98% on Foard soil and 10–20% on Lawton soil.

Species richness of small mammals was not related to carbon or track-cover on either soil. Seven species were captured across all 10 study locations, and captures varied from 3 to 5 species between locations (Table 2). Dominance of *S. hispidus* led to more total animal captures at locations on Lawton soil (Table 2) than locations on Foard soil. *Spermophilus tridecenlineatus* was excluded from analyses because only 1 individual was captured.

Species composition of small mammals differed between soil types (Fig. 3). Sample and species scores indicated relative position in ordination space so that samples or species with similar values were strongly correlated (ter Braak and Verdonschot 1995). Communities on Foard soil demonstrated more variability in species composition than communities on Lawton soil (Fig. 3). Species that prefer more areas with more bare ground or shorter vegetation were more closely associated with samples known to have greater disturbance.

Captures of individual species of small mammals responded in a complex manner when regressed with organic soil carbon and track-cover, so I was unable to calculate the relative influence of long-term and short-term disturbance (Fig. 4, 5). I focused on *S. hispidus, P. maniculatus, C. hispidus*, and *R. fulvescens* for the remainder of the analyses because *P. leucopus* and *R. montanus* had inadequate capture rates. Responses of *S. hispidus, P. maniculatus, C. hispidus*, and *R. fulvescens* followed similar trends to short-term and long-term disturbance although the strength of the relationship varied by soil series and temporality of disturbance (Fig. 4, 5). In general, soil organic carbon explained more variation than did track-cover. Although *S. hispidus* and *P.*

maniculatus were abundant across locations, *S. hispidus* was most abundant at less disturbance and *P. maniculatus* was most abundant at greater disturbance. *C. hispidus* and *R. fulvescens* were captured only on Foard or Lawton locations, respectively. *C. hispidus* increased with both long-term and short-term disturbance, while *R. fulvescens* decreased with long-term disturbance. Captures of *R. fulvescens*, however, were not related to short-term disturbance (Fig. 4, 5).

Plant communities also were related to richness and composition of small mammals. Richness of small mammals was influenced by plant species richness (Fig. 6). Plant communities also were differentiated by an interaction of soil series with disturbance (Table 3). Plant communities on Lawton soil exhibited less variability in composition than plant communities on Foard soil. The 3 most dominant plant species, as calculated by importance values (Table 3), were perennial grasses whose distributions were centered around samples from locations with Lawton soil. Plant species with greater species scores on DCA axis 1 were found in more intensely disturbed locations and were early to mid-seral plants that also tended to be shorter in stature than those with lesser scores (Table 3).

Plant species composition (plant DCA axis 1 sample scores) influenced abundance of *S. hispidus*, *P. maniculatus*, *C. hispidus*, and *R. fulvescens* (Fig. 7). Relationships between plant species composition and *S. hispidus* and *P. maniculatus* were differentiated by soil series in that *S. hispidus* was most abundant on Lawton soil and decreased with change in plant species composition; however, *P. maniculatus* was most abundant on Foard soil and increased change in plant species composition.

DISCUSSION

Plant species composition, a determinant of habitat structure, differed between soil series and intensity over short-term (track-cover) and long-term (soil organic carbon) time scales (Fig. 8). Habitat composition and structure, as altered by recent and past military maneuvers influenced small mammal communities and abundances of individual species in my study. Many studies of grassland small mammals focusing on short-term disturbance, such as fire, have measured animal community dynamics and habitat structure (Abramsky et. al. 1978, Clark et al. 1989, Goertz 1964, Kaufman and Fleharty 1974). Some researchers have included data on plant functional groups to better understand small mammal communities (Grant et al. 1982, Jorgensen and Demarais 1999, Kaufman et al. 2000). Few studies, however, have considered effects of landscape features such as topographic position or grassland type on small mammal communities (Clark et al. 1989, Grant and French 1979, Grant et al. 1982, Orians and Solbrig 1977). My study highlights edaphic factors as an important link between the small mammal and plant communities. Relationships varied between these ecosystem components over short-term (1–2 years) and long-term (decades) time scales. Not only are soils and plant species composition critical to understanding small mammal ecology, but the temporality of external perturbations also influences responses.

Small mammal richness and composition.—My results parallel previous studies in that species replacement rather than change in species richness occurs following grassland disturbance (de la Peña et al. 2003, Diersing and Severinghaus 1984, Clark and Kaufman 1991, Goran et al. 1983, Matlack et al. 2001, Schramm and Willcutts 1985, Severinghaus 1980). Species composition of small mammals on Foard soil, differed from species composition on Lawton soil, and abundances of individual species were related to both short-term and long-term disturbance (Fig. 5, 6). I predicted that small mammals would respond more strongly to short-term disturbance than long-term, but soil organic carbon explained more variation in small mammal abundances than track-cover. Total capture rates may have been affected by the below normal precipitation amounts in 2003, but we were unable to understand the influence of climate with this data set.

Plant community and soils.—Despite observations that small mammal communities varied by soil series, it is unlikely that they responded directly to edaphic factors. Instead, plant community richness and composition responded to soil series especially as soil disturbance acted upon them. At Fort Sill, 2 common soil series, Foard and Lawton Loam (NRCS 2004), produced distinct, but similar, plant communities when undisturbed (e.g., they were both categorized as mixed prairie; Table 3), and plant species composition on Lawton soil varied less across the disturbance gradient than that of Foard locations (Chapter 1). These communities became increasingly dissimilar compositionally when disturbed by military training activities (Chapter 1) because the sodic component (sodium salts) of Foard soil, normally found in the B-horizon (NRCS 2001), is brought in closer contact with roots through loss of topsoil and soil mixing. Exposure to elevated sodicity inhibits osmoregulation in some plants, thus limiting rooting depth which in turn resulted in decreased plant height and productivity and ultimately, different plant (Hopkins et al. 1991, Vepraskas 1994) and animal communities.

Conceptual disturbance model.—In studies where plant productivity was enhanced via nutrient amendments, biomass of small mammal species increased (Abramsky 1978, Grant et. al. 1977, Hall et. al. 1991). Species replacement was attributed to alteration of vegetation structure rather than to the nutrient amendments themselves. Likewise, military maneuvers altered plant species composition, plant height, and litter depth. The change in plant community structure led to change in composition of the small mammal community on the Foard soil. Because plant species composition on Lawton soil varied little, I expected small mammal abundances to be equivalent among those locations. However, *S. hispidus* and *R. fulvescence* clearly responded to long-term disturbance on Lawton soils. Because abundances of small mammal species did vary and are unlikely to respond to soil series directly, there must be other factor(s) driving animal responses on Lawton soil that I did not measure (Fig. 8).

Response of plant and animal communities on Lawton soil to short-term disturbance was unclear because I recorded few quadrats with large amounts of track-cover. This paucity might have occurred because new or existing plants may have colonized gaps created by disturbance on Lawton sites more quickly than Foard sites because of better water infiltration and nutrient availability (Vepraskas 1994, NRCS 2001). Sodium salts tend to disperse soil particles, which impedes movement of water and nutrients (Havlin et al. 1999). Alternatively, trainers at Fort Sill may prefer to conduct maneuvers on Foard locations because of particular traits (e.g. vegetation height and density, nearness to wooded edges or hills).

The relationship between plant species richness and small mammal richness observed in my study (Fig. 7) suggests that preserving plant biodiversity across a landscape benefits other organisms. Conversely, small mammal richness may be more strongly related to climatic conditions such as moisture than plant richness at regional scales (Hawkins and Pausas 2004). Military maneuvers maintain habitat heterogeneity across Fort Sill, which enriches both the small mammal and plant species pools (Chapter 1; Fuhlendorf and Engle 2001).

Application.—Although responses of individual species to military maneuvers were consistent with their life histories (Cameron and Spenser 1981, Dalquest and Horner 1984, Goetz 1964, Paulson 1988, Spencer and Cameron 1982), I explored vegetation and soil dynamics as potential mechanisms influencing small mammal communities. The analysis of interactions of small mammals with vegetation and soils presented here may allow researchers to develop a protocol for using small mammals as biological indicators of habitat condition (Dale and Beyeler 2001, Thomas 1982). For example, my study suggests that 4 small mammal species respond to disturbance, especially over long time scales. *P. maniculatus* and *S. hispidus* represent detector species as defined by McGeoch (2002) because they are ubiquitous and respond to specific habitat conditions. Observing trends over time or across disturbance gradients would allow managers to anticipate ecosystem change preventing irreversible degradation. *C. hispidus* and *R. fulvescens* have more specific requirements and could be considered characteristic species (McGeoch 2002).

Characteristic species of small mammals, such as *C. hispidus* and *R. fulvescens*, can be monitored on a presence-absence basis rather than by observing trends over time. Tracking such species could document habitat degradation, albeit it would not allow managers to take preventative action (McGeoch 2002). Insects such as moths (macrolepidoptera), ground beetles (Carabidae), and dung beetles (Scarabaeidae) have been used as bioindicators because their fidelity and specificity to habitat conditions allow researchers to evaluate ecosystem change (Luff and Woiwod 1994, McGeoch 2002). Combining data from both detector and characteristic species may improve land-management decisions.

Use of bioindicators should include consideration of soil heterogeneity because disturbance can have differential effects on communities within a larger ecosystem classification (i.e., mixed prairie). In my study, when Foard soil was disturbed (e.g., topsoil was lost and soil horizons were mixed), plants exposure to natric conditions increased. Plants adapted to sodic soil and highly disturbed conditions increased at those locations (e.g., *Grindelia papposa, Hordeum* *pusillum*, *Plantago elongata*, and *Xanthisma texanum*). Lawton locations lacking sodic conditions maintained similar species composition across the disturbance gradient.

Failing to couple soil conditions with studies of vegetation and small mammal communities would lead to greater overall variance and less interpretability. Furthermore, small mammal dynamics have been well documented in terms of habitat structure (Abramsky, 1978, Kaufman et al. 1983, Kincaide et al. 1983), but the soil-plant link in small mammal-habitat interactions is often omitted. The results of this study suggest that use of organic soil carbon as a monitoring device for small mammals may prove useful to land managers. Power to predict the response of the small mammal community to disturbance may be enhanced by including this fundamental level of complexity.

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LITERATURE CITED

Abramsky, Z. 1978. Small mammal community ecology: changes in species diversity in response to manipulated productivity. Oecologia 34:113–123.

Anderson, D. W. and D. C. Coleman. 1985. The dynamics of organic matter in grassland soils. Journal of Soil and Water Conservation. March-April:211–216.

Animal Use and Care Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

Baer, S. G., D. J. Kitchen, J. M. Blair, and C. W. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecological Applications 12:1688-1701.

Barrett, G. W., and J. D. Peles (eds.). 1999. Landscape ecology of small mammals. Springer-Verlage, New York.

Burke, I. C., W. K. Lauenroth, and D. P. Coffin. 1995. Soil organic matter recovery in semiarid grasslands: Implications for the conservation reserve program. Ecological Applications 5:793–801.

Burke, I. C., W. K. Lauenroth, M. A. Vinton, P. B. Hook, R. H. Kelly, H. E. Epstein, M. R. Aguiar, M. D. Robles, M. O. Aguilera, K. L. Murphy, and R.

A. Gill. 1998. Plant-soil interactions in temperate grasslands. Biogeochemistry 42:121–143.

Cameron, G. N., and S. R. Spencer. 1981. *Sigmodon hispidus.* Mammalian Species 158:1–9.

Clark, B. K., and D. W. Kaufman. 1991. Effects of plant litter on foraging and nesting behavior of prairie rodents. Journal of Mammalogy 72:502–512.

Clark, B. K., D. W. Kaufman, E. J. Finck, and G. A. Kaufman. 1989. Small mammals in tall-grass prairie: patterns associated with grazing and burning. Prairie Naturalist 21:177–184.

de la Peña, N. M., A. Butet, Y. Delettre, G. Paillat, P. Morant, L. Le Du, and F. Burel. 2003. Response of the small mammal community to changes in western french agricultural landscapes. Landscape Ecology 18:265–278.

Dale, V. H., and S. C. Beyeler. 2001. Challenges in the development and use of ecological indicators. Ecological Indicators 1:3–10.

Dalquest, W. W., and N. V. Horner. 1984. Mammals of north-central Texas. Midwestern State University Press, Wichita Falls, Texas.

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33:43–64.

Diersing, V. E., and W. D. Severinghaus. 1984. The effects of tactical vehicle training on the lands of Fort Carson, Colorado: an ecological assessment. United States Army Construction and Engineering Research Laboratory, Technical Report N-85/03:1–46.

Dodd, M. B., W. K. Lauenroth, I. C. Burke, and P. L. Chapman. 2002. Associations between vegetation patterns and soil texture in the shortgrass steppe. Plant Ecology 158:127–137.

Eiviner, V. T., and F. S. Chapin, III. 2003. Functional matrix: conceptual framework for predicting multiple plant effects on ecosystem processes. Annual Review of Ecology, Evolution and Systematics 34:455–485.

Fehmi, J. S., and J. W. Bartolome. 2002. Species richness and California voles in an annual and a perennial grassland. Western North American Naturalist 62:73–81.

Frank, A. B., D. L. Tanaka, L. Hofmann, and R. F. Follette. 1995. Soil carbon and nitrogen of northern Great-Plains grasslands as influenced by long-term grazing. Journal of Range Management. 48:470–474.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. Bioscience 51:625-632.

Gee, G. W., and J. W. Bauder. 1986. Particle size analysis. Pp. 377–411 in Methods of soil analysis. Part 1, No. 9. Chemical methods (A. Klude ed.). Book series 5:1–1188. Soil Science Society of America.

Gibson, D. J., C. C. Freeman, and L. C. Hulbert. 1990. Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. Oecologia 84:169-175

Goertz, J. W. 1964. The influence of habitat quality upon density of cotton rat populations. Ecological Monographs 34:359-381.

Goran, W. D., L. L. Radke, and W. D. Severinghaus. 1983. An overview of the ecological effects of tracked vehicles on major U.S. army installations. United States Army Construction Engineering Research Laboratory Technical Report N-142:1–75.

Grant, W. E., E. C. Birney, N. R. French, and D. M. Swift. 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. Journal of Mammalogy 63:248–260.

Grant, W. E., and N. R. French. 1980. Evaluation of the role of small mammals in grassland ecosystems: a modeling approach. Ecological modeling 8:15–37.

Grant, W. E., N. R French, and D. M. Swift. 1977. Response of a small mammal community to water and nitrogen treatments in a shortgrass prairie ecosystem. Journal of Mammalogy 58:637–562.

Hagan, W. T. 1976. United States-Comanche relations: the reservation years. Yale University Press, New Haven, Connecticut.

Hall, A. T., P. E. Woods, and . W. Barrett. 1991. Population dynamics of the meadow vole (*Microtus pennsylvanicus*) in nutrient-enriched old-field communities. Journal of Mammalogy 72:332–342.

Harrell, W. C., and S. D. Fuhlendorf. 2002. Evaluation of habitat structural measures in a shrubland community. Journal of Range Management. 55:488–493.

Havlin, J. L., J. D. Beaton, S. L. Tisdale, and W. L. Nelson. 1999. Soil fertility and fertilizers: an introduction to nutrient management. Prentice Hall, Upper Saddle River, New Jersey.

Hawkins, B. A., and J. G. Pausas. 2004. Does plant richness influence animal richness?: the mammals of Catalonia (NE Spain). Diversity and Distributions 10:247-252.

Heske, E. J., J. H. Brown, and S. Mistry. 1994. Long-term experimental study of a Chihuahuan desert rodent community: 13 years of competition. Ecology 75:438–445.

Hill, M. O., and H. G. Gauch, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58.

Hopkins, D. G., M. D. Sweeney, D. R. Kirby, and J. L. Richardson. 1991. Effects of revegetation on surficial soil salinity in panspot soils. Journal of Range Management 44:215-220.

Johnson, L. C., and J. R. Matchett. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82:3377–3389.

Johnson, R., J. W. H. Ferguson, A. S. van Jaarsveld, G. N. Bronner, and C. T. Chimimba. 2002. Delayed responses of small-mammal assemblages subject to afforestation-induced grassland fragmentation. Journal of Mammalogy 83:290–300.

Jorgensen, E. E., and S. Demarais. 1999. Spatial scale dependence of rodent habitat use. Journal of Mammalogy 80:421–429.

Kauffman, D. W., E. J. Finck, and G. A. Kaufman. 1990. Small mammals and grassland fires. Pp. 28–80 in Fire in North American tallgrass prairies (S. L. Collins and L. L. Wallace, eds.). University of Oklahoma Press, Norman.

Kaufman, D. W., and E. D. Fleharty. 1974. Habitat selection by nine species of rodents in north-central Kansas. Southwestern Naturalist 18:443–452.

Kauffman, D. W., and G. A. Kaufman 1990. Small mammals of wheat fields and fallow wheat fields in north-central Kansas. Transactions of the Kansas Academy of Sciences 93:28–37.

Kaufman, D. W., G. A. Kaufman, and B. K. Clark. 2000. Small mammals in native and anthropological habitats in the Lake Wilson area of north-central Kansas. The Southwestern Naturalist 45:45–60.

Kaufman, D. W., G. A. Kaufman, P. A. Fay, J. L. Zimmerman, and E. W. Evans. 1998. Animal populations and communities. Pp. 113–139 in Grassland dynamics (A. K. Knapp, J. M. Briggs, D. C. Hartmett, and S. L. Collins, eds.), Oxford University Press, New York.

Kaufman, D. W., G. A. Kaufman, and E. J. Finck. 1983. Effects of fire on rodents in tallgrass prairie of the flint hills region of eastern Kansas. Prairie Naturalist 15:49–56.

Kaufman, G. A., and D. W. Kaufman. 1997. Ecology of small mammals in prairie landscapes. Pp. 207–243 in Ecology and conservation of Great Plains vertebrates (F. L. Knopf and F. B. Samson, eds.). Springer-Verlag, New York.

Kincaid, W. B., G. N. Cameron, and B. A. Carnes. 1983. Patterns of habitat utilization in sympatric rodents on the Texas coastal prairie. Ecology 64:1471–1480.

Knops, J. M. H., and D. Tillman. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. Ecology 81:88-98.

Ludwig, J. A., and D. J. Tongway. 1995. Spatial organization of landscapes and its function in semi-arid woodlands, Australia. Landscape Ecology 10:51–63.

Luff, M. L., and I. P. Woiwod. 1994. Insects as indicators of land-use change: a European perspective, focusing on moths and ground beetles. Pp. 399–422 in Insects in a changing environment (R. Harrington and N. E. Stork, eds.). Academic Press, London, United Kingdom.

McGeoch, M. A., B. J. Van Rensburg, and A. Botes. 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. Journal of Applied Ecology 39:661–672.

Matlack, R. S., D. W. Kaufman, and G. A. Kaufman. 2001. Influence of grazing by bison and cattle on deer mice in burned tallgrass prairie. American Midland Naturalist 146:361–368.

Milchunas, D. G., K. A. Schulz, and R. B. Shaw. 1999. Plant community responses to disturbance by mechanized military maneuvers. Journal of Environmental Quality 28:1533–1547.

Mobley, H. L., and R. C. Brinlee. 1967. Soil survey, Comanche county, Oklahoma. United States. Government Printing Office, Washington D.C.

Natural Resources Conservation Service. 2001. Official Soil Series Descriptions. United States Department of Agriculture. Lincoln, Nebraska.

Natural Resources Conservation Service 2004a. National soil information system, National Soil Survey Center, Lincoln, Nebraska.

Natural Resources Conservation Service. 2004b. The PLANTS database, version 3.5. National Plant Data Center, Baton Rouge, Louisiana.

Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon, and organic matter. Pp. 961–1010 in Methods of soil analysis. Part 3. Chemical Methods. (D. L. Sparks, ed.). SSSA Book Series: 5. Soils Science Society of America, Book Series 5:1–1390.

Oklahoma Climatological Survey. 2003. Mesonet data. Oklahoma Climatolocal Survey, University of Oklahoma, Norman.

Orians, G. H., and O. T. Solbrig (eds.). 1977. Convergent evolution in warm deserts. Dowden, Hutchinson, and Ross, Inc., Pennsylvania.

Orrock, J. L., J. F. Pagels, W. J. McShea, and E. K. Harper. 2000. Predicting presence and abundance of a small mammal species: the effect of scale and resolution. Ecological Applications 10:1356–1366.

Paulson, D. D. 1988. *Chaetodipus hispidus*. Mammalian species 320:1–4.

Peet, R. K., R. G. Knox, J. S. Case, and R. B. Allen. 1988. Putting things in order: the advantages of detrended correspondence analysis. American Naturalist 131:924–934.

Potter, K. N., H. A. Torbert, H. B. Johnson, and C. R. Tischler. 1999. Carbon storage after long-term grass establishment on degraded soils. Soil Science 164:718–725.

Rowell, D. L. 1994. The determination of the density of soil particles. Pp. 66–67 in Soil science: methods and applications. Longman Scientific & Technical, England.

SAS Institute Inc. 2002. SAS/STAT user's guide. Version 9.01. SAS Institute Inc., Cary NC, USA.

Schramm, P., and B. J. Willcutts. 1983. Habitat selection of small mammals in burned and unburned tallgrass prairie. Pp. 49–55 in Eighth North American prairie conference. (R. Brewer, ed.). Western Michigan University, Kalamazoo.

Schuman, G. E., J. D. Reeder, J. T. Manley, R. H. Hart, and W. A. Manley. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecological Applications 9:65–71.

Schlesinger, W.H. 1986. Changes in soil carbon storage and associated properties with disturbance and recovery. Pp. 194–220 in The changing carbon cycle: a global analysis (J. R. Trabalka, and D. E. Reichle, eds.). Springer-Verlag, New York.

Severinghaus, W. D., R. E. Riggins, and W. D. Goran. 1980. Effects of tracked vehicle activity on terrestrial mammals and birds at Fort Knox, Kentucky. Transactions of the Kentucky Academy of Sciences 41:15–26.

Silva, M. 2001. Abundance, diversity, and community structure of small mammals in forest fragments in Prince Edward Island National Park, Canada. Canadian Journal of Zoology 79: 2063–2071.

Sims, J. T. 1996. Lime requirement. P. 491–515 in Methods of soil analysis. Part 3. Chemical Methods (D.L. Sparks, ed.). Soil Science Society of America Book Series 5:1–1390.

Spencer, J. R., and G. N. Cameron. 1982. *Reithrodontomys fulvescens* Mammalian Species 174:1–7.

ter Braak, C. J. F. 1987. Ordination. Pp. 91–173 in Data analysis in community ecology (R. H. Jongman, C. J .F. ter Braak, and O. F. R. van Tongeren, eds.). Pudoc, Wageningen, The Netherlands.

ter Braak, C. J. F., and P. Šmilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York.

ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57:255–289.

Thomas, W. T. 1982. Needs for and approaches to wildlife habitat assessment. Transactions of the North American Wildlife and Natural Resources Conference 47:35-46.

Tiessen, H., J. W. B. Stewart, and J. R. Bettany. 1982. Cultivation effects on the amounts and concentration of carbon, nitrogen, and phosphorus in grassland soils. Agronomy Journal 74:831–835.

Tyrl, R. J., T. G. Bidwell, and R. E. Masters. 2002. Field guide to Oklahoma plants. Oklahoma State University, Stillwater.

United States Department of Agriculture. 1954. Diagnosis and improvement of saline and alkali soils. Agriculture Handbook no. 60. United States Department of Agriculture, Riverside, California.

Vepraskas, M. J. 1994. Plant response mechanisms to soil compaction. Pp. 263–287 in Plant-environment interactions (R. E. Wilkinson ed.). Marcel Dekker, Inc., New York.

White, P. S. and S. T. A. Pickett. 1985. Natural Disturbance and patch dynamics: an introduction. Pp. 3–13 in (S. T. A. Pickett and P. S. White eds.), The ecology of natural disturbance and patch dynamics. Academic Press, Inc., Orlando.

Table 1. Soil and vegetation characteristics ($\bar{X}$ ± SD) of sampling locations at Fort Sill, Oklahoma, soil series (F -Foard, L -Lawton).

Soil series-Location	Plant height (cm)	Litter depth (cm)	Angle of obstruction (degrees)	Bare ground	Carbon	Track cover	Plant richness
				(%)			
F-1	79 ± 19	13 ± 7	87 ± 35	3 ± 9	1.6 ± 0.2	3 ± 9.9	61
F-2	80 ± 13	11 ± 5	86 ± 32	6 ± 7	1.5 ± 0.1	0.5 ± 2.7	42
F-3	66 ± 18	2 ± 2	83 ± 30	27 ± 14	0.9 ± 0.2	36 ± 30.4	65
F-4	46 ± 27	1 ± 2	64 ± 30	85 ± 22	0.5 ± 0.1	98 ± 0.0	43
F-5	79 ± 6	3 ± 2	85 ± 14	26 ± 16	0.8 ± 0.1	35 ± 28.0	66
L-1	102 ± 13	7 ± 5	88 ± 28	11 ± 6	1.2 ± 0.1	10 ± 17.4	53
L-2	92 ± 15	8 ± 5	88 ± 25	8 ± 9	1.2 ± 0.2	11 ± 21.7	60
L-3	108 ± 27	6 ± 4	88 ± 23	11 ± 10	2.9 ± 0.4	17 ± 23.9	71
L-4	116 ± 17	5 ± 4	89 ± 20	7 ± 8	2.4 ± 0.4	17 ± 25.6	70
L-5	93 ± 13	4 ± 2	88 ± 31	10 ± 9	2.2 ± 0.2	20 ± 20.0	65

Table 2. Total small mammal captures, number of individuals, and richness resulting from 4,800 trap nights at 10 locations varying in disturbance across Fort Sill, Oklahoma. Soil series, (F -Foard, L -Lawton).

		Location										
Species	Captures	F-1	F-2	F-3	F-4	F-5	L-1	L-2	L-3	L-4	L-5	Total
Chaetodipus hispidus	Total	0	0	14	13	9	0	0	0	0	0	36
	Individuals	0	0	6	9	7	0	0	0	0	0	22
Peromyscus leucopus	Total	0	1	0	6	4	0	0	3	1	1	16
	Individuals	0	1	0	1	3	0	0	3	1	0	9
Peromyscus maniculatus	Total	6	4	11	45	5	1	2	20	19	7	120
	Individuals	4	4	7	18	4	1	2	8	9	5	62
Reithrodontomys fulvescens	Total	0	0	0	0	0	1	2	9	21	4	37
	Individuals	0	0	0	0	0	1	2	13	6	3	25
Reithrodontomys montanus	Total	1	5	3	0	1	0	1	1	3	1	16
	Individuals	1	3	2	0	1	0	1	3	1	1	13
Sigmodon hispidus	Total	35	67	6	4	5	127	126	194	126	158	848
	Individuals	25	32	4	4	5	31	43	44	79	62	329
Spermophilus tridecenlineatus	Total	0	0	1	0	0	0	0	0	0	0	1
	Individuals	0	0	1	0	0	0	0	0	0	0	1
	Total											1074
	Individuals											461
	Richness	3	4	5	4	5	3	4	5	5	5	7

Table 3. Characteristics of the 40 most important plant species as calculated by importance values on an anthropogenically disturbed mixed prairie. DCA axis 1 species scores indicate the central point of that species' distribution in ordination space. Greater species scores indicate more intense disturbance. Life history traits: longevity (A-Annual, P-Perennial), life form (F-Forb, G-Grass, L-Legume), stature (T-Tall, M-Mid, S-Short, W-Woody), seral stage late, (E-Early, M-Mid, L-Late) (Tyrl et al. 2002, NRCS 2004b).

Species	DCA axis 1 species score	Importance value	Life history	Seral stage
Desmanthus illinoensis	-1.1	12.4	PLM	L-E
Monarda clinopodioides	-1.1	11.2	AFM	M
Amorpha canescens	-0.8	19.3	PLW	L
Elymus canadensis	-0.8	20.1	PGT	M-L
Panicum virgatum	-0.6	35.3	PGT	L
Ruellia humilis	-0.4	25.1	PFS	M-L
Helianthus maximiliani	-0.3	42.9	PFT	L
Psoralidium tenuiflorum	-0.3	72.6	PLM	L
Andropogon gerardii	0.0	25.7	PGT	L
Galium virgatum	0.0	18.6	AFS	E
Oxalis corniculata	0.0	16.9	AFS	M-L
Dichanthelium oligosanthes var. scribnerianum	0.4	122.8	PGM	M-L
Krameria lanceolata	0.4	32.5	PFM	M-L
Sporobolus compositus	0.4	140.7	PGT	M-L
Solidago missouriensis	0.5	20.7	PFM	M
Schizachyrium scoparium	0.6	193.8	PGM	L
Symphyotrichum ericoides	0.6	83.2	PFM	L-E
Erigeron strigosus	0.9	14.8	AFM	E-M
Mimosa nuttallii	0.9	47.9	PLM	L-E
Sorghastrum nutans	0.9	101.2	PGT	L
Calylophus serrulatus	1.1	32.2	PFM	M-L
Ambrosia psilostachya	1.3	96.6	AFS	M-L
Aster sp.	1.3	48.7	PFS	L-E
Hedyotis nigricans	1.3	29.7	PFS	L-E
Sporobolus cryptandrus	1.5	26.2	PGM	E-M
Yucca glauca	1.5	18.7	PFW	M-L
*Bromus japonicus**	1.6	67.1	AGM	E
Bouteloua hirsuta	2.0	14.2	PGS	M-L
Bouteloua curtipendula	2.1	14.7	PGM	M-L
Amsonia ciliata	2.3	19.0	PFS	E
Guara coccinea	2.5	13.6	PFM	E-M
Plantago wrightiana	2.5	15.6	PFS	E-M
Amphiachyris dracunculoides	2.6	18.9	AFM	E-M
Chaetopappa asteroides	2.8	14.1	AFS	E

Table 3 continued.

Species	DCA Axis 1 species score	Importance value	Life history	Seral stage
Plantago elongata	2.8	14.2	AFS	E-M
Juncus sp.	2.9	18.5	PGM	L
Liatris punctata var nebraskana	3.0	14.4	PFM	M-L
Thelesperma filifolium	3.1	27	PFM	E-M
Hordeum pusillum	3.6	21.9	AGS	E
Plantago patagonica	3.7	30.4	AFS	E-M

* Introduced species.

Figure Legends

Fig. 1.—Permanent sampling design used in each of 10 study locations to access small mammals and plants. A 3 x 5 small mammal trapping grid was established between vegetation transects (✩ = 1 station). Plant and soil sampling was done in 1 x 1-m quadrats and scaled up to 60 m^2.

Fig. 2.—Short-term (track-cover) disturbance as function of long-term (soil organic carbon), which occurred on Foard soil but on Lawton soil ($P = 0.08$).

Fig. 3.—Plot of small mammal sample scores produced by detrended correspondence analysis (DCA). Polygons were drawn around samples of the same soil series. Axis 1 species and samples appeared to be influence by an interaction of soil with vehicular disturbance. Eigenvalues for axis 1 and 2 were 0.468 and 0.042 with total inertia of 0.600; axis 1 and 2 accounted for 78% and 7% of the variance in species data, respectively.

Fig. 4.—Abundances of 4 small mammal species as predicted by long-term disturbance (carbon): a) greater abundances of *S. hispidus* were recorded with less disturbance on both soil series; b) greater abundances of *P. maniculatus* occurred with increased disturbance at locations on Foard soil, but there was no relationship on Lawton soil ($P = 0.12$); c) greater abundances of *C. hispidus* occurred with increased disturbance on Foard soil; and d) greater abundances of *R. fulvescens* occurred in less disturbance locations on Lawton soil.

Fig. 5.—Abundances of 4 small mammal species as predicted by short-term disturbance (track-cover): a) *S. hispidus* demonstrated a relationship on soil series, but the Lawton relationship was mildly significant; b) greater abundances of *P. maniculatus* occurred with more disturbance at locations on Foard soil, but there was no relationship on Lawton soil (*P* = 0.10); c) greater abundances of *C. hispidus* increased with short-term disturbance on Foard soil; and d) no relationship was detected for *R. fulvescens* on Lawton soil (*P* = 0.41).

Fig.6.—Species richness of small mammal as a function of plant species richness, which occurred on Lawton soil but not on Foard soil (*P* = 0.74).

Fig. 7.—Abundances of 4 small mammal species as predicted by plant species composition (DCA axis 1): a) abundances of *S. hispidus* decreased with change in plant species compositon (DCA axis 1) across soil series, but those on Foard soil were not (*P* = 0.12); b) *P. maniculatus* increased with change in plant species composition on Foard soil, but not on Lawton soil (*P* = 0.11); c) C. *hispidus* increased with change in plant species composition on Foard soil; and d) *R. fulvescens* decreased with change in plant species composition on Lawton soil.

Fig. 8.—Conceptual model of a small mammal community response to disturbance in mixed prairie: long-term disturbance refers to soil carbon relationships and short-term disturbance refers to track-cover. Soil disturbance

by military vehicles results in levels of carbon fluctuation intermediate to the effects of cultivation and grazing or fire (Frank et. al. 1995, Schuman et. al. 1999, Johnson et. al. 2001). Because I recorded a narrow range of short-term disturbance on Lawton soil, I was only able to hypothesize the relationships that would result following short-term disturbance events..

Fig. 1.

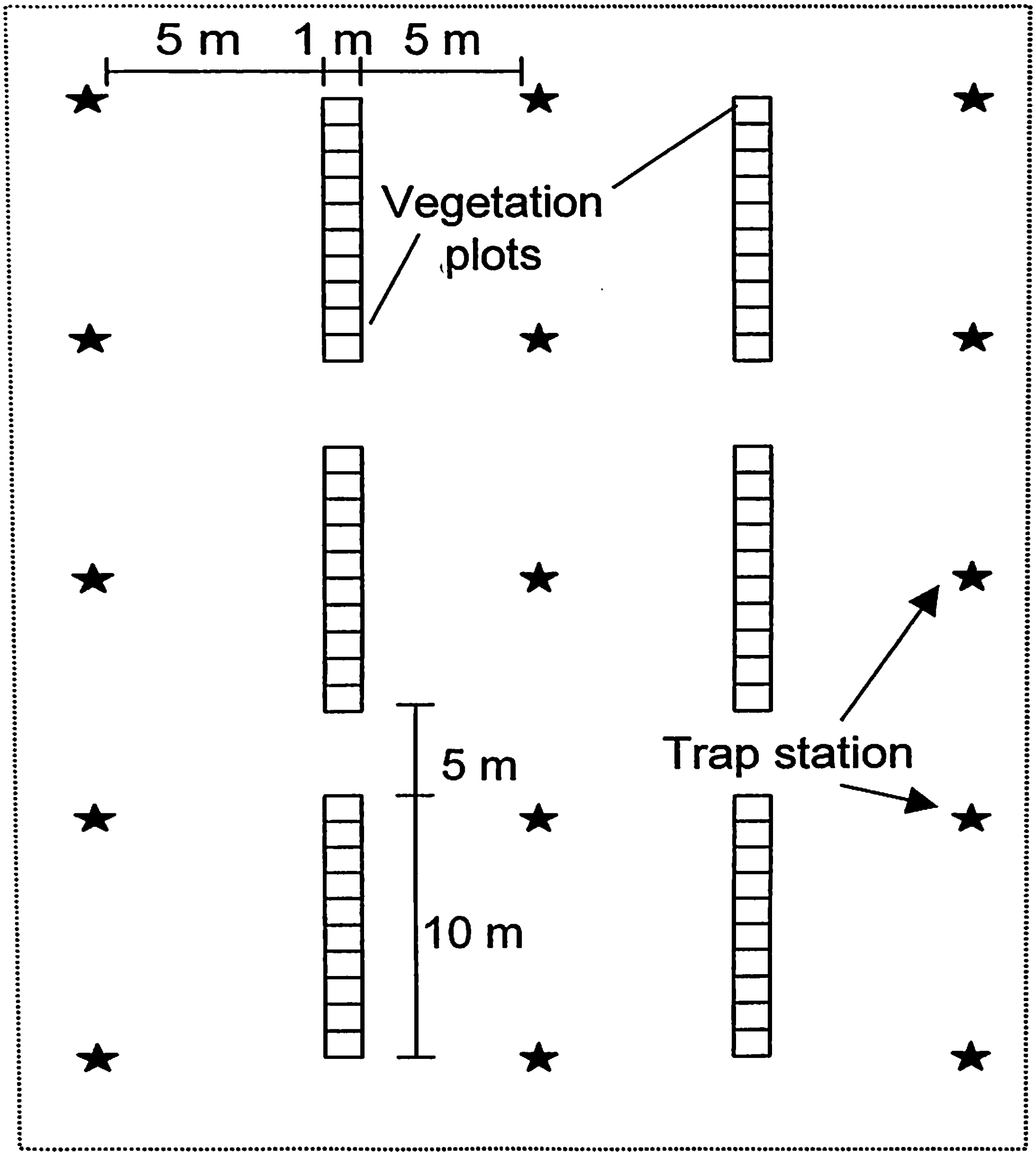


Fig. 2.

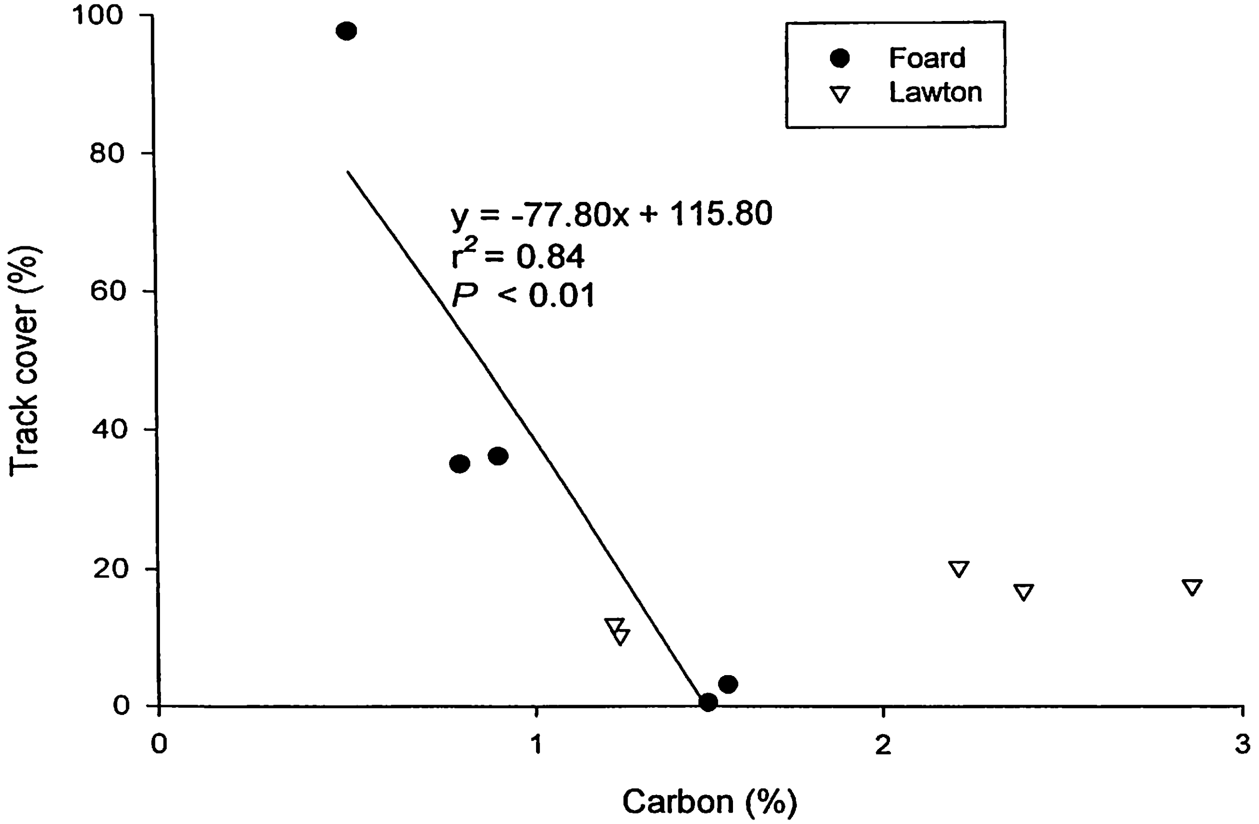

100
80
60
40
20
0
0
1
2
3
Track cover (%)
Carbon (%)
● Foard
▽ Lawton
y = -77.80x + 115.80
r² = 0.84
P < 0.01

Fig. 3.

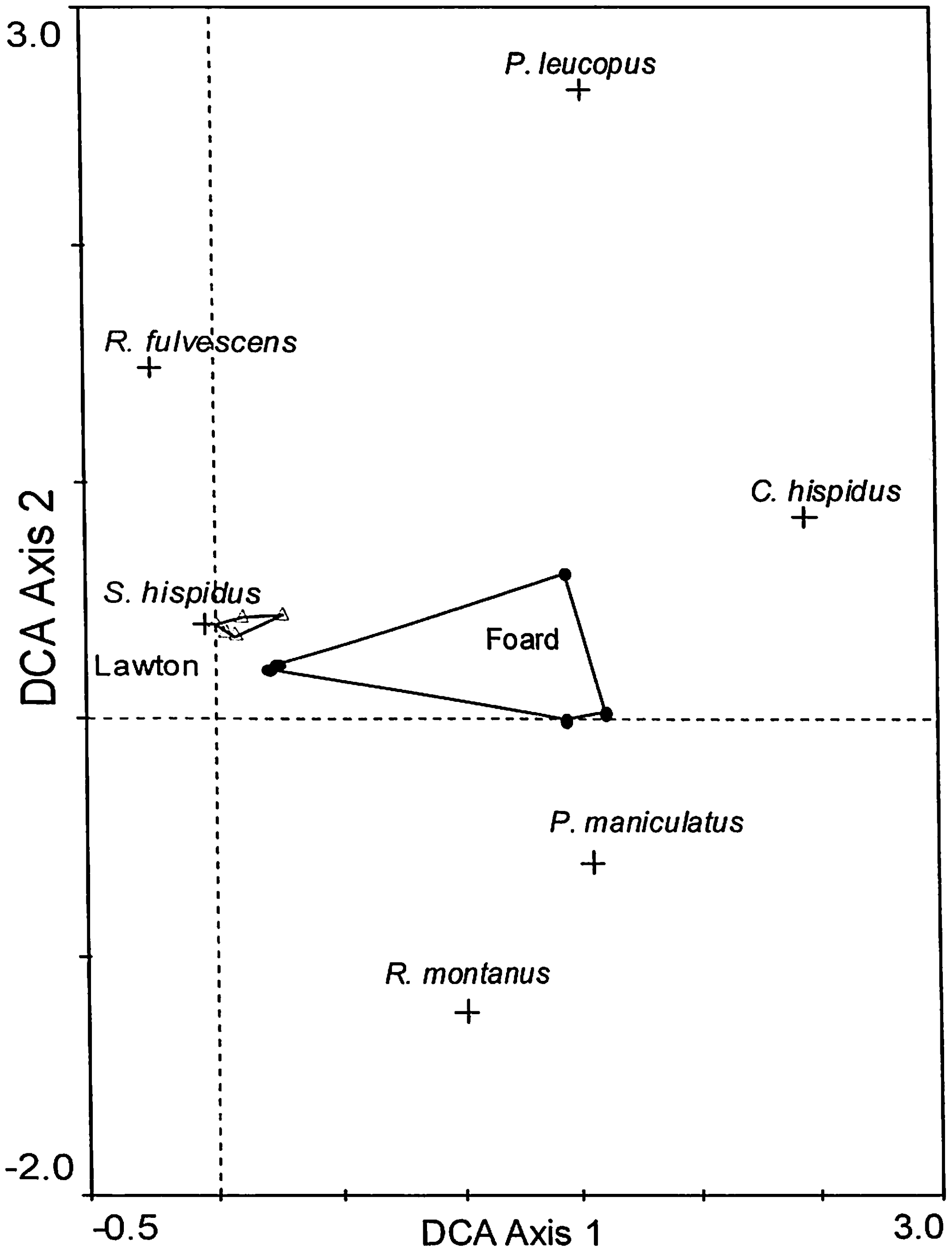
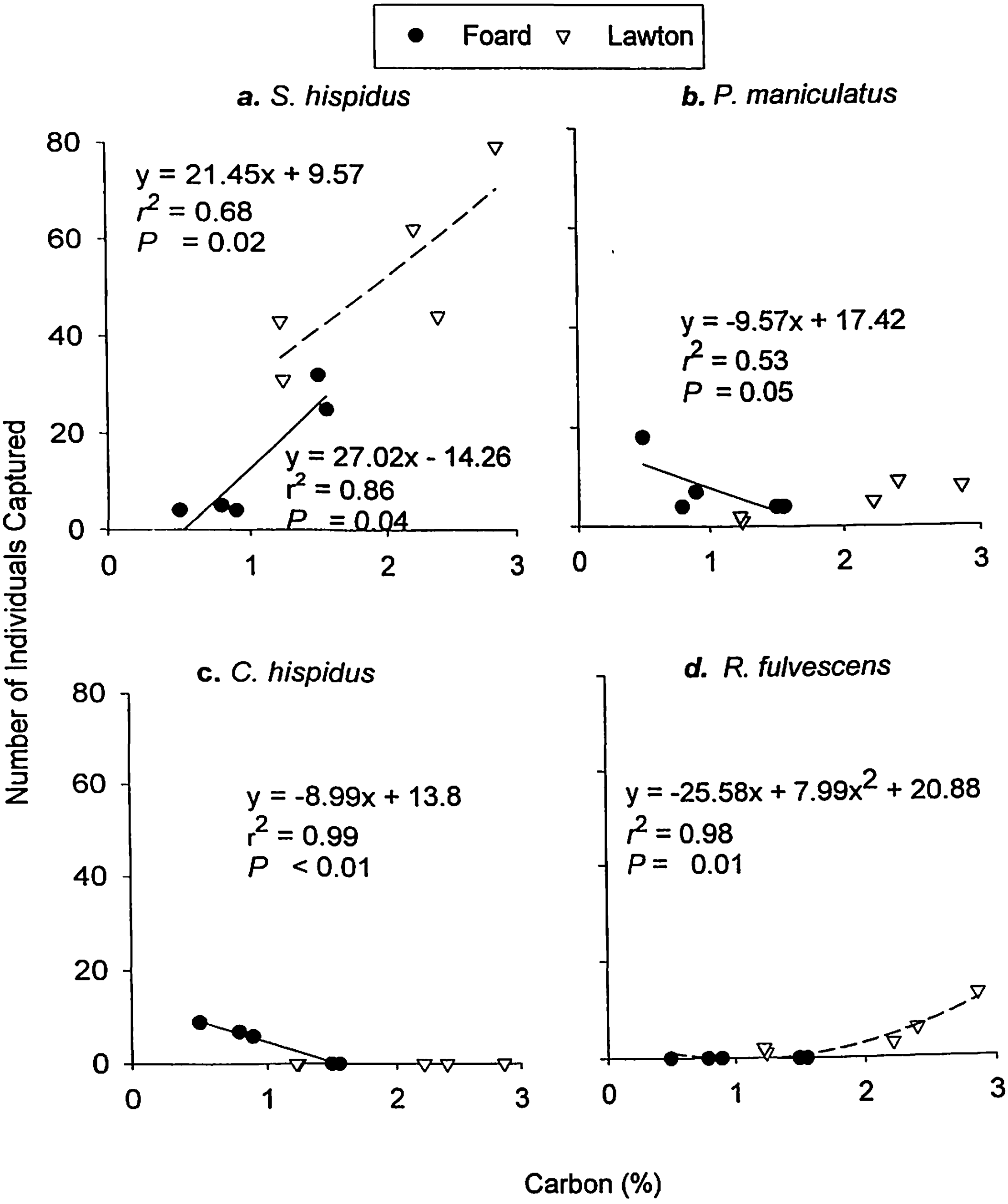

3.0
P. leucopus
R. fulvescens
C. hispidus
S. hispidus
Foard
Lawton
DCA Axis 2
P. maniculatus
R. montanus
-2.0
-0.5
DCA Axis 1
3.0

Fig. 4.



● Foard ▽ Lawton
a. S. hispidus
b. P. maniculatus
c. C. hispidus
d. R. fulvescens
y = 21.45x + 9.57
r2 = 0.68
P = 0.02
y = 27.02x - 14.26
r2 = 0.86
P = 0.04
y = -9.57x + 17.42
r2 = 0.53
P = 0.05
y = -8.99x + 13.8
r2 = 0.99
P < 0.01
y = -25.58x + 7.99x2 + 20.88
r2 = 0.98
P = 0.01
0
20
40
60
80
0
1
2
3
Number of Individuals Captured
Carbon (%)

Fig. 5.

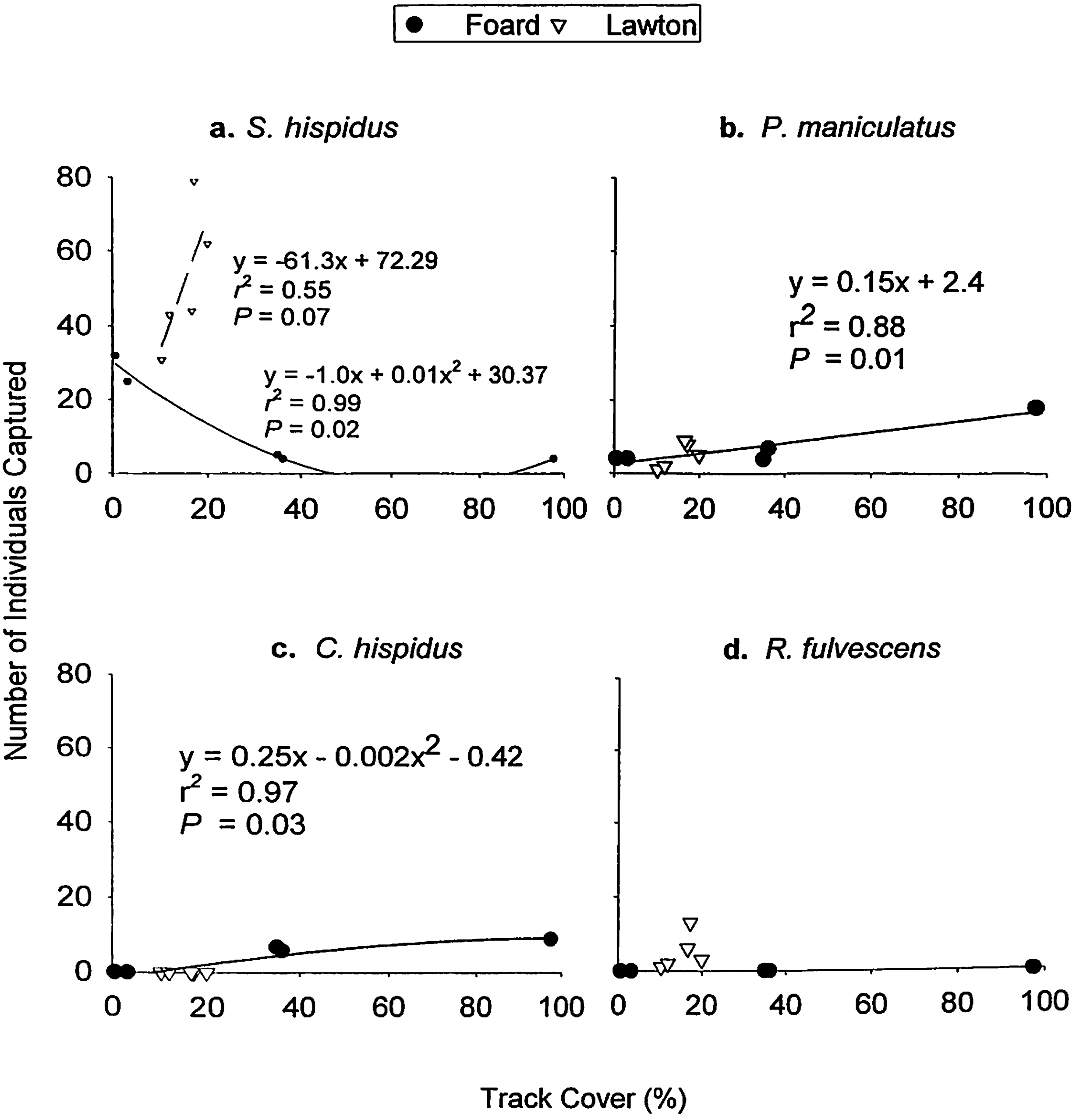

● Foard ▽ Lawton
a. S. hispidus
b. P. maniculatus
c. C. hispidus
d. R. fulvescens
y = -61.3x + 72.29
r² = 0.55
P = 0.07
y = -1.0x + 0.01x² + 30.37
r² = 0.99
P = 0.02
y = 0.15x + 2.4
r² = 0.88
P = 0.01
y = 0.25x - 0.002x² - 0.42
r² = 0.97
P = 0.03
0
20
40
60
80
100
Number of Individuals Captured
Track Cover (%)

Fig. 6

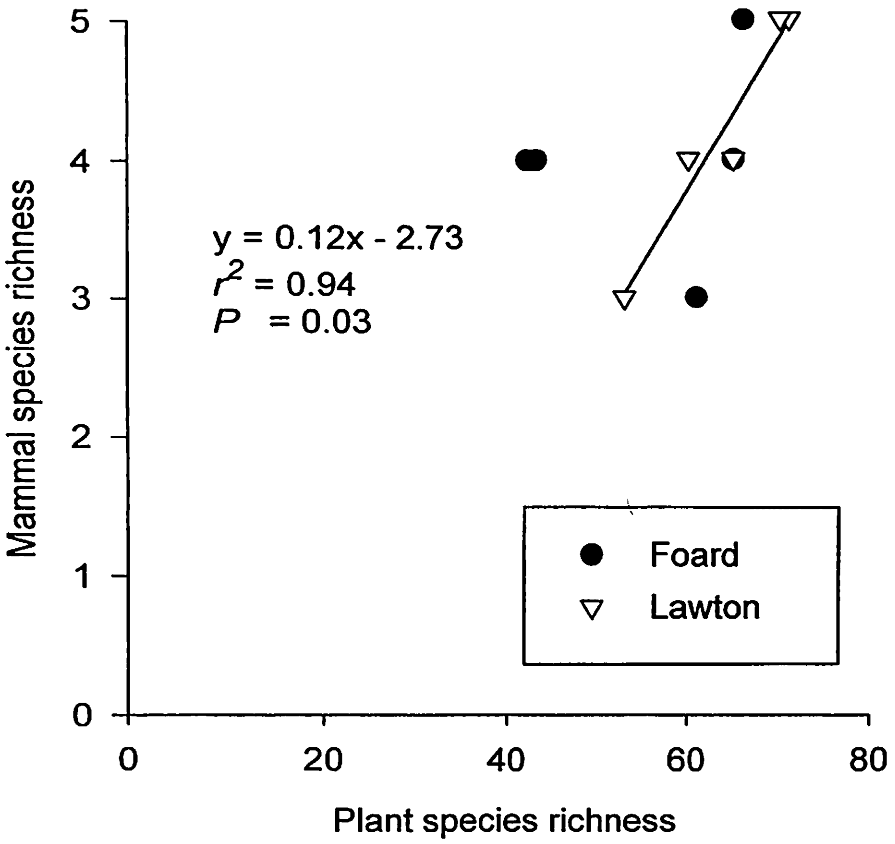

y = 0.12x - 2.73
r^2 = 0.94
P = 0.03
Foard
Lawton
Mammal species richness
Plant species richness
0
1
2
3
4
5
0
20
40
60
80

Fig. 7.

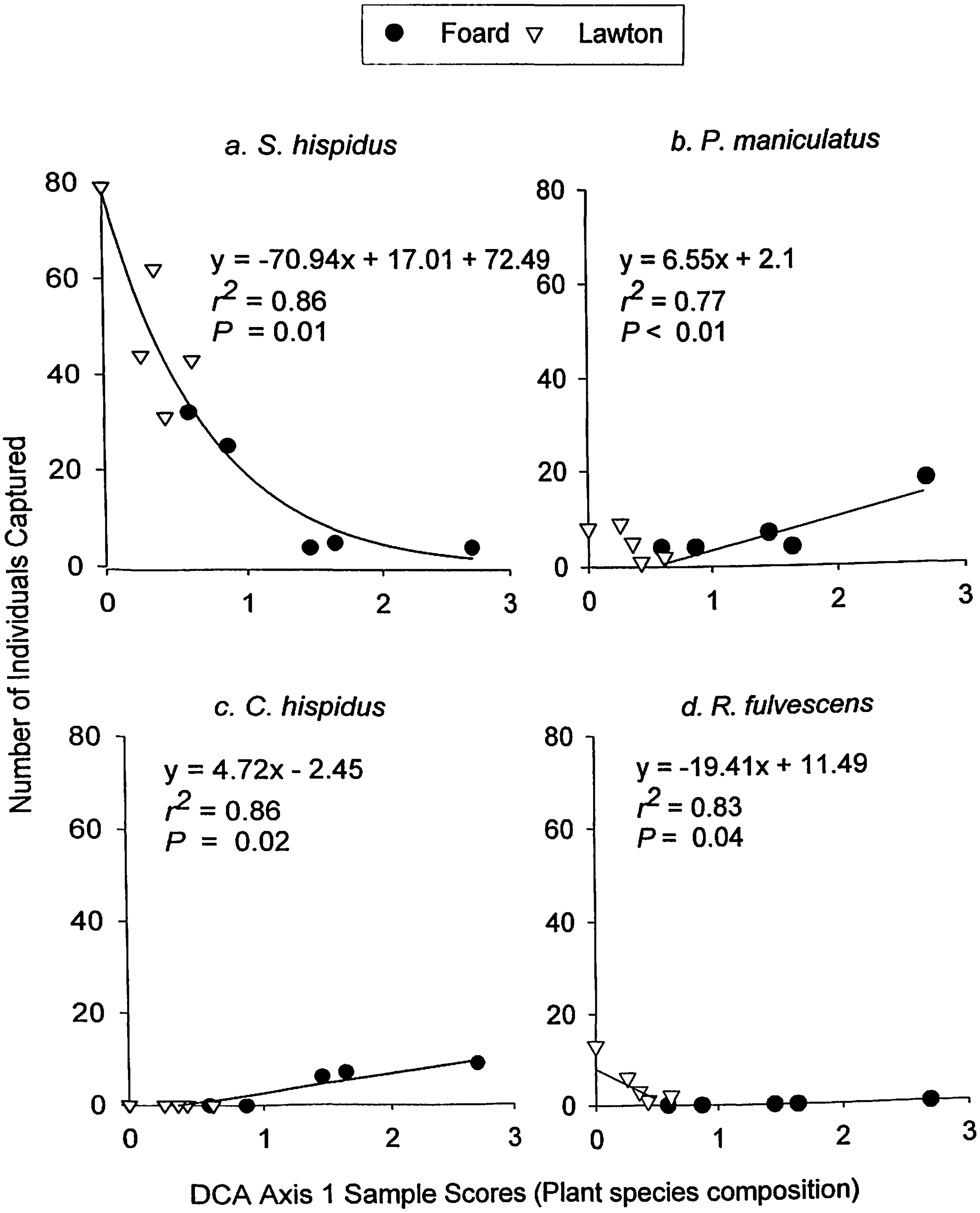
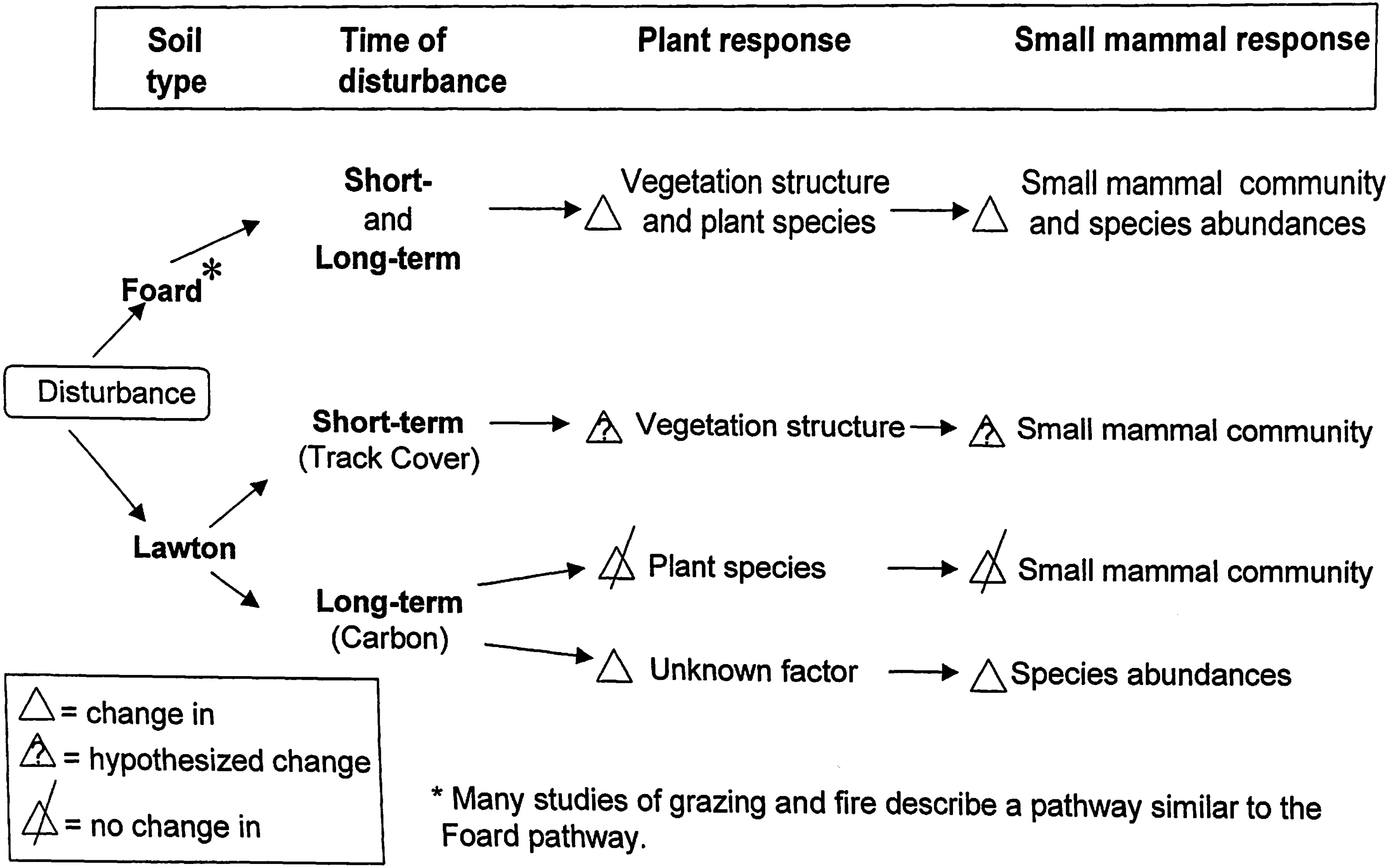

● Foard ▽ Lawton
a. S. hispidus
y = -70.94x + 17.01 + 72.49
r2 = 0.86
P = 0.01
b. P. maniculatus
y = 6.55x + 2.1
r2 = 0.77
P < 0.01
c. C. hispidus
y = 4.72x - 2.45
r2 = 0.86
P = 0.02
d. R. fulvescens
y = -19.41x + 11.49
r2 = 0.83
P = 0.04
0
20
40
60
80
0
1
2
3
Number of Individuals Captured
DCA Axis 1 Sample Scores (Plant species composition)

Fig. 8.



* Many studies of grazing and fire describe a pathway similar to the Foard pathway.

APPENDIX

Species recorded at 10 sampling locations across Fort Sill during spring and fall 2003. Species are listed in alphabetical order.

Acalypha
Acalypha monococca
Achillea millefolium
Aegilops cylindrica
Allium sp.
Ambrosia artemiisofolia var. elatior
Ambrosia psilostachya var. lindheimerana
Amorpha canescens
Amsonia ciliata
Andropogon gerardii
Apiaceae
Apocynum cannabinum
Aristida oligantha
Aristida purpurea
Aristida purpurascens
Artemisa ludoviciana var. mexicana
Asclepias asperula ssp. capricornu
Asclepias stenophylla
Asclepias verticillata
Aster oblongifolium
Aster sp.
Baptisia australis var. minor
Baptisia bracteata var. glabrescens
Bothriochloa saccharoides var. torreyana
Bouteloua curtipendula
Bouteloua gracilis
Bouteloua hirsuta
Brickellia eupatorioides var. corymbulosa
Bromus japonicus
Buchloe dactyloides
Callirhoe involucrata
Calylophus berlandieri ssp. pinifolius
Calylophus serrulatus
Capsella bursa-pastoris
Carex sp.
Celtis laevigata
Centaurea americana
Chaetopappa asteroides
Chamecrista fasciulata
Chaerophyllum tainturieri
Chamaesyce prostrata
Cirsium undulatum
Conyza canadensis var. canadensis
Conyza canadensis var. glabrata
Coreopsis lancolata
Coreopsis tinctoria
Croton capitatus
Croton sp.
Croton texensis
Cuscuta sp.
Dalea candida
Dalea enneandra
Dalea multiflora
Dalea purpurea
Dalea sp.
Danthonia spicata
Daucus pusillus
Desmanthus illinoensis
Desmanthus leptolobus
Dichanthelium oligosanthes var. scribnerianum
Diodia teres
Echinacea angustifolia
Eleocharis baldwinii
Elymus canadensis
Elytrigia reptans
Eragrostis capillaris

Eragrostis curtipedicellata
Eragrostis intermedia
Eragrostis sessilispica
Eragrostis spectabilis
Erigeron annuus
Erigeron sp.
Erigeron strigosus
Eriogonum longifolium
Euphorbia marginata
Euphorbia spathulata
Evolvulus pilosus
Foeniculum vulgare
Froelichia gracilis
Galium virgatum
Gaura coccinea
Geranium carolinianum
Grindelia papposa
Gutierrezia dracunculoides
Hedeoma hispida
Hedyotis nigricans
Helenium amarum
Helianthus annuus
Helianthus maximiliani
Helianthus sp.
Heterotheca canescens
Hordeum pusillum
Hypericum drummondii
Juncus sp.
Koeleria macrantha
Krameria lanceolata
Krigia dandelion
Lactuca serriola
Lamiaceae
Lepidium virginica
Leptochloa cognatum
Lespedeza capitata
Lesquerella gracilis
Lesquerella sp.
Liatris punctata var. nebraskana
Linum rigidum
Linum sulcatum
Lithospermum incisum
Lobelia puberula
Mimosa nuttallii
Monarda clinopodioides
Monarda fistulosa
Muehlenberia capillaris
Nassella leucotricha
Neptunia lutea
Nothoscordum bivalve
Oenothera laciniata
Onagraceae sp.
Opuntia macrorhiza
Oxalis corniculata
Packera plattensis
Palafoxia rosea
Panicum capillare
Panicum cur
Panicum obtusum
Panicum virgatum
Panium dichotomiflorum
Paspalum distichum
Penstemon sp.
Phalaris caroliniana
Physalis sp.
Plantago elongata
Plantago patagonica
Plantago rhodosperma
Plantago sp.
Plantago wrightiana
Poa arachnifera
Polygonum tenue
Polytaenia nuttallii
Prunus angustifolia
Psoralidium tenuiflorum
Ptilimnium capillaceum
Ratibida columnifera
Rayjacksonia annua
Rudbeckia hirta
Ruellia humilis
Sabita campestris
Salvia azurea
Schizachyruim scoparium
Scutellaria wrightii
Senecio vulgaris
Silphium laciniatum
Sisyrinchium angustifolium
Solanum dimidaiatum
Solanum rostratum
Solidago missouriensis
Sorghastrum nutans
Sorghum halepense

Sporobolus compositus
Sporobolus cryptandrus
Sporobolus pyramidatus
Stenosiphon linifolius
Stillingia sylvatica
Symphoricarpos orbiculatus
Symphyotrichum ericoides
Talinum parviflorum
Tephrosia virginiana
Thelesperma filifolium
Toxicodendron radicans
Tradescantia ohiensis
Tragia betonicifolia
Tragopogon dubius
Tridens albescens
Tridens flavus
Triodanis leptocarpa
Veronia baldwinii
Vulpia octoflora
Xanthisma texanum
Yucca glauca
unk15
unk19
unk24
unk30
unk36
unk38
unk48
unk49
unk53
unk59
unk64

VITA

Sherry Ann Leis

Candidate for the Degree of

Master of Science

Thesis: EFFECTS OF MILITARY TRAINING ON SOIL, VEGETATION, AND THE SMALL MAMMAL COMMUNITY IN A MIXED PRAIRIE

Major field: Plant and Soil Science

Biographical:

Personal data: Born in Sheboygan Falls, Wisconsin, On April 16, 1973.

Education: Graduated from Sheboygan Falls High School, Sheboygan Falls, Wisconsin in June 1991; received Bachelor of Science degrees in Anthropology and Environmental Biology from Beloit College, Beloit, Wisconsin in May 1995. Completed the requirements for the Master of Science degree with a major in Plant and Soil Science at Oklahoma State University in December 2004.

Experience: Worked as an agroforester in Gambia, West Africa as a Peace Corps Volunteer 1995-97; worked as an environmental educator at the Ellwood H. May Environmental Park, Sheboygan, Wisconsin, 1999-2000; worked as a prairie restoration assistant with the Aldo Leopold Foundation, Baraboo, Wisconsin, 2000; employed by the Institute of Ecosystem Studies as a research assistant to the director, Millbrook, New York, 2000-2002; employed as a research assistant at Oklahoma State University, Department of Plant and Soil Sciences, 2002-2004.

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