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Old-field grassland successional dynamics following cessation of chronic disturbance

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Abstract.
Question: Does increasing *Festuca* canopy cover reduce plant species richness and, therefore, alter plant community composition and the relationship of litter to species richness in old-field grassland?
Location: Southeastern Oklahoma, USA.
Methods: Canopy cover by species, species richness, and litter mass were collected within an old-field grassland site on 16, 40 m × 40 m plots. Our study was conducted during the first three years of a long-term study that investigated the effects of low-level nitrogen enrichment and small mammal herbivory manipulations.
Results: Succession was altered by an increase in abundance of *Festuca* over the 3-yr study period. Species richness did not decline with litter accumulation. Instead, *Festuca* increased most on species-poor plots, and *Festuca* abundance remained low on species-rich plots.
Conclusions: *Festuca* may act as an invasive transformer-species in warm-season dominated old-field grasslands, a phenomenon associated more with invasions of cool-season grasses at higher latitudes in North America.

Keywords: *Festuca arundinacea*; Heavy grazing; Redundancy Analysis (RDA); Species richness.

Nomenclature: Anon. (1986).

Introduction

Grazing is a keystone disturbance that shaped the development and maintenance of the North American tallgrass prairie (Knapp et al. 1998). In temperate mesic grasslands dominated by native warm-season grasses, disturbance by grazing maintains species richness through its influence on succession and resource availability (Collins 1987; Collins & Steinauer 1998; Smith & Knapp 1999). Large herbivores continually influence vegetation structure and community composition through defoliation and trampling of vegetation (Collins & Steinauer 1998). Secondary succession in both native and old-field (cultivated then abandoned) grasslands after removal of heavy grazing usually results in an increase in late-successional warm-season grasses (Freeman 1998; Engle et al. 2000), an increase in litter accumulation that decreases species richness (Collins 1987; Carson & Peterson 1990; Foster & Gross 1998), and a decrease in abundance of non-dominant grasses and forbs (Weaver 1968; Knapp et al. 1998).

However, the presence of exotic species may alter the usual secondary succession in old-field grasslands following grazing removal (Tremmel & Peterson 1983; Fike & Niering 1999). In much of North America, *Festuca arundinacea* is an invasive perennial grass that is native to Eurasia (Gibson & Newman 2001). Its superior competitive ability conferred by an endophytic fungal symbiont (Clay 1990; Bacon 1995; Clay & Holah 1999; Matthews & Clay 2001) may lead to its dominance in native and old-field grasslands and thereby alter species composition (Clay & Holah 1999) and nutrient cycling (Gay et al. 1996).

The widespread use of *Festuca* for forage, turf, and soil conservation purposes began in the 1940s, and *Festuca* gained status as a commonly planted species in the eastern US (Ball et al. 1993; Hoveland 1993). Although *Festuca* is considered by pastoralists to be a valuable forage species in planted pastures, native and old-field grasslands lacking disturbance may be at risk of *Festuca* invasion, which can result in *Festuca* becoming a transformer species as defined by Richardson et al. (2000). Studies of *Festuca* have focused on the effects of species richness and plant-soil interactions of endophyte-infected *Festuca* (Clay & Holah 1999; Matthews & 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 relatively small amounts of *Festuca* in natural grasslands.

We assumed that *Festuca* alters vegetation dynamics and succession in warm-season old-field grasslands released from heavy grazing. Our objective was to describe vegetation dynamics in an old-field grassland released from chronic heavy grazing, dominated by warm-season grasses, and invaded by *Festuca*. We predicted that increasing *Festuca* would reduce species richness and therefore alter plant community composition and the relationship of litter to species richness. If this prediction were to hold and *Festuca* were to have clear ecosystem impacts, then *Festuca* would fit the designation of an invasive-transformer species (Richardson et al. 2000). Our study was conducted in the first three years of a long-term study that investigated the effects of low-level nitrogen enrichment and small mammal herbivory manipulations.

Methods

This study was conducted in southeastern Oklahoma at the Center for Subsurface and Ecological Assessment Research (CSEAR), operated by the US EPA, R.S. Kerr Environmental Research Center (Ada, OK). Cultivation at the site was abandoned around 1950. Herbaceous vegetation naturally re-established, and during the last half century the old-field grassland was grazed on a continuous basis until January 1998. Dominant vegetation consisted of early to mid-successional grasses and forbs including *Aristida oligantha*, *Andropogon virginicus*, *Ambrosia psilostachya*, and *Aster ericoides*. There were also exotic species present including *Festuca arundinacea* and *Cynodon dactylon*. The predominant soil type is Burleson clay (fine, montmorillonitic, thermic, Udic Pellusterts) (Anon. 1973). Annual precipitation is 990 mm, which predominantly occurs from April through October (Anon. 2000).

This old-field grassland has been the focus of an interdisciplinary study in which 16 plots of 40 m × 40 m received a factorial arrangement of nitrogen and small mammal herbivory exclusion treatments. Nitrogen was applied in the form of 34% NH_4NO_3 4 × during the year (February, May, August, and November) with a total of 16.3 kg-N.ha^{-1}.yr^{-1}. Small mammal herbivory was manipulated using 2.5 cm chain-link fence ca. 2 m in height. The treatments included (1) no nitrogen and no fence; (2) nitrogen and no fence; (3) no nitrogen and fence; (4) nitrogen and fence. To determine if species composition varied among treatments, we performed Redundancy Analysis (RDA) using CANOCO version 4 (ter Braak & Šmilauer 1998). To test for a nitrogen effect on canopy cover, nitrogen was the explanatory variable and fence was the covariable. To test for a fence effect, fence was used as the explanatory variable and nitrogen was a covariable. Because no treatment effects were detected for nitrogen ($P = 0.46$) or fence ($P = 0.14$), we performed all subsequent analyses at the plot level without regard to treatment.

We sampled 25 0.1-m^2 quadrats in herbaceous vegetation in May 1999, 2000, and 2001 for canopy cover and species richness. Canopy cover was estimated by species with the Daubenmire (1959) cover class method, and analysed by functional group. The grass and sedge functional groups were based on photosynthetic pathway and origin and included (1) cool-season native grasses; (2) *Festuca arundinacea* – a cool-season introduced grass; (3) warm-season native grasses, and (4) warm-season introduced grasses; (Waller & Lewis 1979; Hatch & Pluhar 1993; Stubbendieck et al. 1997). Forbs were separated by nitrogen fixing ability into non-legume forbs and legumes (Anon. 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. Litter was harvested from five 0.1-m^2 quadrats per plot in August 1998, 1999, and 2000. Litter mass was dried at 60 °C in a forced-air oven until reaching a constant weight.

We calculated average quadrat canopy cover ($n = 25$) for each species by plot in 1999, 2000, and 2001. To investigate community composition, we performed an RDA on the species data 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 our prediction that *Festuca* would alter the relationship of species richness to litter accumulation, we used regression analysis (Anon. 1991) to examine relationships among (1) species richness and litter mass and (2) species richness and *Festuca* cover. To determine if a plot's composition and species richness changed as *Festuca* increased, or alternatively to determine if *Festuca* increased on plots with respect to a plot's composition or richness, we calculated a Jaccard Similarity Index (Jongman et al. 1995) as follows,

$$S_J = c/(a + b + c) \quad (1)$$

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.

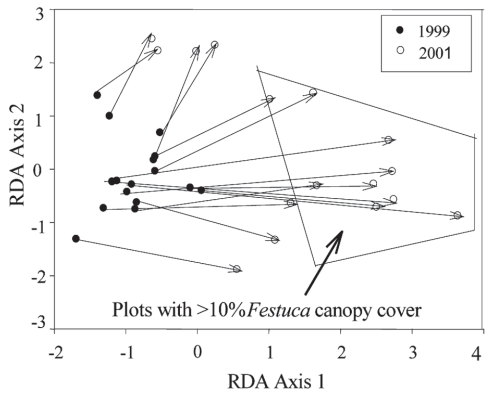

Fig. 1. Site scores for axes 1 and 2 of the Redundancy Analysis following grazing removal in an old-field grassland from 1999 (●) to 2001 (❍). Axis 1 is represented by increasing *Festuca* canopy cover and has an eigenvalue of 0.135 ($P = 0.01$).

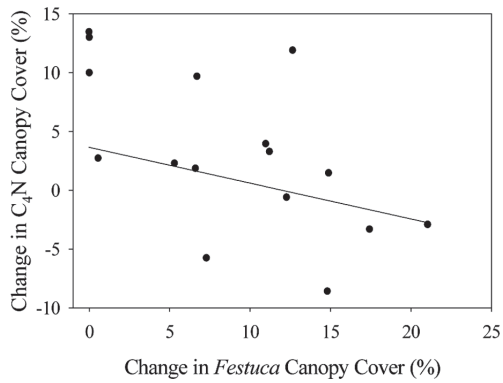

Fig. 2. Plot of the correlation between the change in *Festuca* canopy cover and the change in warm-season native canopy cover from 1999 to 2001 ($P = 0.04$; $r = -0.56$).

Results

Vegetation dynamics were explained by increasing abundance of *Festuca*. The change in species composition within plots is visually represented in the ordination diagram in which plots with the greatest amount of *Festuca* (> 10% canopy cover) are located in the right half of the diagram (Fig. 1). *Festuca* cover increased nearly five-fold on average across plots from 1999 to 2001 (Table 1), which is reflected along RDA Axis 1.

Festuca was correlated with the two dominant functional groups, warm-season native grasses and non-legume forbs that represented most of the species and total canopy cover (75% in 1999). Warm-season native grass cover was not correlated with *Festuca* cover in the first two growing seasons (1999: $P = 0.13$, 2000: $P = 0.77$) when *Festuca* cover was less, but by 2001 *Festuca* canopy cover was correlated negatively ($P < 0.01$, $r = -0.71$) with warm-season native grass cover. However, plots with the greatest warm-season native grass cover (e.g. 28%) had the smallest amount of *Festuca* cover (e.g. 0.7%) in 2001, and plots with low warm-season native grass canopy cover (e.g. 6.9%) had the greatest amount of *Festuca* cover (e.g. 21.9%). The relationship appears to be causal in that, on the average, warm-season native grasses decreased most on plots where *Festuca* increased most (Fig. 2).

Table 1. Mean and standard error (SE) of species richness and *Festuca* canopy cover in an Oklahoma old-field grassland ($n = 16$).

	Species richness		*Festuca* canopy cover (%)	
Year	Mean	SE	Mean	SE
1999	44	± 2	2.3	± 0.6
2000	37	± 1	4.9	± 1.0
2001	41	± 2	10.9	± 2.0

The dominance of two abundant non-legume forbs determined the overall influence of *Festuca* on the non-legume forb functional group. Non-legume forb cover was positively correlated ($P = 0.03$, $r = 0.53$) to *Festuca* canopy cover in 1999 when mean *Festuca* cover was 2.3%. But with greater *Festuca* canopy cover in 2000 and 2001, non-legume forb canopy cover and *Festuca* canopy

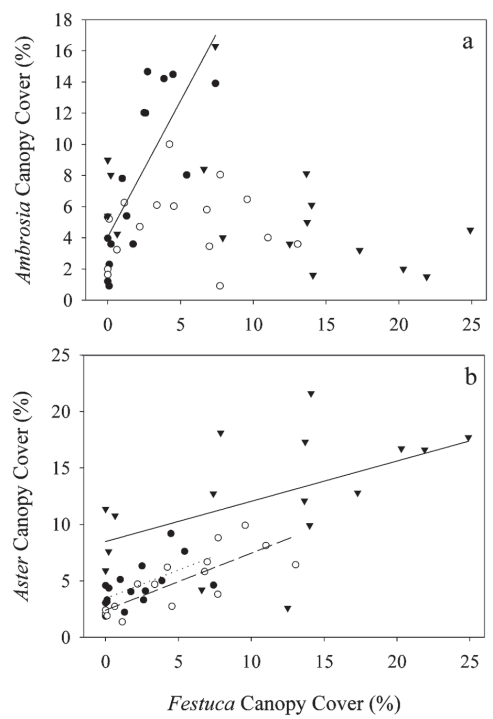

Fig. 3a. Correlation between *Festuca* and *Ambrosia* canopy cover in (●) 1999 ($P < 0.01$, $r = 0.80$); (❍) 2000 ($P = 0.74$) and (▼) 2001 ($P = 0.07$). **b.** Correlation between *Festuca* canopy cover and *Aster* canopy cover, 1999 ($P = 0.02$; $r = 0.59$), 2000 ($P < 0.01$; $r = 0.80$), and 2001 ($P = 0.03$; $r = 0.53$).

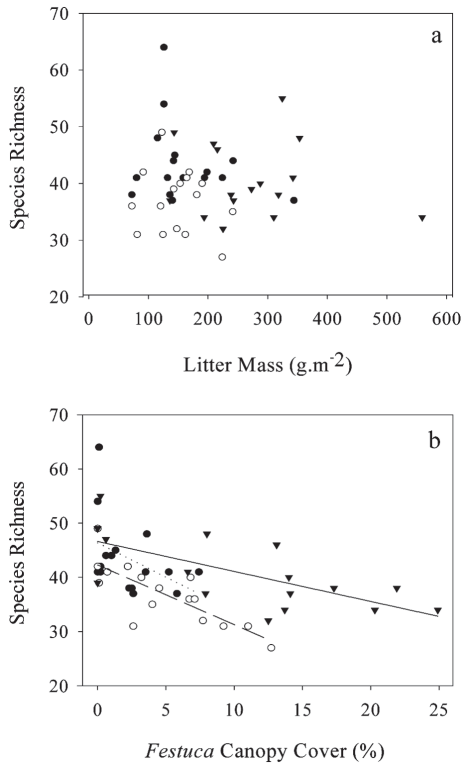

Fig. 4a. Species richness as a function of litter mass. Regression models were not significant in (●) 1999 ($P = 0.36$); (❍) 2000 ($P = 0.56$) and (▼) 2001 ($P = 0.69$). **b.** Species richness Y as a function of *Festuca* cover X. Regression model for 1999 not significant ($P = 0.11$); for 2000 significant ($P < 0.01$), with $Y = 42.3 - 1.1X$, $r^2 = 0.62$; for 2001 significant ($P < 0.01$), with $Y = 46.6 - 0.5535X$, $r^2 = 0.46$.

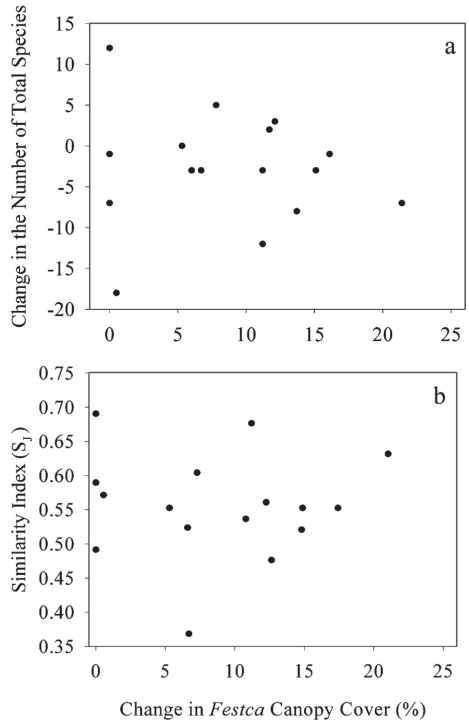

Fig. 5a. Change in *Festuca* canopy cover against change in the number of total species on 16 study plots from 1999 to 2001 ($P = 0.76$). **b.** Plot of the correlation between change in *Festuca* canopy cover from 1999 to 2001 and the Jaccard Similarity Index (change in species presence) ($P = 0.99$).

cover were not correlated ($P > 0.1$). *Ambrosia* canopy cover, which accounted for 20% of the non-legume forb canopy cover in 2001, was positively correlated with *Festuca* canopy cover in 1999 (Fig. 3a), but not in 2000 or 2001. Plots in which *Festuca* canopy cover was greatest, *Ambrosia* abundance was low. *Aster* canopy cover, which accounted for 44% of the non-legume forb canopy cover in 2001, was positively correlated with *Festuca* canopy cover in all three years (Fig. 3b). *Aster* canopy cover increased from 1999 to 2001 and was the most abundant non-legume forb in 2001. The loss of canopy cover contributed by minor non-legume forb species was accounted for by an increase in *Aster* canopy cover.

Species richness was not correlated to litter mass (Fig. 4a), but species richness was negatively related to *Festuca* canopy cover (Fig. 4b). However, the change in *Festuca* canopy cover was not correlated with the change in the total number of species from 1999 to 2001 (Fig. 5a). Furthermore, *Festuca* canopy cover increased on plots that were both similar and dissimilar in species presence from 1999 to 2001 (Fig. 5b).

Discussion

We expected grazing cessation in this seral old-field grassland with *Festuca arundinacea* to result in community vegetation changes that follow successional patterns observed elsewhere in old-field grasslands released from heavy grazing (Engle et al. 2000). Instead, a five-fold increase in *Festuca* accounted for much of the post-grazing successional trajectory and also was associated with a decrease in the dominant functional group, warm-season native grasses. Species richness did not decline with increases in *Festuca*; rather, *Festuca* increased on plots with low species richness.

We observed a distinct separation in ordination space among old-field grassland plots in the three years following grazing cessation that represented increasing abundance of *Festuca* over time. On plots in which *Festuca* cover exceeded 10%, *Festuca* increased by replacing warm-season native grasses, which ordinarily dominate post-disturbance succession in mid-continental warm-season grasslands (Collins & Steinauer 1998). Our findings contrast with other tall-grass prairie studies, where, in the absence of an invasive transformer, vegetation changes within native grassland plots over a 3-yr period are chronosequences from early- to late-successional

species (Collins & Adams 1983; Engle et al. 2000). In our plots, successional dynamics, in terms of functional group dominance but not in terms of species richness, are explained by increasing abundance of *Festuca* rather than by increasing mid- and late-successional warm-season native grasses.

Unlike temperate mesic grasslands, species richness was not correlated to litter accumulation in this old-field grassland, nor did species richness decline with increasing abundance of *Festuca*. Our study provides an exception to numerous observations that accumulation of litter in the absence of disturbance reduces species richness in temperate mesic grasslands in North America (Knapp & Seastedt 1986; Carson & Peterson 1990; Facelli & Pickett 1991; Foster & Gross 1998). Because the absence of disturbance promotes litter accumulation, one would expect an increase in litter mass over time and a decline in species richness with cessation of grazing. However, the presence of *Festuca* may alter the long-term relationship between litter and species richness. *Festuca* has high litter quality, including rapid decomposition and reduced litter accumulation (Wieder et al. 1983). Therefore, an increase in *Festuca* may reduce accumulated litter mass compared to mesic grasslands with no *Festuca*.

Even though canopy cover of *Festuca* was low, we predicted its abundance to be negatively correlated with species richness in this old-field grassland dominated by warm-season native grasses. However, *Festuca* did not influence species richness. Rather, *Festuca* became more abundant on species-poor plots than on species-rich plots. Therefore, although *Festuca* canopy cover increased on some plots, mean *Festuca* abundance remained low throughout the study and a causal relationship was not detected between *Festuca* canopy cover and species richness. Our results contrast to studies in which *Festuca,* as the dominant vegetation component, influenced vegetation dynamics by decreasing species richness (Clay & Holah 1999) and by decreasing litter accumulation (Wieder et al. 1983).

In other ecosystems where exotic species can become dominant, the exotics change community composition and alter ecosystem properties (Masters & Sheley 2001). Our observations suggest that the short-term response of *Festuca* to grazing release may be a previously unrecognized parallel in some respects to that of *Bromus tectorum* in the Intermountain region of the western US (DiTomaso 2000; Belnap & Phillips 2001; Masters & Sheley 2001) and *B. inermis* in northern latitudes (Bragg 1995; Bowles et al. 2003). *B. tectorum* invades and spreads rapidly, altering community composition and historic fire regimes. *B. tectorum* produces more litter and provides more fuel compared to native grasses and shrubs, thus increasing fire frequency (D'Antonio & Vitousek 1992; DiTomaso 2000). In the northern mesic prairie, *B. inermis* increases when fire is absent, whereas both cool- and warm-season native grasses decrease. The shift in the plant community from native grasses to *B. inermis* is associated with a decline in species richness (Bowles et al. 2003).

In our study, *Festuca* did not reduce species richness, but *Festuca* dominated the successional trajectory, which is consistent with *Festuca* functioning as an invasive-transformer species by exerting clear ecosystem impacts (Richardson et al. 2000). In manipulated grasslands seeded to *Festuca*, *Festuca* exerts even greater influence as an invasive-transformer species by reducing litter accumulation (Wieder et al. 1983), reducing species richness (Clay & Holah 1999), and altering nitrogen dynamics through greater uptake of nitrate nitrogen than native warm-season grasses (Gay et al. 1996). Our conclusions are based on short-term change following cessation of heavy grazing, but if *Festuca* continues to increase in our study old-field grassland, we expect it ultimately to influence ecosystem function similar to that in monocultures and simple mixtures of *Festuca*. The potential consequences of *Festuca* invasion in the southern grassland region dominated by native warm-season grasses are striking given these grasslands, unlike their more northern counterparts (e.g. *B. inermis* invasion), have not yet experienced significant invasion by cool-season grass species.

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