VEGETATION DYNAMICS FOLLOWING CESSATION OF SEVERE DISTURBANCE IN AN OLD FIELD

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NOMENCLATURE

Plant nomenclature follows Great Plains Flora Association (1986)

CHAPTER I

THE IMPORTANCE OF TOPOEDAPHIC GRADIENTS IN AN OKLAHOMA OLD FIELD

Abstract

Topography often dictates soil resource availability in grasslands. Our objective was to determine if an old-field grassland that exhibited little topographic variation had an underlying soil nitrogen gradient. To address this objective, we evaluated the relationship between species canopy cover and topoedaphic variables (soil solution chemistry, soil texture, and spatial attributes). Species canopy cover was sampled within 3, 1 x 1-m quadrats on 16, 40 x 40-m plots. A soil sample was collected in the center of each quadrat at two depths (0 to 15 cm and 15 to 30 cm) and analyzed for soil solution chemistry, and soil texture. Locations for each quadrat were determined by measuring an easting and northing distance from a fixed point, and elevation was determined using a transit level. Even though little measurable topographic variation was evident across the study area, the dominant spatial gradients were correlated with nitrogen. When the influence of the topoedaphic gradients was removed, underlying gradients of phosphorus and pH emerged.

Introduction

Old fields have been used as the classic system for modeling secondary successional dynamics of grasslands (Albertson and Tomanek 1965; Collins and Adams 1983; Inouye et al. 1987). Old fields are a unique type of grassland resulting from cultivation, abandonment, and natural revegetation. Natural revegetation of old fields serves as a template for studies of grassland processes. Old-field vegetation is influenced by competition (Tilman 1982; Cahill 1999), allelopathy (Wilson and Rice 1968; Stowe 1979), fire (Collins et al. 1995; Engle et al. 2000), and herbivory (Collins 1987; Hartnett and Fay 1998). As in other terrestrial ecosystems, natural heterogeneity of plant-available soil nutrients via topographic variation likely influences vegetation dynamics, but the topic has received little attention.

Old fields have also been used to investigate the plant-soil relationships of secondary succession on nutrient-poor soils (Christensen and MacAller 1985; Kalisz 1986; Pastor et al. 1987; Robertson et al. 1988; Dormaar et al. 1990; Gross et al. 1995). Soil properties, including nitrogen (Wedin and Tilman 1990; Knops and Tilman 2000), soil organic matter (Zedler and Zedler 1969), phosphorus, potassium, calcium, magnesium, and pH (Kalisz 1986) change during succession. For example, nitrogen is usually the most limiting nutrient to plant growth during the first 40 to 60 years of old-field succession (Gleeson and Tilman 1990), and through time resource limitation can shift from nitrogen to light availability (Tilman 1988).

Nitrogen limitation occurs in both tallgrass prairie (Risser et al. 1981; Knapp et al. 1998) and old fields (Pastor et al. 1987; Tilman 1988; Gleeson and Tilman 1990). Soil nitrogen is influenced by management practices, topography, and season (Abrams et al.

1986; Knapp et al. 1993; Turner et al. 1997). In many old fields, nutrients are lost because of cultivation, but through succession following cultivation, nutrient levels slowly recover. For example, in Minnesota old fields early-successional species were associated with low nitrogen levels and late-successional species were associated with high nitrogen levels (Tilman 1987). Topography influences a mobile nutrient such as nitrogen and management practices in combination with topography affect nitrogen availability. In tallgrass prairie of Kansas, nitrogen availability was greater on unburned upland sites than compared to burned lowland sites (Turner et al. 1997). Nitrogen availability also changes with season in that soil microbial activity occurs between soil temperatures of 10 and 60 °C (Brady and Weil 1999).

Although not a resource gradient, topography has been related to vegetation patterns in grasslands (Schimel et al. 1991; Knapp et al. 1993; Ruess and Seagle 1994; Turner et al. 1997), because topography influences soil chemistry. Nitrogen, in particular, is associated with a topographic gradient and can influence plant productivity and physiology in tallgrass prairie (Knapp et al. 1993; Turner et al. 1997). The relationship of topography with nitrogen and thus with vegetation composition in old fields is uncertain. In grasslands lacking clearly discernable drainage patterns (i.e. uplands and lowlands), one might expect topoedaphic gradients other than topography to influence vegetation. Hence, we examined a nutrient-poor old field that exhibited relatively little topographic variation to test the hypothesis that nitrogen, exclusive of topography, is the overlying gradient upon which vegetation is distributed.

Methods

The study area is located in Pontotoc County, Oklahoma, which is owned and maintained by the United States Environmental Protection Agency, Robert S. Kerr Environmental Research Center in Ada, Oklahoma. The study area is abandoned farmland. At the time of cultivation, the old field was subjected to erosion, which resulted in losses of topsoil and soil nutrients. Following re-establishment of herbaceous vegetation, ca. 1950, and the old field was heavily grazed until January of 1998. The dominant soil consists of Burleson clay (fine, montmorillonitic, thermic, Udic Pellusterts) (USDA-SCS 1973), and the primary vegetation was dominated by the early to mid-seral species *Aristida oligantha*, *Andropogon virginicus*, *Ambrosia psilostachya*, and exotic species including *Festuca arundinacea* and *Cynodon dactylon.*

We sampled vegetation and soils in August of 1998. Three 1 x 1-m quadrats were sampled for species canopy cover per plot on 16, 40 x 40-m contiguous plots using the Daubenmire cover class method (Bonham 1989). A soil sample was collected in the center of each quadrat at two depths (0 to 15 cm and 15 to 30 cm), dried in a forced air oven at 60 °C, and ground to pass a 2 mm sieve. Soils were analyzed for nitrate-nitrogen, ammonium-nitrogen, potassium, phosphorus, organic matter, pH, and soil texture.

Methods described for soil analyses follow Zhang et al. (1998). Soil nitrate was extracted with 0.25% calcium sulfate, analyzed on a flow injection analyzer, and quantified by using cadmium reduction chemistry. Soil ammonium was extracted with indophenol blue on a flow injection analyzer. Soil potassium was extracted with 0.2% Mehlich III and analyzed using inductively coupled plasma. Soil phosphorus was extracted with the potassium extract and 0.267% ascorbic acid color complex and analyzed on a spectrophotometer at 880 nm. Organic matter was determined by the loss on-ignition method. Soil pH was measured with a glass electrode in a 1:1 soil:water solution. The hydrometer method was used to determine soil texture.

To determine the topographic changes across the study area, we measured an easting and northing distance and elevation at each quadrat. The southwest corner of the study area was the fixed point in which an easting distance and northing distance were measured. Elevation was determined using a transit level from two fixed points within the study area. The easting, northing, and elevation measurements provide a three-dimensional value for each quadrat, which was used to evaluate topographic differences across the study area (Fig. 1).

We analyzed the vegetation data with partial canonical correspondence analysis (pCCA) using CANOCO version 4 (ter Braak and Šmilauer 1998) to determine if there was a difference in soil properties by depth. We found that the 15 to 30 cm soil properties did not explain variation beyond that explained by the 0 to 15 cm soil properties (P=0.325). In a nutrient depleted old field that has lost topsoil to erosion, we determined it was unnecessary to analyze soil properties at two subsoil depths. The soil fractions of sand and clay were used in analysis and silt was removed because sand and clay were determined as the soil fractions that would most limit nutrient availability. This was done to avoid elimination of variables by CANOCO, because the program detects linear combinations of variables that add to 100%.

To determine how species are distributed on this old field, we investigated the relationship between vegetation and topoedaphic variables with canonical correspondence analysis (CCA) using CANOCO. CCA is a direct gradient analysis that constructs ordination axes from linear combinations of environmental variables that maximize species scores (Jongman et al. 1995). The topoedaphic variables used in this analysis were nitrate-nitrogen, ammonium-nitrogen, potassium, phosphorus, organic matter, pH, soil texture, easting, northing, and elevation. In the event that we found a topographic gradient was important in vegetation distribution, we wanted to identify the underling important soil properties. Hence, we used pCCA to factor out the influence of topographic variation.

Results

Our results indicate a two-tiered system of soil-related gradients influenced vegetation. The first tier consisted of topographic gradients, which explained much of the vegetation distribution in this old field (Table 1). The topographic gradients were two-dimensional and represent the east-west (CCA Axis 1) and north-south (CCA Axis 2) topographic environmental variables (Fig. 2). Of the other soil variables contributing to vegetation distribution, nitrogen was correlated with the topographic gradient (Fig. 2), indicating that nitrogen varied topographically even with an average slope of 1% and relief of 3.1 m. Species associated with the easting gradient included *Amphiachyris dracunculoides* (Amdr), *Sporobolus asper* (Spas), *Croton texensis* (Crte), and species associated with the northing gradient included *Aristida oligantha* (Arol), *Carex*, and *Stylosanthes biflora* (Stbi) (Fig. 2).

The second tier of gradients, revealed by factoring out topographic variation, were phosphorus (pCCA Axis 1) and pH (pCCA Axis 2) (Fig. 3). Nitrogen was not an important environmental gradient in the ordination. *Sporobolus* and *Amphiachyris*, which were associated with the easting gradient, were associated with the phosphorus gradient when spatial variation was factored out (Fig. 3). *Festuca arundinacea* (Fear) was associated with the environmental variable of elevation, but with spatial variation removed *Festuca* was associated with the phosphorus gradient (Fig. 3).

Discussion

Among the topoedaphic gradients influencing plant community composition that we included in this study of old-field vegetation, topography was of primary importance. Topographic gradients influence resource availability of nitrogen and water in tallgrass prairie ecosystems (Turner et al. 1997). Nitrogen is usually the most limiting nutrient in grasslands, especially old fields (Inouye et al. 1987; Knops and Tilman 2000) and the variation in soil nitrogen influences vegetation. We found nitrogen was associated with topographic gradients, which indicated that the topography-nitrogen gradient was an important component in explaining old-field vegetation distribution.

Lacking distinct topographic variability in this old field, we expected minimal importance of topography as a gradient and we expected other gradients including nitrogen to emerge. Even with little topographic variation, topography remained the overlying gradient in explaining the distribution of species. In a suite of comprehensive studies on topoedaphic and plant relationships, studies on the Konza Prairie Research Natural Area in the Flint Hills of Kansas demonstrated the influence of topography on nitrogen availability, soil water availability, and aboveground biomass production (Schimel et al. 1991; Knapp et al. 1993; Benning and Seastedt 1995). The topographic variability is distinct between uplands and lowlands at Konza and relief within watersheds is usually 50 m with discernible changes in parent material (Knapp et al. 1993; Benning and Seastedt 1995; Briggs and Knapp 1995; Turner et al. 1997). Plant nitrogen concentration was highest on the uplands (Schimel et al. 1991), whereas total soil water was greatest on the lowland sites (Knapp et al. 1993; Benning and Seastedt 1995). In a 10-year study on the Konza Prairie, net primary production was greater on lowland sites compared to upland sites with seasonal evaporation most strongly correlated to aboveground biomass production (Benning and Seastedt 1995).

Our results show that in an old field with much less topographic variation than what occurs at Konza, nitrogen is not the most important variable, but rather nitrogen is dictated by topography. Topography results in subtle small-scale variability that can be difficult to detect even though it is well established that slight changes in toposequence can influence soil properties (Brady and Weil 1999). Hence, topography is a contributing factor to spatial heterogeneity of soil properties (Robertson et al. 1988; Gross et al. 1995) and topography can control the availability of mobile plant available nutrients in the soil.

One could expect a topographically homogeneous old field to have a dominating gradient other than nitrogen, because nitrogen is spatially arranged via topography. Removing the topographic gradients with pCCA, the primary underlying gradient was phosphorus and nitrogen was no longer a dominating soil gradient. This could be the result of the level of phosphorus, an immobile nutrient, was more related to land-use history, particularly cultivation, than to topography (James and Wells 1990; Brady and Weil 1999).

Floristic composition of this old field was dependent primarily on topoedaphic variation, such that the primary environmental gradient influencing old-field vegetation was topography associated with nitrogen. With slight changes in relief, we expected the topographic influence on vegetation distribution to be of secondary importance or possibly non-existent. However, we found topography to be an important environmental variable. Nitrogen was associated with topography and the interaction between these two variables was present at slopes ranging from 0 to 2%. The relationship between topographic variation and soil properties demonstrates the importance of soil spatial heterogeneity in arranging vegetation patterns, and supports hypotheses that plant communities are structured in response to plant available soil nutrients (Tilman 1982; Robertson et al. 1988; Tilman 1988). But when topographic variation was held constant, nitrogen was no longer a dominant soil property and the underlying gradient became phosphorus. Phosphorus is an immobile nutrient and phosphorus levels are a reflection of cultivation rather than topography as compared to nitrogen. The spatial pattern of vegetation in this old field was associated with a phosphorus gradient imbedded within a topography-nitrogen gradient.

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Table 1. Interset correlations between environmental variables with CCA axis 1 and 2 and pCCA axis 1 and 2 for a mid-successional old field. Bold axis scores indicate the variable most correlated with the respective axis.

Environmental Variable	CCA Axis 1	CCA Axis 2	pCCA Axis 1	pCCA Axis 2
Easting	**0.5840**	0.2028	----	----
Northing	0.4202	**-0.4287**	----	----
Elevation	-0.0906	-0.3987	----	----
Phosphorus	-0.3770	-0.2417	**-0.5801**	-0.0166
pH	0.5618	-0.2762	0.3092	**-0.5590**
Nitrate (NO_3-N)	0.3002	0.0352	0.4044	-0.1091
Ammonium (NH_4-N)	-0.5563	-0.0211	-0.3743	0.1845
Potassium	0.1753	-0.2824	0.0264	-0.2968
Organic matter	0.0625	-0.3013	-0.0877	-0.2181
Sand	-0.3998	0.1209	0.0211	0.2239
Clay	0.4665	-0.0839	0.1405	-0.1667

Table 2. Scientific names of species present in a mid-successional old field.

Species Code	Scientific Name	Canopy Cover (%)
Amdr	*Amphiachyris dracunculoides*	31
Amps	*Ambrosia psilostachya*	75
Anvi	*Andropogon virginicus*	48
Arol	*Aristida oligantha*	90
Aser	*Aster ericoides*	83
Bola	*Andropogon saccharoides*	63
Buda	*Buchloe dactyloides*	40
Carex	*Carex spp.*	8
Crte	*Croton texensis*	29
Cyda	*Cynodon dactylon*	46
Fear	*Festuca arundinacea*	35
Melu	*Medicago lupulina*	54
Pafl	*Paspalum floridanum*	6
Pasp	*Panicum sphaerocarpon*	31
Spas	*Sporobolus asper*	31
Stbi	*Stylosanthes biflora*	8

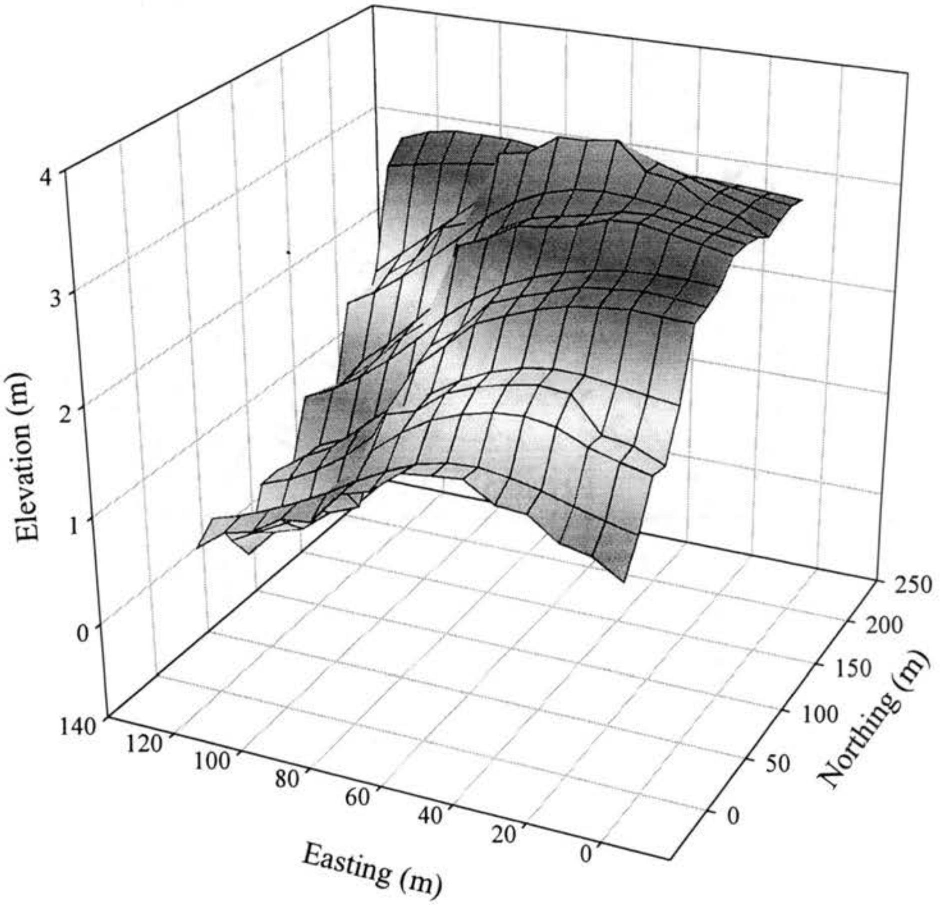

Fig. 1. Three-dimensional plot of the topographic variables northing, easting, and elevation of a mid-successional old field located in Oklahoma, USA. The highest elevation is found at the north end and the lowest elevation is the southeast corner. Mean slope for the east-west and north-south gradients is 1% with relief varying 3.1m over the entire study area.

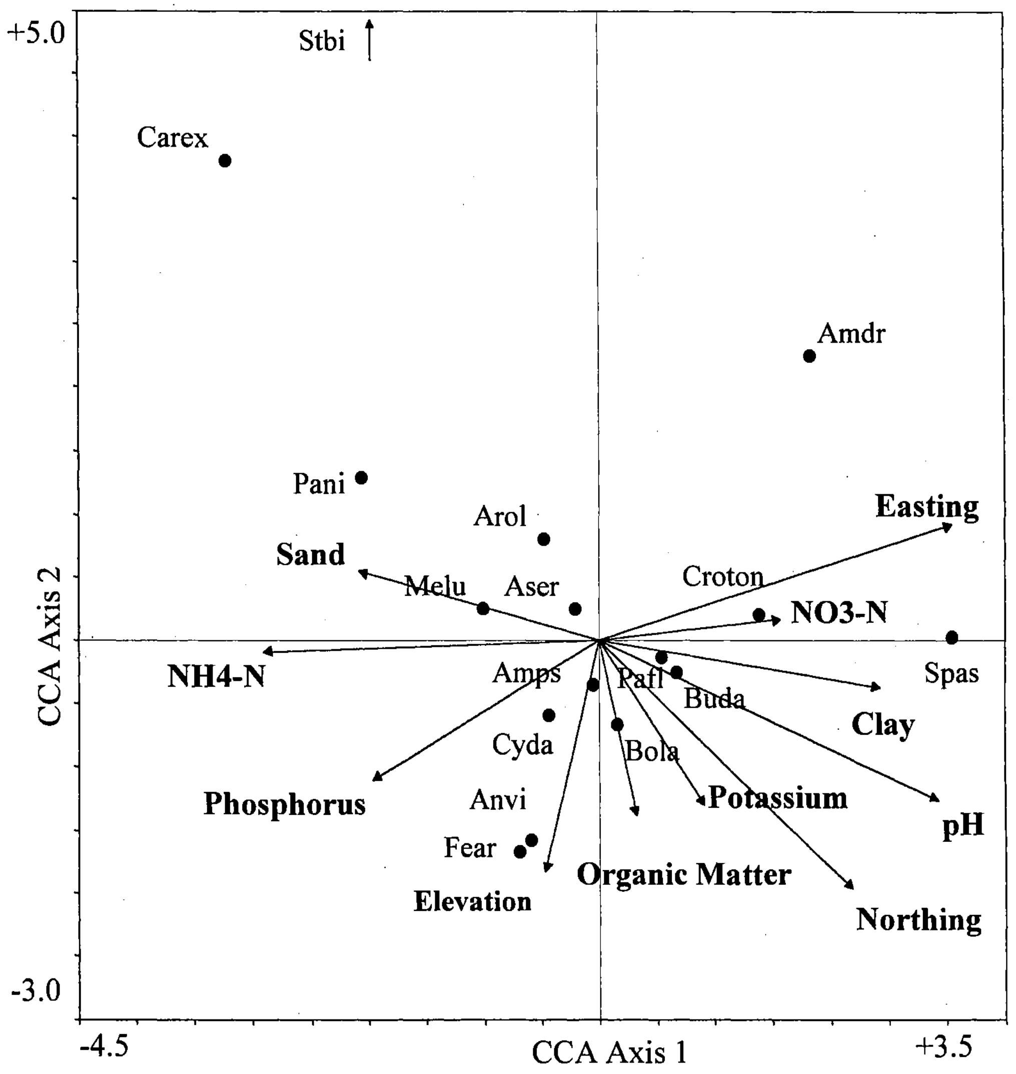

Fig. 2. Plot of the first two axes of canonical correspondence analysis (CCA) ordination on a mid-successional old field with species represented by closed circles and environmental variables represented by arrows. Species abbreviations are given in Table 2. The Monte Carlo test of significance found that both the first CCA axis (F = 5.207; P = 0.005) and the overall model (F = 2.007, P = 0.005) were significant. The first two axes accounted for 55% of the extracted variation in the species-environment relationship with axis 1 having an eigenvalue of 0.18 and axis 2 with an eigenvalue of 0.12. The first axis is represented by an east-west topographic gradient and the second axis is represented by a north-south topographic gradient.

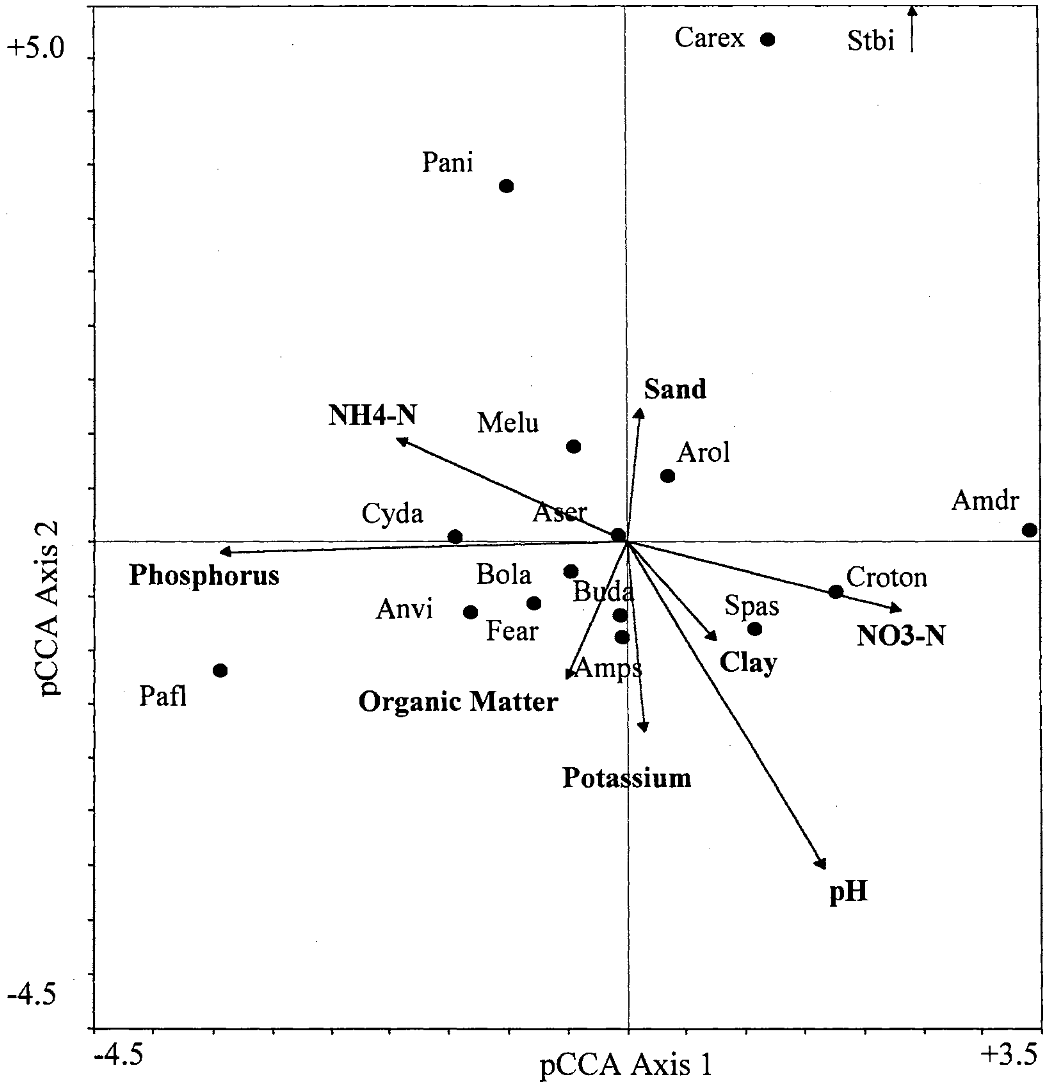

Fig. 3. Plot of the first two axes of a partial canonical correspondence analysis (pCCA) ordination on a mid-successional old field with species represented by closed circles and environmental variables represented by arrows. The pCCA factored out the topographic environmental variables of northing, easting, and elevation. Species abbreviations are given in Table 2. The Monte Carlo test of significance found that both the first pCCA axis (F = 3.421; P = 0.005) and the overall model (F = 1.466, P = 0.005) were significant. The first two axes accounted for 60% of the extracted variation in the species-environment relationship with axis 1 having an eigenvalue of 0.10 and axis 2 with an eigenvalue of 0.07. The first axis is represented by a phosphorus gradient and the second axis is represented by a pH gradient.

CHAPTER II

ABOVE- AND BELOWGROUND PROCESSES IN AN OKLAHOMA OLD FIELD FOLLOWING CESSATION OF GRAZING

Abstract

In the tallgrass prairie, response of above- and belowground processes to disturbance is predictable. Our objective was to examine short-term changes in above- and belowground phytomass and tissue nitrogen and carbon in an Oklahoma old field following cessation of heavy grazing. Above- and belowground primary production and tissue quality were sampled at the peak of the growing season in 1998, 1999, and 2000 on 16, 40 x 40-m plots. Among the above- and belowground processes evaluated, only aboveground primary production followed similar patterns compared to published values for tallgrass prairie. For the three years of this study, aboveground primary production increased following the cessation of grazing similar to tallgrass prairie. The remaining processes of aboveground tissue quality, root mass, and root nitrogen and carbon more resembled these processes in heavily grazed tallgrass prairie and not tallgrass prairie released from grazing. Aboveground plant nitrogen concentration was stable and aboveground plant carbon concentration decreased over three years. Root mass was variable, root nitrogen and carbon concentrations decreased over the three year study

period. The severity of disturbance, cultivation and grazing, combined with drought conditions in 1998 may have altered normal short-term patterns expected for this old field.

Introduction

Disturbance drives above- and belowground phytomass and plant tissue quality. Disturbance factors such as fire (Collins 2000; Engle and Bidwell 2001) and grazing (Axelrod 1985; Knapp et al. 1999) are important components in maintaining North American tallgrass prairie. Varying the frequency and intensity of disturbance can increase or decrease above- and belowground phytomass (Turner et al. 1993; Biondini et al 1998). For example, in the tallgrass prairie, frequent fires increase aboveground production compared to unburned prairie, whereas aboveground production decreases with infrequent fire (Knapp et al. 1998). As grazing intensity increases from moderate to heavy, aboveground production usually decreases (Hazell 1967; Briske and Heitschmidt 1991), and continuous heavy grazing can shift the plant community (Weaver 1954), decrease primary productivity (Branson 1985), and alter nutrient cycling (Briske and Heitschmidt 1991). Disturbance can increase or decrease tissue quality. For example, plant tissue C:N increases with burning (Ojima et al. 1994) because fire volatilizes plant nitrogen, which affects the phytomass nitrogen pool and increases C:N of plant tissue. Whereas grazing decreases plant tissue C:N (Risser and Parton 1982; Hobbs et al. 1991) through the return of nitrogen by fecal deposition, and consumption of plant carbon.

Disturbance history, including disturbance severity is one of several major elements that constrain the role of current disturbance as a driver in grasslands.

Cultivation is a severe type of irreversible disturbance. Old fields are a type of grassland that have been disturbed by cultivation and then allowed to revegetate naturally. Old fields vary in successional stage, nutrient availability, and production potential, which can alter the vegetation response to disturbance. For example, an old field disturbed by cultivation and heavy grazing did not have a similar vegetation response to burning as compared to late-successional tallgrass prairie (Engle et al. 2000). However, old fields that resemble tallgrass prairie in structure and species would be expected to follow similar patterns of vegetation response as tallgrass prairie.

Precipitation influences the severity of disturbance factors on grasslands. In the tallgrass prairie annual precipitation ranges from 600 to 1200 mm (Sims et al. 1978; Risser et al. 1981) compared to the precipitation range of 300 to 600 mm for xeric to mesic grasslands (Sala et al. 1988; Lane et al. 2000). This precipitation difference contributes to the resilience of tallgrass prairie following disturbance. For example, annual or biennial fires are a common disturbance in the Flint Hills region of the tallgrass prairie because precipitation supports the production of fine fuel. In xeric grasslands, fires are not as frequent because primary production is limited by precipitation. Precipitation not only drives primary production, but also tissue quality. Tissue quality is less in higher precipitation areas of the Great Plains and tissue quality increases in areas with less precipitation (Vinton and Burke 1997). With high precipitation, grasslands require frequent disturbance to maintain tissue quality. Therefore, the role of disturbance changes depending on mean annual precipitation.

In the long-term, removal of grazing or fire in tallgrass prairie decreases aboveground primary production, increases litter accumulation, and decreases tissue quality (Knapp and Seastedt 1986; Johnson and Matchett 2001). However, removal of heavy grazing increases short-term aboveground primary productivity (Engle et al. 2000). Patterns of production and plant tissue quality following cessation of heavy grazing in an old field within the tallgrass prairie region should mirror these patterns in tallgrass prairie. Therefore, the objective of this study was to examine short-term changes in above- and belowground phytomass and tissue nitrogen and carbon in a severely eroded old field located within the tallgrass prairie region following the cessation of grazing.

Methods

This work was performed on an old-field grassland in Pontotoc County, Oklahoma, approximately 16 km west of Ada, Oklahoma. The area is owned and maintained by the United States Environmental Protection Agency, Robert S. Kerr Environmental Research Center in Ada, Oklahoma. The old field was abandoned from cultivation about 1950 and subsequently it revegetated naturally. The dominant soil is Burleson clay (fine, montmorillonitic, thermic, Udic Pellusterts) (USDA-SCS 1973), and the primary vegetation consists of the early to mid-seral species *Aristida oligantha*, *Andropogon virginicus*, *Ambrosia psilostachya*, and exotic species including *Festuca arundinacea* and *Cynodon dactylon*. Pontotoc County has a continental climate with a mean annual temperature of 16.7°C, a January mean of 4.2°C, and a July mean of 28.2°C. Annual precipitation averages 990 mm with most precipitation occurring from April to October (NOAA). The study area consists of 16, 40 by 40-m plots that received nitrogen amendments and herbivory exclosure treatments in a factorial arrangement. Nitrogen amendments consisted of four annual applications of 34% ammonium nitrate for a total of 48 kg N ha^{-1} yr^{-1}. The small mammal exclosures consisted of a 2.5 cm chain link fence built to a height of 2 m. The four treatments included 1) no nitrogen and no exclosure, 2) nitrogen and no exclosure, 3) no nitrogen and exclosure, and 4) nitrogen and exclosure. Above- and belowground phytomass, plant nitrogen, and carbon did not differ among treatments (Fig. 1) ($P>0.05$), so values were averaged across treatments.

We sampled aboveground current year's growth in August of 1998, 1999, and 2000 within a 0.1-m^2 quadrat with five samples per plot. Current year's growth was removed at the soil surface and litter collected within each quadrat. Current year's growth and litter were dried at 60°C in a forced-air oven until reaching a constant weight, then ground to pass a 1.0-mm mesh screen. Nitrogen and carbon concentration of current year's growth and litter was determined using the dry combustion method and analyzed on the Leco CN-2000 (Jones and Case 1990; Zhang et al. 1998).

Belowground samples were harvested in August of 1998, 1999, and 2000 for belowground mass, nitrogen, and carbon. Three root cores were sampled per plot. Each core had a diameter of 7.6 cm and sampled to a depth of approximately 30 cm. The root cores were soaked overnight and the roots washed to remove soil particles. The recovered root mass included both live and dead roots and rhizomes. Roots were then dried and ground to pass a 1.0-mm mesh screen and analyzed for nitrogen and carbon concentration using the dry combustion method.

Results

Aboveground primary production increased during the study, but tissue quality remained largely unchanged. Aboveground primary production increased nearly two-fold over three growing seasons (Table 1). We expected plant nitrogen concentration to increase with increased aboveground primary production, but plant nitrogen remained stable for three years following cessation of grazing. Plant carbon concentration decreased following the cessation of grazing resulting in lower plant tissue C:N by 2000 (Table 1).

Root nitrogen and root carbon decreased following the cessation of grazing, whereas root mass varied over the three years of the study (Table 1). In 1998, root mass exceeded aboveground phytomass, but in 1999 and 2000, production was greatest aboveground. The AG:BG phytomass ratio varied by a factor of three because root mass declined in 1999 as aboveground primary production increased. Even though both root nitrogen and carbon declined, root C:N increased.

Discussion

Cultivation and heavy grazing are two disturbances in grasslands that alter short- and long-term recovery of primary productivity and plant tissue quality. Cultivation reduces above- (Bazzaz 1968) and belowground primary productivity through soil erosion and soil nutrient loss. Heavy grazing also reduces above- (Herbel and Anderson 1959; Hazell 1967) and belowground primary production (Schuster 1964) and favors grazing tolerant species (Weaver 1954). Cessation of heavy grazing reduces the dominance of grazing tolerant species (e.g. *Aristida oligantha*) and increases aboveground primary productivity (Gillen et al. 1987; Engle et al. 2000). This shift in species composition following cessation of grazing alters the concentration of plant tissue nitrogen. Early successional species have lower concentrations of plant tissue nitrogen than compared to late successional species (Redente et al. 1992), and plant nitrogen would be expected to increase following cessation of grazing. In this study, we investigated the short-term changes in aboveground primary production, root mass, and tissue nitrogen and carbon in a severely eroded old field following the cessation of grazing.

In tallgrass prairie, cessation of heavy grazing increases aboveground primary production, and among the factors investigated in this study, only aboveground primary production increased. Aboveground tissue quality, root mass, and root nitrogen and carbon, which have predictable patterns following cessation of grazing in tallgrass prairie, did not have predictable patterns in our old field. In particular, our results indicated that aboveground primary production increased in the first few years after removal of heavy grazing. Even with the loss of topsoil during cultivation, patterns of aboveground primary production of our old-field site was comparable with studies on tallgrass prairie in which grazing was removed (Fig. 2). For example, in a heavily grazed grassland in southern Oklahoma aboveground primary production increased following cessation of grazing on an old field and tallgrass prairie site (Engle et al. 2000). Although the old-field site was cultivated, it was on a site with deeper soils than compared to the tallgrass prairie site. Aboveground primary production increased nearly two-fold over two years, whereas aboveground mass on the tallgrass prairie site only increased by 14%. In north central Oklahoma, aboveground primary production increased with the cessation of heavy grazing in an old field also with shallow soils (Fig. 2), but the increase was only 10% over two growing seasons (Gillen et al. 1987). Although aboveground primary production in old fields and tallgrass prairie varies by site, both grasslands demonstrate increases in primary production with the cessation of heavy grazing.

The severity of grazing and release from grazing alter patterns of aboveground primary production in tallgrass prairie. Heavy grazing in tallgrass prairie decreases primary production in both the short- and long-term. Whereas the removal of heavy grazing increases aboveground primary production in the short-term, but primary production would decrease in the long-term because of litter accumulation (Table 2). Aboveground primary production increased on our old-field site similar to the aboveground production response in other old fields and tallgrass prairie sites (Fig. 2). As aboveground primary production increases with the removal of grazing, nitrogen and carbon concentrations also change.

Aboveground tissue quality in our old-field site did not resemble tissue quality patterns observed in other studies in tallgrass prairie following the removal of heavy grazing (Table 2). We were unable to find studies that reported changes in aboveground plant nitrogen following heavy grazing, but in the tallgrass prairie of Kansas, moderate grazing increased aboveground plant nitrogen concentrations compared to no grazing (Turner et al. 1993). Therefore, we expected a decline in nitrogen concentration of aboveground plant tissue, but plant nitrogen did not change. A shift in species composition from more early seral species with low tissue nitrogen concentration to fewer late seral species with high tissue nitrogen concentration (Redente et al.1992) may explain the unchanged plant nitrogen.

Belowground primary production and root nitrogen and carbon did not parallel aboveground response to cessation of grazing as expected. Root mass is highly variable among years in tallgrass prairie with no clear relationship between root production and aboveground primary production (Milchunas and Lauenroth 1993; Lauenroth et al. 1994). Even though heavy grazing reduces root mass (Weaver 1954; Schuster 1964), root mass is also influenced greatly by precipitation (Hayes and Seastedt 1987; Rice et al. 1998). In our study, precipitation (Fig. 3) appeared to be associated with root mass. Following an intense growing season drought in 1998, root mass was lowest in 1999 (Fig. 4). Root mass did not increase with cessation of grazing, in fact belowground production was non-directional. Others studies in the tallgrass prairie have also reported variable root production over time with grazing and with no grazing (Table 2). For example, root mass increased in ungrazed tallgrass prairie of Kansas, whereas root mass decreased in ungrazed tallgrass prairie of Oklahoma (Fig. 4). Variation in root mass in other grassland studies and our old field indicates factors other than disturbance control short-term root production.

Although root mass in tallgrass prairie and aboveground primary production do not appear to be related, cessation of heavy grazing may alter this relationship. Because the response of aboveground primary production is more rapid than root growth following the cessation of grazing, increased root mass may not be detected in our old field for several growing seasons. Heavy grazing reduces root mass compared to moderately grazed and ungrazed grasslands (Schuster 1964; Risser et al. 1981), and the removal of heavy grazing increases long-term root production (Schuster 1964). In our old-field site, heavy grazing and cultivation may be restricting root production compared to a grassland without severe disturbance. Even though root mass did not increase in the short-term, we expect a long-term increase in root mass.

Root tissue quality, as indexed by root nitrogen concentration, decreases with heavy grazing (Turner et al. 1993), so we expected a short-term increase in root nitrogen with the cessation of heavy grazing. But, belowground tissue quality was more similar to heavily grazed tallgrass prairie than tallgrass prairie with grazing removed (Table 2). In our old-field site, the short-term decreases in root nitrogen and carbon are not indicative of long-term patterns observed elsewhere. Although continual heavy grazing reduces stored carbon in tallgrass prairie (Turner et al. 1993), carbon storage should increase because of increased root production following the cessation of heavy grazing.

The severity of disturbance in grasslands alters short-term above- and belowground processes. Cessation of heavy grazing increased aboveground primary production, whereas aboveground tissue quality, root mass, and root nitrogen and carbon were more characteristic of heavily grazed tallgrass prairie. Even with drought conditions the first growing season following cessation of heavy grazing, aboveground primary production increased. The increase in aboveground primary production may have occurred at the expense of belowground production, thus the explanation for variable root mass in the short-term. However, we expect root mass and belowground carbon storage to increase in the long-term.

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Table 1. Aboveground phytomass, root mass, and above- and belowground tissue quality for an old-field site in southeast Oklahoma following the cessation of heavy grazing.

	Old-Field Site		
	1998	1999	2000
Aboveground			
Phytomass (g/m^2)	182	262	347
Plant nitrogen (%)	0.8	0.8	0.8
Plant carbon (%)	43	41	36
AG C:N	54	51	45
Belowground			
Root mass (g/m^2)	222	105	209
Root nitrogen (%)	0.7	0.6	0.5
Root carbon (%)	42	41	36
BG C:N	60	68	72
AG:BG mass	0.8	2.5	1.7

Table 2. Comparison of patterns in aboveground phytomass, root mass, and above- and belowground tissue quality in moderate grazed tallgrass prairie, tallgrass prairie with no grazing, an old-field site following cessation of heavy grazing, heavily grazed tallgrass prairie, and tallgrass prairie following cessation of heavy grazing.

	Moderate Grazing		Heavy Grazing		
	Tallgrass Prairie		Old-Field Site	Tallgrass Prairie	
Component	Under Disturbance (compared to no disturbance)	No Grazing	Cessation of Disturbance	Under Disturbance (compared to no disturbance)	Cessation of Disturbance
Aboveground					
Phytomass	↑[1, 5, 6, 8]	↓[1, 5, 6, 8]	↑	↓[2, 3]	↑[7, 11]
Plant nitrogen (%)	↑[8]	↓[8]	No change	↑	↓
AG C:N	↓	↑	↓	↓	↑
Belowground					
Root mass	↑ to ↓[4, 10]	↓[4]	Nonlinear fluctuation	↓[8, 12]	↑
Root nitrogen (%)	↑[9, 12]	↓	↓	↓[8, 9]	↑ to ↓
BG C:N	↓[12]	↑	↑	↑[8]	↓
AG:BG mass	↓	↑	↑	↓	↑

Table 2. Continued.

1. Kelting (1954), Oklahoma, tallgrass prairie, no grazing 20 years prior to study, mowed 10 years prior to study.
2. Herbel and Anderson (1959), Kansas, tallgrass prairie, varying grazing intensities.
3. Hazell (1967), Oklahoma, tallgrass prairie, heavy grazed annually.
4. Sims and Singh (1978a), Oklahoma, tallgrass prairie, ungrazed for 20 years prior to study.
5. Sims and Singh (1978b), Oklahoma, tallgrass prairie, ungrazed for 20 years prior to study.
6. Risser et al. (1981), Oklahoma, tallgrass prairie, ungrazed for 20 years prior to study.
7. Gillen et al. (1987), Oklahoma, tallgrass prairie, heavily grazed prior to study.
8. Turner et al. (1993), Kansas, tallgrass prairie, three mowing intensities and three mowing heights, no grazing 10 years prior to study.
9. Benning and Seastedt (1997), Kansas, tallgrass prairie, plots mowed annually.
10. Biondini et al. (1998), North Dakota, mixed-grass prairie, no grazing for 16 years prior to study.
11. Engle et al. (2000), Oklahoma, tallgrass prairie and old field, heavily grazed prior to study.
12. Johnson and Matchett (2001), Kansas, tallgrass prairie, no grazing for 5 years prior to study.

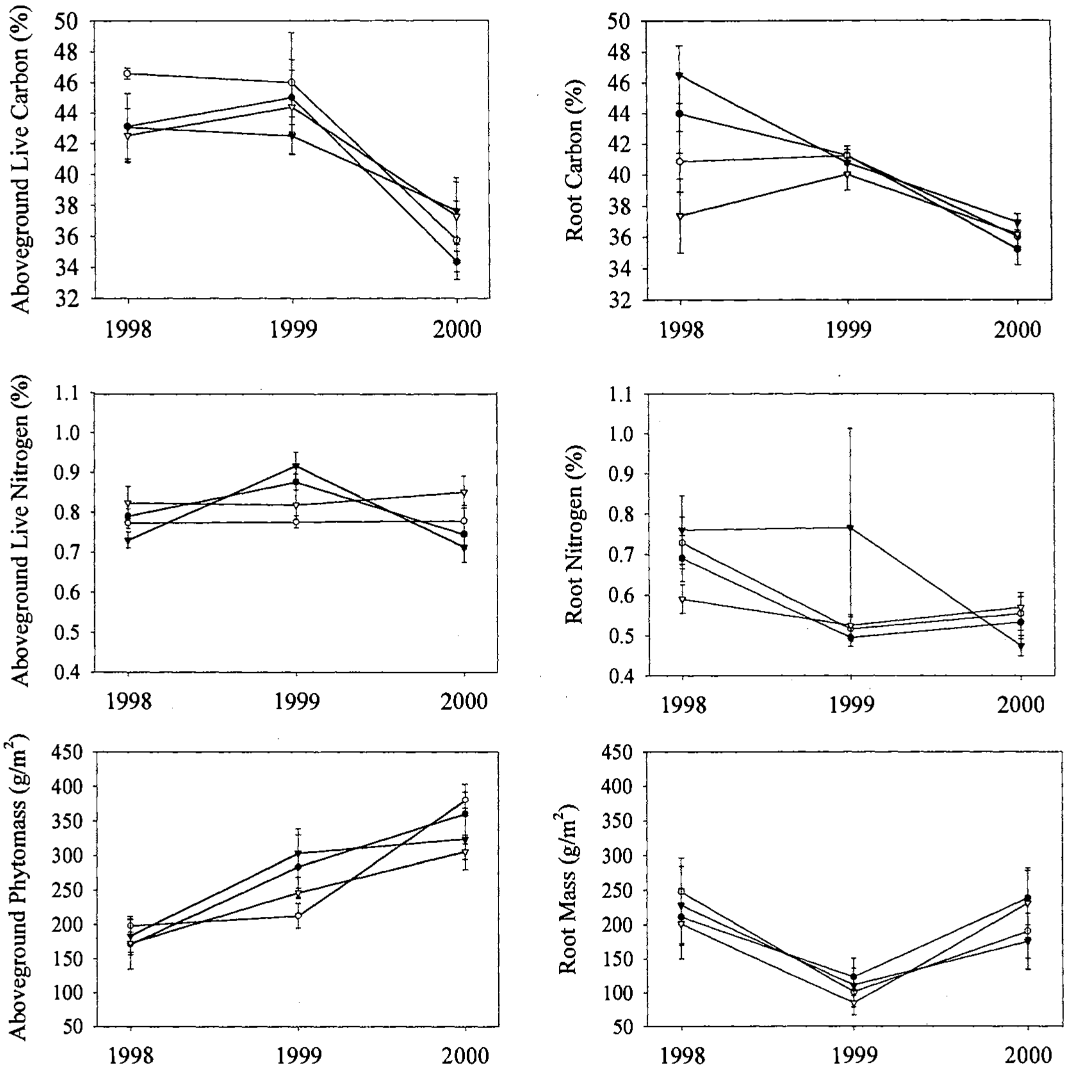

Fig. 1. Aboveground phytomass (g/m^2), root mass (g/m^2), above- and belowground carbon (%) and nitrogen (%) for a mid-successional old field in southeast Oklahoma in 1998, 1999, and 2000. Means in 1998 are pre-treatment with treatments applied in 1999 and 2000, ● = no nitrogen and no exclosure, ○ = nitrogen and no exclosure, ▼ = no nitrogen and exclosure, and ▽= nitrogen and exclosure.

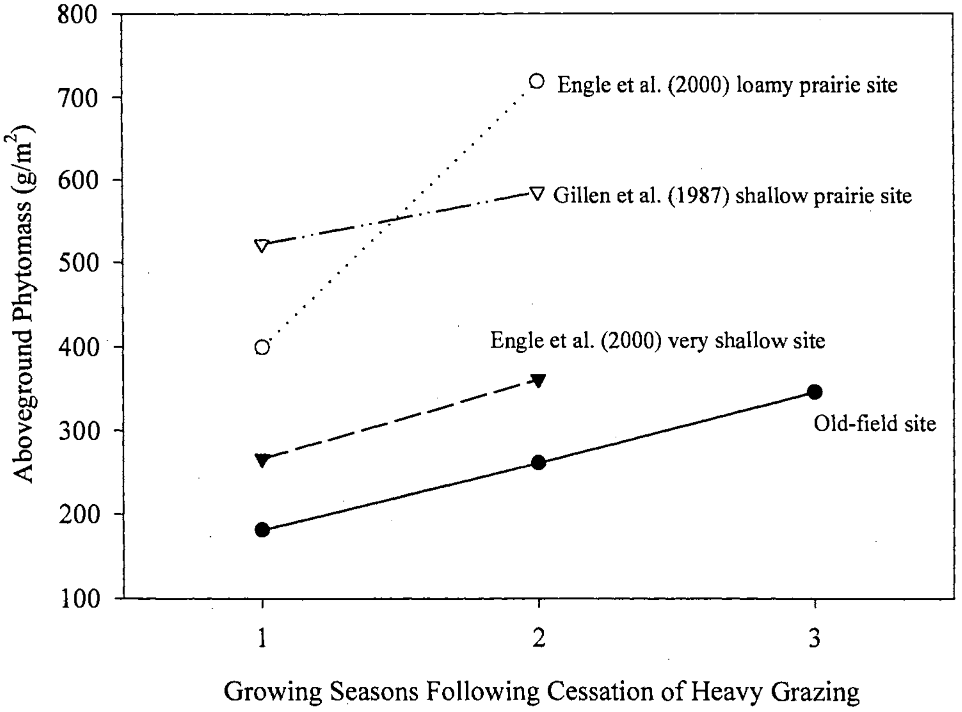

Fig. 2. Comparison of aboveground primary production following cessation of heavy grazing in tallgrass prairie and old-field sites in Oklahoma. Tallgrass prairie sites include Gillen et al. (1987) shallow prairie site and Engle et al. (2000) very shallow site. Old fields include Engle et al. (2000) loamy prairie site and the old field study site in southeast Oklahoma.

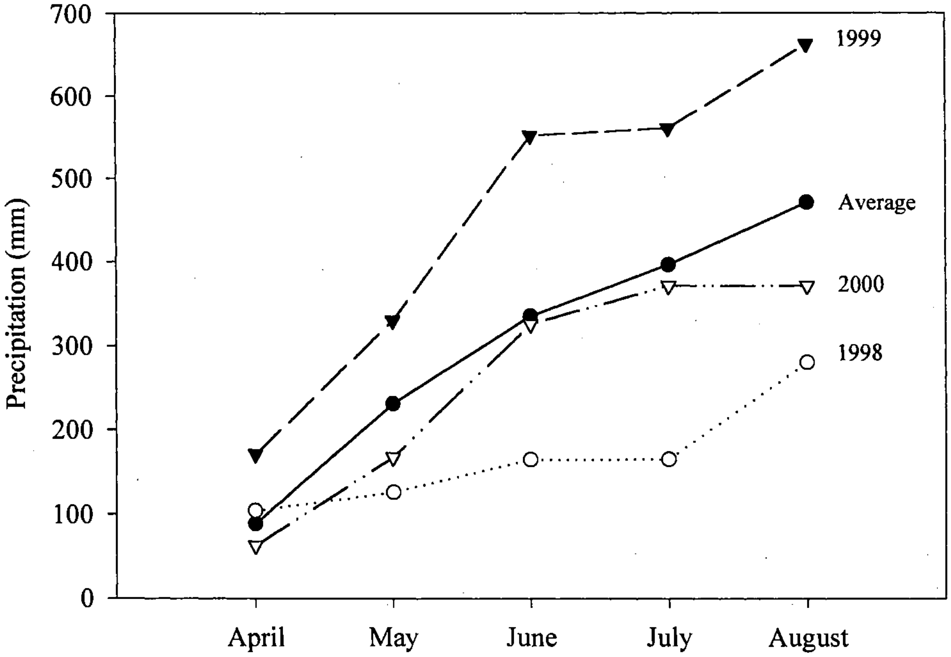

Fig. 3. Growing-season precipitation for Ada, Oklahoma in 1998, 1999, 2000, and the long-term (30-year) average.

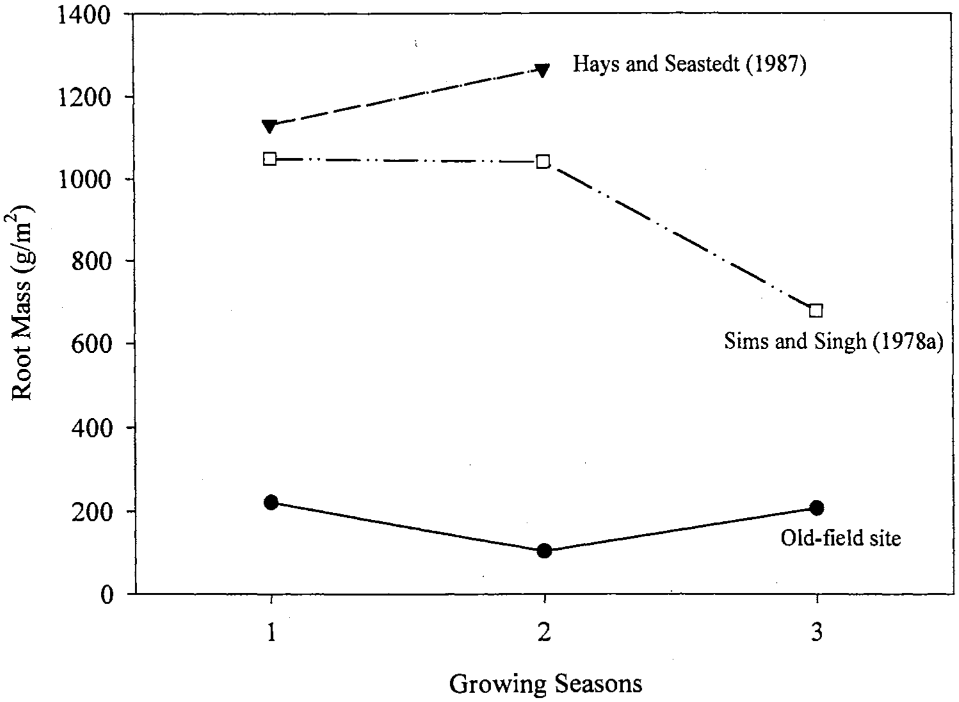

Fig. 4. Comparison of root mass on ungrazed tallgrass prairie of Kansas and Okalahoma and root mass for the old field study site in southeast Okalahoma following cessation of heavy grazing. Sims and Singh (1978a), Hayes and Seastedt (1987), and the old-field site used root cores sampled to 30 cm and included total root mass (both live and dead portions of roots and rhizomes).

CHAPTER III

OLD-FIELD SUCCESSIONAL DYNAMICS FOLLOWING CESSATION OF SEVERE DISTURBANCE

Abstract

In grasslands dominated by warm-season grasses, community composition and successional patterns can be altered by disturbance and exotic species invasions. Our objective was to describe vegetation dynamics following cessation of severe disturbance, which was heavy grazing by cattle, in an old-field grassland subject to invasion by *Festuca arundinacea*, an exotic grass. Specifically, we evaluated changes in plant community composition and investigated the relationships between species richness and litter accumulation and between species richness and abundance of *Festuca*. Vegetation data consisted of canopy cover by species, species richness, and litter mass collected on 16, 40 x 40-m plots within an old-field site in southeastern Oklahoma, USA. The usual successional patterns following cessation of heavy grazing, annuals followed by perennial bunchgrasses and ending in mature prairie, were altered by *Festuca*, which increased in abundance over the three-year study period. However, species richness was not correlated to abundance of *Festuca*. Moreover, the expected negative correlation between litter accumulation and species richness demonstrated in other mesic grasslands was not present in this old field. *Festuca* and species richness were negatively correlated,

but on plots in which *Festuca* increased species richness did not decrease. Instead, *Festuca* increased most on species-poor plots and *Festuca* abundance remained low on species-rich plots. We conclude that not only does *Festuca* influence plant community composition, the dynamics of *Festuca* invasion are influenced by plant species richness.

Introduction

Exotic species influence ecosystem processes and secondary succession in grasslands. Invasion theory suggests that areas of low species diversity are more prone to invasion than areas with high species diversity (Elton 1958). Experiments have reported evidence that both support (MacArthur and Wilson 1967; Tilman 1982; Tilman 1997) and contradict (Robinson and Quinn 1988; Vitousek et al. 1996; Smith and Knapp 1999) this theory. However, in addition to species richness, succession and disturbance may also influence plant invasions on grasslands. Succession can influence the establishment of the invader through changes in vegetation and nutrient availability (Masters and Sheley 2001). Disturbance can affect resource availability and increase potential sites available for the invading species to establish (Grubb 1977). Grazing in tallgrass prairie can increase species richness by its influence on succession and resource availability (Collins 1987; Collins and Steinauer 1998; Smith and Knapp 1999).

Grazing is a keystone process that historically shaped the development and maintenance of the tallgrass prairie (Knapp et al. 1998). Large herbivores continually influence vegetation structure and community composition through removal and trampling of vegetation (Collins and Steinauer 1998). When grazing is removed, the dominant warm-season matrix grasses increase in abundance and the non-dominant minor grasses and forbs decrease (Weaver 1968; Knapp et al. 1998). The removal of grazing becomes the successional driver resulting in the increase of late-successional warm-season grasses (Freeman 1998; Engle et al. 2000). Therefore, the removal of grazing in a plant community that has been continuously grazed at moderate to heavy rates will result in generally predictable vegetation changes (Booth 1941; Inouye et al. 1987; Collins 1990; Engle et al. 2000). However, the invasion or introduction of exotic species may alter the usual secondary succession of a grassland following grazing (Tremmel and Peterson 1983; Fike and Niering 1999).

Festuca arundinacea is invasive and competitive, which may lead to it becoming a dominant component of native grasslands and possibly altering species composition (Clay and Holah 1999) and nutrient cycling (Gay et al. 1996). The widespread use of *Festuca* for forage, turf, and soil conservation purposes began in the 1940's, and *Festuca* gained status as a commonly planted species in the eastern US (Ball et al. 1993; Hoveland 1993). *Festuca* has been studied with the focus on the effects of endophyte-infected *Festuca* versus uninfected *Festuca* on species richness and plant-soil interactions (Clay and Holah 1999; Matthews and Clay 2001). These studies were primarily concerned with the difference between endophyte-infected and uninfected *Festuca* in monocultures and simple mixtures, rather than the overall effect of *Festuca* in natural grasslands.

Removal of grazing in heavily grazed old fields of the Southern Great Plains can be the driver of vegetation resulting in litter accumulation and increases in late-successional species (Engle et al. 2000). However, vegetation dynamics and successional paths may be altered when an exotic species is present. The objective of our study was to describe vegetation dynamics in a warm-season dominated old-field grassland subject to invasion by *Festuca*, an exotic species. We hypothesize that *Festuca* has no influence on community composition or the abundance (canopy cover) of any species or group of species. We also hypothesize that species richness is a function of litter accumulation as demonstrated in similar grasslands (Collins 1987; Carson and Peterson 1990; Foster and Gross 1998) and species richness is not influenced by *Festuca.*

Methods

This study was conducted on an old field in Pontotoc County, Oklahoma, USA. The area was abandoned from cultivation around 1950 and herbaceous vegetation naturally re-established. During the last half century, the grassland has been subjected to heavy livestock grazing until January 1998. Dominant vegetation consists of the early to mid-successional grasses and forbs including *Aristida oligantha*, *Andropogon virginicus*, *Ambrosia psilostachya*, and *Aster ericoides.* There are also exotic species present including *Festuca arundinacea* and *Cynodon dactylon.* The predominant soil type is Burleson clay (fine, montmorillonitic, thermic, Udic Pellusterts) (USDA-SCS 1973). Annual precipitation is 990 mm, which predominantly occurs from April through October (NOAA).

The study area is part of an interdisciplinary study and the 16, 40 x 40-m plots received a factorial arrangement of nitrogen and herbivory exclusion treatments. Nitrogen was applied in the form of 34% ammonium nitrate four times during the year (February, May, August, and November) with a total of 48 kg N ha^{-1} yr^{-1}. Exclosures were constructed using 2.5 cm chain link fence approximately 2 m in height with the primary purpose of excluding small mammal herbivory. The treatments included 1) no nitrogen and no exclosure, 2) nitrogen and no exclosure, 3) no nitrogen and exclosure, and 4) nitrogen and exclosure. To determine if canopy cover varied by treatment we performed redundancy analysis (RDA) using CANOCO version 4 (ter Braak and Šmilauer 1998). To test for a nitrogen effect on canopy cover, nitrogen was the explanatory variable and exclosure a covariable. To test for an exclosure effect, exclosure was used as the explanatory variable and nitrogen was a covariable. Because no treatment effects were detected for nitrogen (P=0.46) or exclosure (0.14), all analyses were performed at the plot level.

We sampled herbaceous vegetation in May of 1999, 2000, and 2001 for canopy cover and species richness. Twenty-five 0.1 m^2 quadrats were sampled per plot to determine canopy cover using the Daubenmire cover class method (Bonham 1989). Canopy cover was collected by species and analyzed by functional group. The determination of the grass and sedge functional groups was based on photosynthetic pathway and origin and included cool-season native grasses, *Festuca arundinacea* (*Festuca* a cool-season introduced grass), warm-season native grasses, and warm-season introduced grasses (Waller and Lewis 1979; Hatch and Pluhar 1993; Stubbendieck et al. 1997). Forbs were separated by nitrogen fixing ability into non-legume forbs and legumes (Great Plains Flora Association 1986). Analyses of non-legume forbs were at both the species and functional group level. Species richness was determined through an extensive search of species present in the entire plot. In August of 1998, 1999, and 2000, litter was harvested from five 0.1 m^2 quadrats per plot. Litter mass was then dried at 60°C in a forced-air oven until reaching a constant weight.

The three most abundant species were *Festuca arundinacea*, *Aster ericoides*, and *Ambrosia psilostachya.* Of these three species, only *Festuca* had a negative relationship with species richness. We only investigated *Festuca* in relation to community composition, litter mass, and species richness, because *Festuca* has been shown to decrease species richness and alter the plant community (Clay and Holah 1999; Spyreas et al. 2001).

Because we detected no differences in canopy cover among treatments, we investigated the influence of *Festuca* on community composition. We calculated average canopy cover (n=25) for each species by plot in 1999, 2000, and 2001. To investigate community composition patterns, we performed an RDA using species data by plot and year with *Festuca* as the explanatory variable. We also examined relationships between *Festuca* canopy cover and functional group canopy cover using Pearson's correlation coefficients (r).

To test the hypothesis that species richness is a function of litter accumulation (and not *Festuca* abundance), we used regression analysis (SAS 1991) to examine the relationships of 1) species richness and litter mass and 2) species richness and *Festuca* cover. To determine if a change in plot composition including a change in species richness was associated with an increase in *Festuca* abundance, or alternatively, *Festuca* increased on plots with respect to its composition or richness, we calculated a Jaccard Similarity Index (Jongman et al. 1995) as follows,

$$S_J = c/(a+b+c)$$

where, a = the number of unique species in a plot in 1999, b = the number of unique species in a plot in 2001, and c = the number of species shared by the plot in 1999 and

2001. A similarity index of 1.0 would indicate no change in species presence over time, whereas a similarity index of zero would indicate a complete change in species presence over time. We then used correlation to determine if a change in *Festuca* canopy cover was accompanied by a change in species presence of plots.

Results

We expected grazing cessation to result in community vegetation changes that follow successional patterns observed elsewhere in old fields released from heavy grazing (Engle et al. 2000), but the vegetation dynamics in this old field were explained most clearly by increasing abundance of *Festuca.* The change in species abundance by plot is demonstrated in Figure 1 in which plots with the greatest amount of *Festuca* (>10% canopy cover) are located in the right half of the ordination diagram. *Festuca* cover increased nearly five-fold from 1999 to 2001 (Table 1), which is reflected along RDA Axis 1.

The community data do not support the hypothesis that *Festuca* has no influence on the abundance of any species or group of species. Of the possible 15 correlations between functional group canopy cover and *Festuca* canopy cover, only two were correlated (Fig. 2). However, the correlations occurred between the two dominant functional groups and *Festuca.* The two functional groups, warm-season native grasses and non-legume forbs, were dominants, representing the majority of the total canopy cover (e.g. 75% in 1999). A negative relationship between *Festuca* canopy cover and warm-season native grass cover in 2001 indicates that *Festuca* may be increasing at the expense of warm-season native grasses. Warm-season native grass cover was negatively correlated to *Festuca* cover in 2001, but was not correlated with *Festuca* cover in the first two growing seasons when *Festuca* cover was less (Fig. 2a). In 2001, plots with larger amounts of *Festuca* contained less warm-season native grasses than plots with little *Festuca*. However, an inspection of the change in warm-season grass cover and *Festuca* canopy cover over time indicated that an increase in *Festuca* canopy cover did not coincide with a decrease in warm-season native grass canopy cover. Plots with the highest warm-season native grass canopy cover had the least amount of *Festuca* cover, and plots with low warm-season native grass canopy cover had the greatest amount of *Festuca* cover.

The dominance of two non-legume forbs masked the overall influence of *Festuca* on the non-legume forb functional group. Non-legume forb cover was positively correlated to *Festuca* canopy cover in 1999 when *Festuca* cover was <7% (Fig. 2b). But with greater *Festuca* canopy cover in 2000 and 2001, non-legume forb canopy cover and *Festuca* canopy cover were not correlated. The two dominant species *Ambrosia* and *Aster* accounted for 64% of the non-legume forb canopy cover (Table 2), with the remaining 36% representing the other 43 non-legume forb species. Canopy cover of many of these minor species was correlated with *Festuca* canopy cover in 2001 (Table 2). *Ambrosia* canopy cover was positively correlated with *Festuca* canopy cover in 1999 (Fig. 4), but not in 2000 or 2001. Plots in which *Festuca* canopy cover was greatest, *Ambrosia* abundance was low. *Aster* canopy cover was positively correlated with *Festuca* canopy cover in all three years (Fig. 5). *Aster* canopy cover increased from 1999 to 2001 and was the most abundant non-legume forb in 2001 consisting of 44% of the total canopy cover of non-legume forbs. The loss of canopy cover contributed by minor non-legume forb species was accounted for by an increase in *Aster* canopy cover.

Because species richness is a function of litter accumulation in tallgrass prairie (Collins 1987; Carson and Peterson 1990; Foster and Gross 1998), we hypothesized that *Festuca* in our old field would not alter this negative relationship. Species richness was not related to litter mass (Fig. 6), but species richness was greatest when *Festuca* cover was low (Fig. 7). However, if the association between *Festuca* cover and species richness was causal (i.e. as *Festuca* increases species richness decreases), an increase in *Festuca* canopy cover on a plot over time would necessarily be accompanied by a decrease in the total number of species on that plot.

However, the change in *Festuca* canopy cover was not correlated to the change in the total number of species from 1999 to 2001 (Fig. 8). For example, the same number of species were lost (n=5) in a plot where *Festuca* canopy cover increased by 20% and in another plot where *Festuca* canopy cover did not change from 1999 to 2001 (Fig. 8). Furthermore, *Festuca* canopy cover increased on plots that were both similar and dissimilar in species presence from 1999 to 2001 (Fig. 9), which indicates *Festuca* did not cause species replacement. Because neither the change in the number of total species nor the change in species presence (similarity index) was negatively correlated with the change in *Festuca* cover, we determined that the relationship between *Festuca* cover and species richness was not causal. Rather, *Festuca* increased more on lower richness plots.

Discussion

We investigated changes in community composition, functional group canopy cover, and species richness in a grassland dominated by warm-season grasses following the cessation of heavy grazing and containing small amounts of *Festuca*. Other studies have examined vegetation dynamics of *Festuca* monocultures or simple mixtures (Wieder et al. 1983; Clay and Holah 1999; Matthews and Clay 2001). *Festuca* is an invasive and competitive species that overrides vegetation dynamics in monocultures and simple mixtures, so the concern this plant might dominate in old fields is a legitimate concern to restoration.

We expected plots to be chronosequences representing the change in plot species composition from early- to late-successional species (Collins and Adams 1983; Engle et al. 2000) consistent with cessation of grazing as the factor most influencing the plant community (Engle et al. 2000). However, our community data showed a distinct separation among plots over time representing the increase in *Festuca* canopy cover. In the three years following removal of herbivory, changes in plot species composition were expressed with increasing abundance of *Festuca* and not increases in late-successional species. The increase in *Festuca* canopy cover altered successional dynamics. At less than 10% *Festuca* cover, increases in warm-season grasses were expected in this mid-successional grasslands. But as *Festuca* cover exceeded 10%, *Festuca* became the driver of succession in place of warm-season native grasses.

In this old field, the alteration of carbon and nitrogen cycling by *Festuca* is possibly the most important altered ecosystem process. Cool-season grasses have low carbon to nitrogen ratios compared to warm-season grasses and lack bundle sheath cells, which results in higher quality leaf tissue and litter (Waller and Lewis 1979; Coyne et al. 1995). *Festuca* is more capable of capturing elevated nitrate-nitrogen than warm-season species thereby reducing the potential risk of nitrate leaching (Gay et al. 1996). For example, in an upland hardwood forest of Oklahoma, herbicide-induced mortality of the hardwoods followed by overseeding with *Festuca* resulted in *Festuca* sequestering more nitrate-nitrogen compared to overseeding with a warm-season introduced grass, *Bothriochloa ischaemum* var. *ischaemum*, or native vegetation (Gay et al. 1996). Increased abundance of *Festuca* would increase decomposition rates, however, through early growth in the spring and late growth in the fall, *Festuca* is able to monopolize nitrogen uptake compared to warm-season grasses. Although *Festuca* increases litter decomposition and the return of nitrogen, uptake of nitrogen by warm-season grasses may be prevented by *Festuca.*

Successional dynamics were altered with cessation of grazing and *Festuca* abundance increased. In only three years following grazing removal, *Festuca* changed the expected successional patterns. Exotic species such as Eurasian forbs are common in early- to mid-successional old fields (Tilman 1997), but through succession these invasive forbs are replaced by native vegetation (Inoyue et al. 1987). Exotic species can become dominant, changing the community composition and further affecting ecosystem properties (Masters and Sheley 2001). For example, *Bromus tectorum* has become a problem species in the Intermountain region of the western US (DiTomaso 2000; Belnap and Phillips 2001; Masters and Sheley 2001). *Bromus* invades and spreads rapidly, which alters the community composition and the historic fire regime. *Bromus* produces more litter and provides more fuel compared to native grasses and shrubs, thus increasing fire frequency (D'Antonio and Vitousek 1992; DiTomaso 2000). Soil biota are also influenced by *Bromus* invasions, however, opposite results were observed in *Stipa* vs. *Hilaria* grasslands invaded by *Bromus*. For example, soil invertebrates increased in the *Hilaria-Bromus* community and decreased in the *Stipa-Bromus* community (Belnap and Phillips 2001). This variable response of soil biota to *Bromus* invasion may be controlled by the dominant species or interacting factors between trophic levels (Belnap and Phillips 2001).

Exotic species that threaten grasslands are the result of intentional or accidental introductions. *Festuca* was first introduced in the eastern US and became a common species used for livestock forage, soil conservation, and turfgrass (Ball et al. 1993). The specific invasion process that led to *Festuca* becoming established in our old field is unknown, but *Festuca* may have invaded from local populations or cattle may have been the vectors allowing *Festuca* to establish. Although *Festuca* is a valuable species in planted pastures, native grasslands lacking disturbance may be at risk of *Festuca* invasion resulting in *Festuca* becoming an undesirable species that alters ecosystem properties.

Our data do not support the hypothesis that species richness is a function of litter accumulation as compared to other grasslands in which the accumulation of litter reduced species richness (Knapp and Seastedt 1986; Carson and Peterson 1990; Facelli and Pickett 1991; Foster and Gross 1998). The absence of disturbance promotes litter accumulation, and with cessation of grazing we expected an increase in litter mass over time and a decline in species richness. However, the presence of *Festuca* may be altering the expected relationship between litter and species richness. *Festuca* has high litter quality, which leads to rapid decomposition and reduced litter accumulation (Wieder et al. 1983). The increase in *Festuca* may be reducing the amount of litter mass produced compared to an old field with no *Festuca*.

We expected that the low canopy cover of *Festuca* would not influence species richness in an old field dominated by warm-season native grasses. But on species-poor plots, *Festuca* became more abundant compared to species-rich plots. *Festuca* canopy cover increased on some plots, but the mean *Festuca* abundance remained low throughout the study and a causal relationship was not detected between *Festuca* canopy cover and species richness. However, studies in which *Festuca* was the major vegetation component showed that *Festuca* influenced vegetation dynamics by causing decreased species richness (Clay and Holah 1999) and decreased litter accumulation (Wieder et al. 1983).

In three years of this study, *Festuca* abundance increased and altered community composition and short-term succession without decreasing species richness. *Festuca* increased most in species-poor plots in which more opportunities exist for establishment. Unlike tallgrass prairie, species richness was not affected by litter accumulation in this old field. Invasion of *Festuca* had little to no influence on vegetation dynamics in the short-term, rather the influence of *Festuca* may be determined in the long-term with distinct changes in community composition. At this point, it is uncertain if *Festuca* will continue to increase in abundance or if *Festuca* will be maintained the current low abundance. To prevent a shift in species composition from late-successional warm-season grasses to a grassland dominated by *Festuca*, moderate levels of disturbance may need to be implemented. The long-term relationships between community composition and species richness with increasing *Festuca* need to be investigated in order to identify a threshold of *Festuca* dominance in grasslands.

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Table 1. Mean ($\bar{x}$) and standard error (SE) of species richness and *Festuca* canopy cover in an Oklahoma old field (n=16).

	Species Richness		*Festuca* Canopy Cover	
Year	$\bar{x}$	SE	$\bar{x}$	SE
1999	44	±2.0	2.3	±0.6
2000	37	±1.0	4.9	±1.0
2001	41	±2.0	10.9	±2.0

Table 2. Non-legume forb canopy cover (%) in 2001 and the correlations between non-legume forb species and *Festuca* canopy cover. Species with trace canopy cover represented values less than 0.1%.

Forb Species	Cover (%)	Forb vs *Festuca* (r)	P-value
Aster ericoides	13.0	0.5217	0.0382
Ambrosia psilostachya	6.0	-0.4437	0.0852
Amphiachyris dracunculoides	2.0	-0.3122	0.2392
Daucus pusillus	1.4	0.0831	0.7598
Monarda citriodora	1.0	-0.2215	0.4096
Asclepias syriaca	1.0	0.3532	0.1797
Erigeron strigosus	1.0	-0.5262	0.0363
Eryngium leavenworthii	1.0	0.0628	0.8172
Pyrrhopappus multicaulis	0.5	-0.1304	0.6304
Croton texensis	0.4	0.5913	0.0159
Solidago rigidia	0.3	-0.3527	0.1803
Cirsium undulatum	0.3	-0.0818	0.7633
Potentilla recta	0.3	-0.0384	0.8877
Galium boreale	0.3	0.1010	0.7097
Solidago gigantea	0.2	-0.2670	0.3175
Dracopis amplexicaulis	0.2	0.2200	0.4130
Hedeoma hispidium	0.2	-0.5236	0.0374
Sisyrinchium campestre	0.2	-0.1039	0.7017
Euphorbia marginata	0.1	0.1983	0.4616

Table 2. Continued.

Forb Species	Cover (%)	Forb vs *Festuca* (r)	P-value
Achillea millefolium	0.1	-0.2129	0.4286
Rudbeckia hirta	0.1	-0.5563	0.0252
Vernonia baldwinii	0.1	-0.3269	0.2165
Ratibida columnifera	0.1	0.0821	0.7623
Antennaria neglecta	0.1	-0.5168	0.0404
Oenothera linifolia	0.1	-0.5902	0.0161
Plantago patagonica	0.1	-0.3824	0.1438
Cerastium vulgatum	0.1	-0.3072	0.2472
Cirsium altissimum	0.1	0.1044	0.7003
Castilleja indivisa	0.1	-0.4608	0.0724
Oxalis stricta	Trace	-0.2852	0.2842
Liatrus punctata	Trace	-0.3619	0.1684
Scutellaria parvula	Trace	-0.3304	0.2133
Dacus carota	Trace	-0.36189	0.1684
Plantago aristata	Trace	-0.3619	0.1684
Triodanis perfoliata	Trace	0.0487	0.8578
Oenothera speciosa	Trace	0.0778	0.7747
Linum rigidum	Trace	-0.0287	0.9159
Chenopodium album	Trace	0.1262	0.6415
Gnaphalium obutsifolium	Trace	0.1436	0.5956

Table 2. Continued.

Forb Species	Cover (%)	Forb vs *Festuca* (r)	P-value
Urtica dioica	Trace	0.3094	0.2436
Physalis virginiana	Trace	-0.1007	0.7107
Hymenppapus artemisiifolius	Trace	-0.3421	0.1947
Senecio spp.	Trace	0.1011	0.7096
Cocculus carolinus	Trace	-0.3619	0.1684

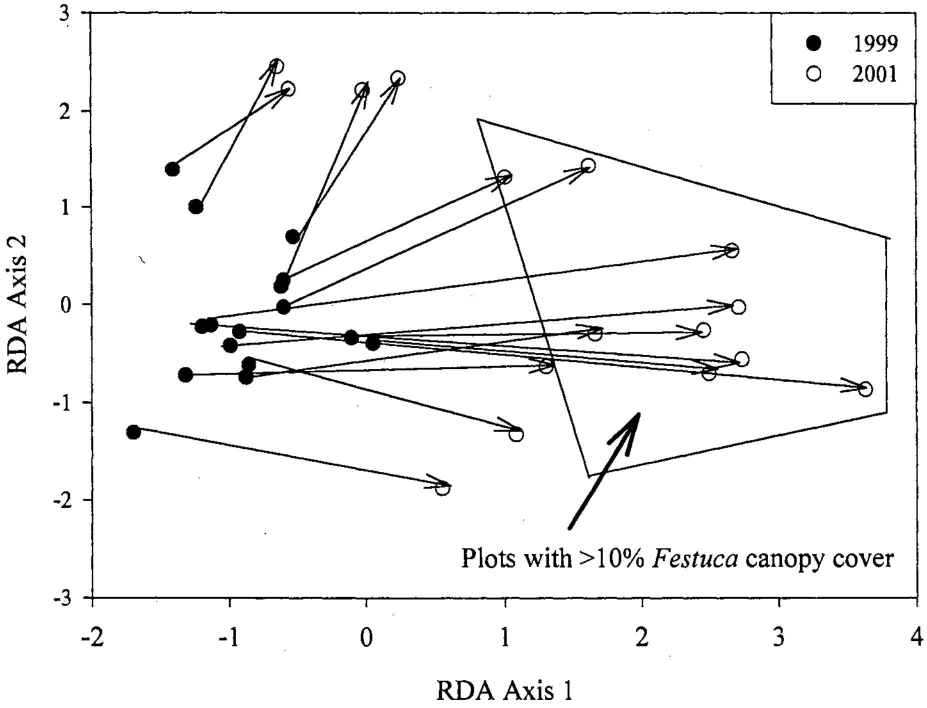

Fig. 1. Site scores for the first two axes of the redundancy analysis (RDA) following the removal of grazing in an Oklahoma old-field grassland from 1999 (●) to 2001 (○). RDA axis 1 is represented by increasing *Festuca* canopy cover and has an eigenvalue of 0.135 (P=0.005).

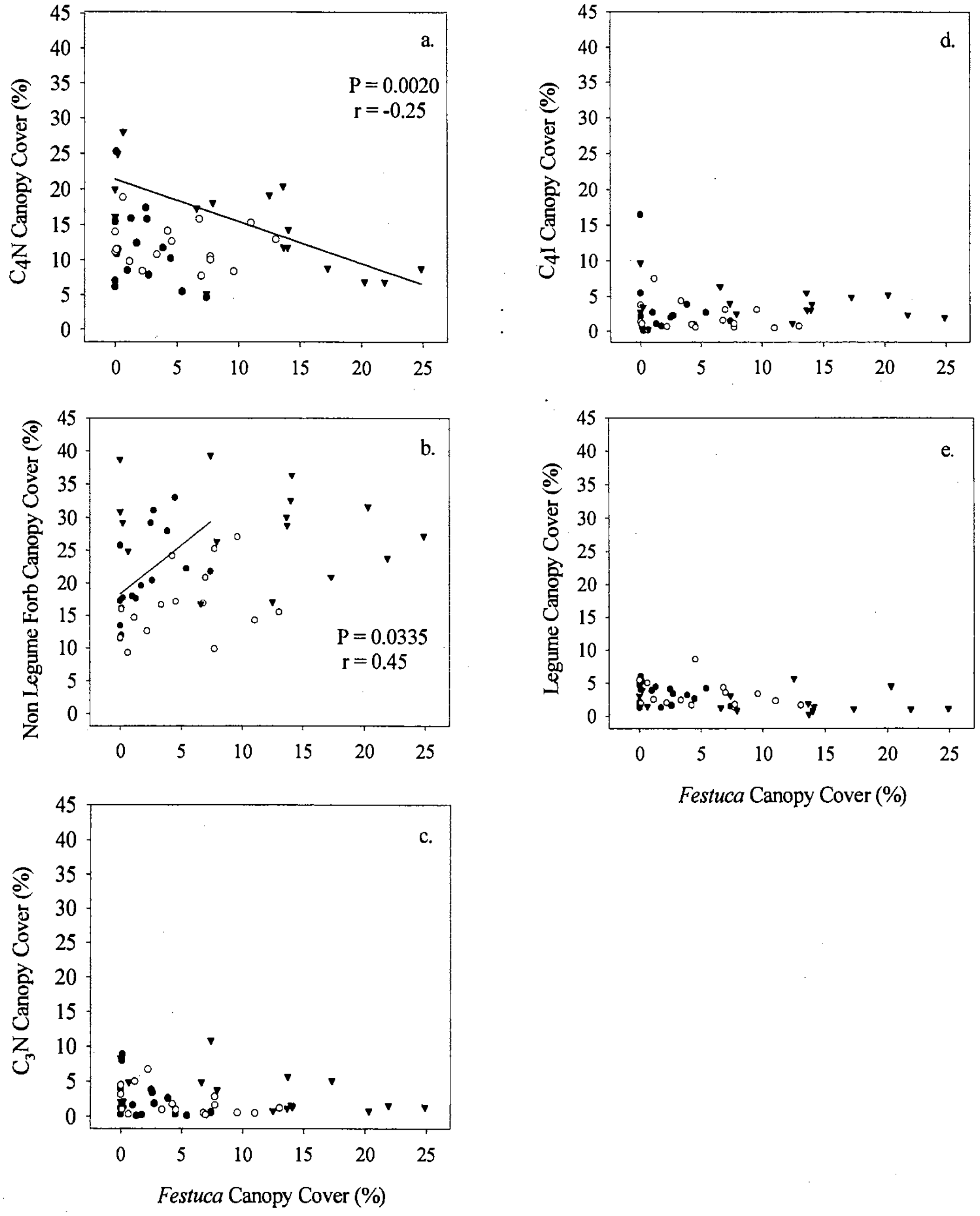

Fig. 2. Correlation between *Festuca* canopy cover and functional group canopy cover on an Oklahoma old field from 1999 to 2001. A. Correlation between *Festuca* canopy cover and warm-season native (C_4N) grass canopy cover in 1999 (P = 0.1305), 2000 (P = 0.7644), and 2001 (P = 0.0020, r = -0.25). B. Correlation between *Festuca* canopy cover

and non-legume forb canopy cover in 1999 ($P = 0.0335$, $r = 0.45$), 2000 ($P = 0.1176$), and 2001 ($P = 0.4915$). C. Correlation between *Festuca* canopy cover and cool-season native (C_3N) grass cover in 1999 ($P = 0.1286$), 2000 ($P = 0.0743$), and 2001 ($P = 0.0963$). D. Correlation between *Festuca* canopy cover and warm-season introduced (C_4I) grass cover in 1999 ($P = 0.4052$), 2000 ($P = 0.3284$), and 2001 ($P = 0.5304$). E. Correlation between *Festuca* canopy cover and legume canopy cover in 1999 ($P = 0.2099$), 2000 ($P = 0.4615$), and 2001 ($P = 0.5953$). ● = 1999 , ○ = 2000, and ▼ = 2001.

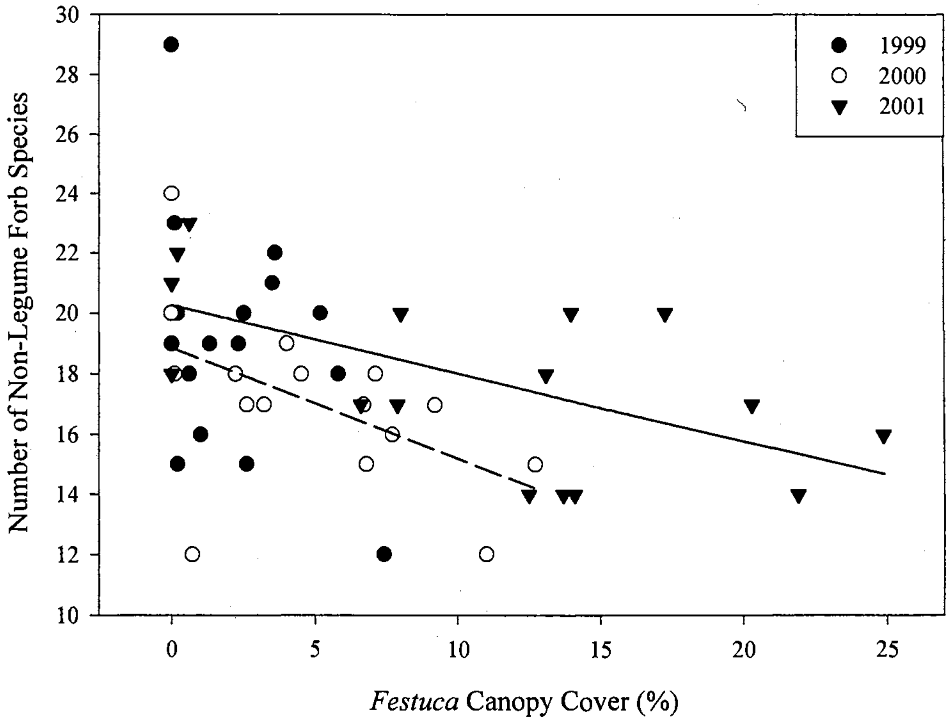

Fig. 3. Correlation between *Festuca* canopy cover and the number of non-legume forb species in 1999 (P = 0.1458.), 2000 (P = 0.0445), and 2001 (P = 0.0127).

● = 1999 , ○- - - -○ = 2000, and ▼—▼ = 2001.

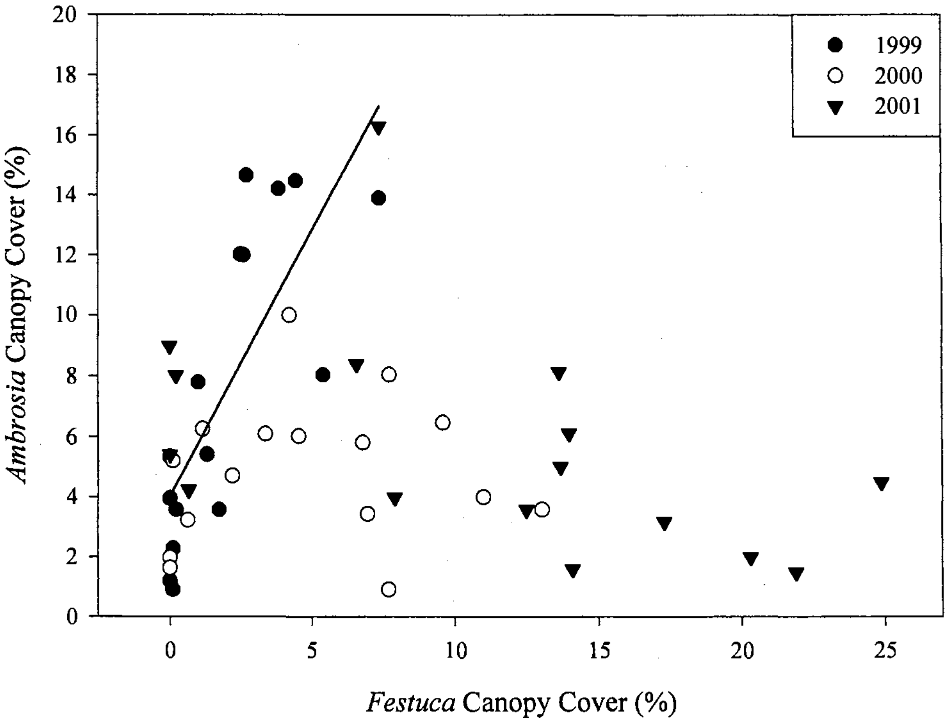

Fig. 4. Correlation between *Festuca* canopy cover and *Ambrosia* canopy cover in 1999 (P= 0.0005, r = 0.80), 2000 (P = 0.7425), and 2001 (P = 0.0688). ● = 1999, ○ = 2000, and ▼ = 2001.

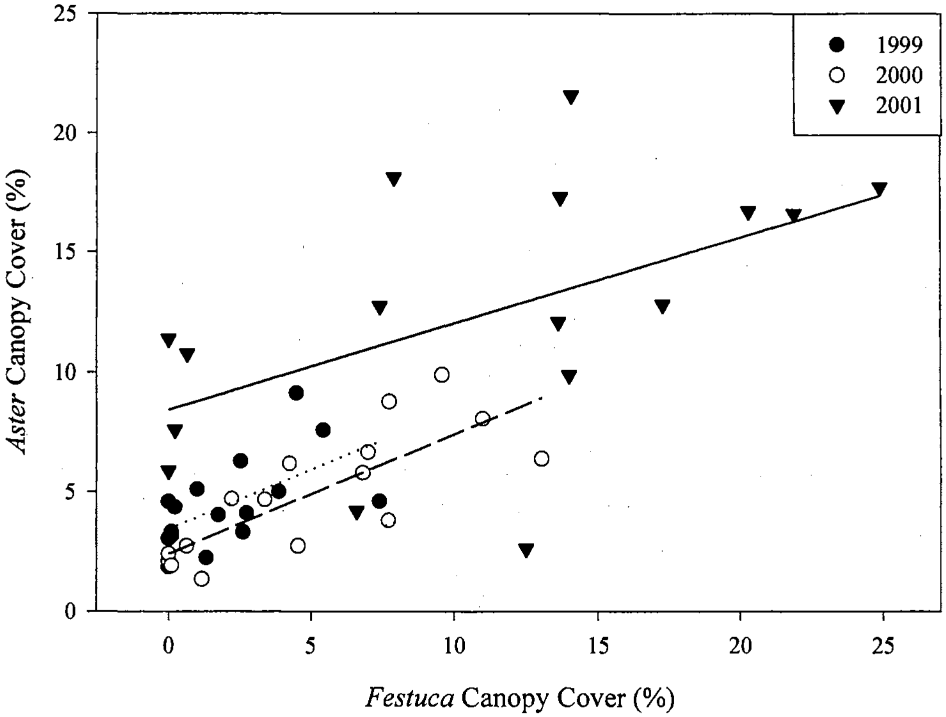

Fig. 5. Correlation between *Festuca* canopy cover and *Aster* canopy cover, 1999 (P = 0.0164, r= 0.59), 2000 (P = 0.0002, r = 0.80), and 2001 (P = 0.0349, r = 0.53). ●···● = 1999 , ○- - - -○ = 2000, and ▼—▼ = 2001.

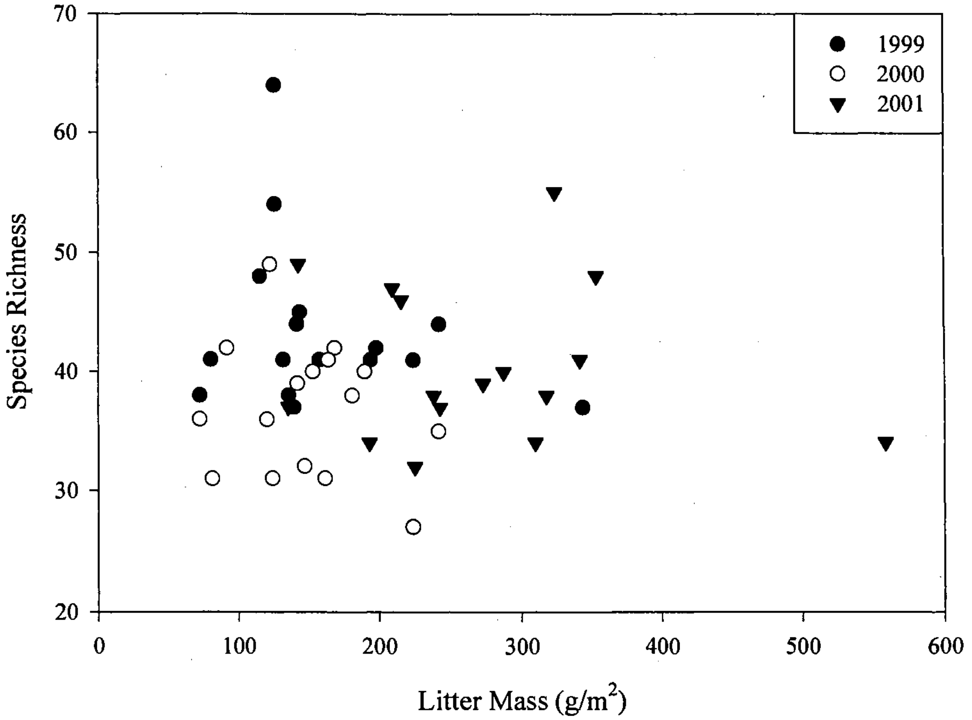

Fig. 6. Plot of species richness as a function of litter mass. Regression models were not significant in 1999 (P = 0.3616), 2000 (P = 0.5560), and 2001 (P = 0.6913). ● = 1999, ○ = 2000, and ▼ = 2001.

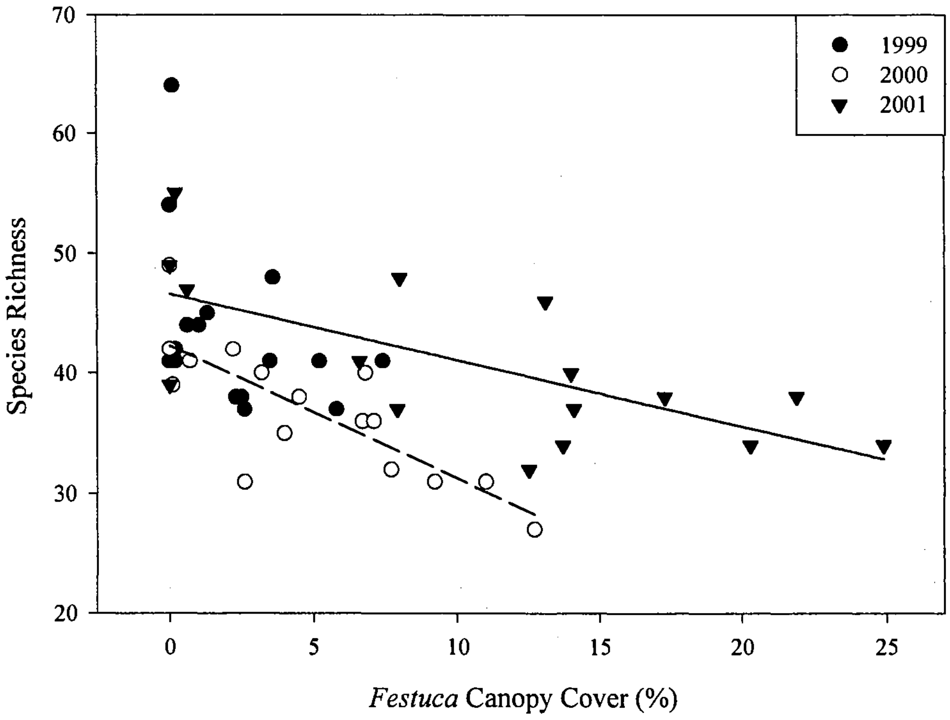

Fig. 7. Plot of species richness as a function of *Festuca* cover. Regression model in 1999 was not significant (P = 0.1069). Regression model in 2000 was significant (P = 0.0003), with Y = 42.3 – 1.1X where Y = species richness and X = *Festuca* canopy cover; R^2 = 0.62. Regression model in 2001 was significant (P = 0.0039), with Y = 46.6 – 0.5535X where Y = species richness and X = *Festuca* canopy cover; R^2 = 0.46. ● = 1999 , ○- - - -○ = 2000, and ▼—▼ = 2001.

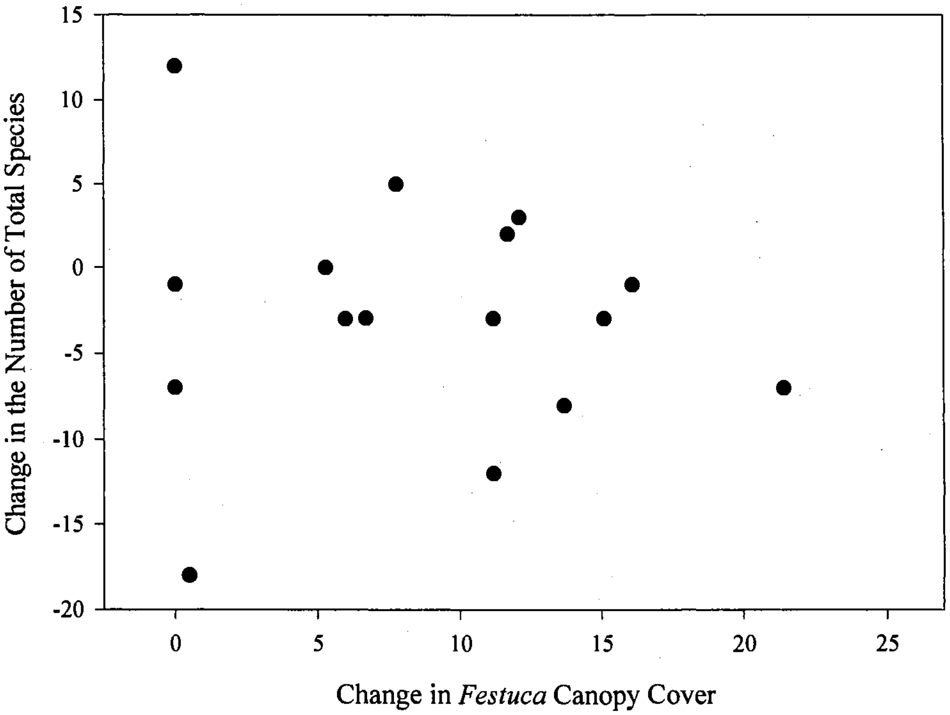

Fig. 8. Plot of the correlation between the change in *Festuca* canopy cover and the change in the number of total species on study plots (n=16) from 1999 to 2001 (P = 0.7636).

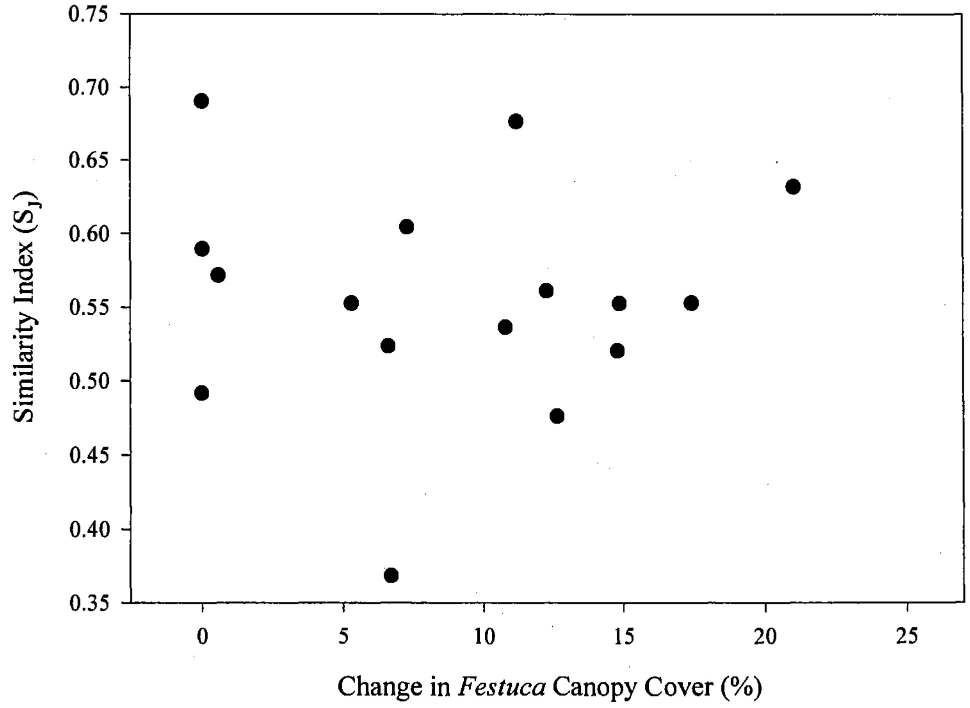

Fig. 9. Plot of the correlation between the change in *Festuca* canopy cover from 1999 to 2001 and the Jaccard Similarity Index (change in species presence) (P = 0.9953).

2

VITA

Susan Jean Tunnell

Candidate for the Degree of

Doctor of Philosophy

Thesis: VEGETATION DYNAMICS FOLLOWING CESSATION OF SEVERE DISTURBANCE IN AN OLD FIELD

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Personal Data: Born in Blair, Nebraska, on July 22, 1972, the daughter of Richard and Marlene Mullins.

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