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The Combined Influence of Grazing, Fire, and Herbaceous Productivity on Tree–Grass Interactions

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Introduction

Although *Juniperus* communities are native to most regions of North America, they have proliferated in many areas of the Great Basin and Great Plains that historically supported grasslands, shrublands, and savannas. Explanations for the observed increases in *Juniperus* dominance, as well as other woody plant communities, are the subject of ongoing debate. The balance between herbaceous and woody vegetation is regulated by complex interactions between climate (e.g., amount and seasonality of rainfall), soils (e.g., soil texture and depth), and disturbance regimes (e.g., fire, gazing, browsing) (Walker 1987; Scholes and Archer 1997; Higgins et al. 2000). Changes in one or more of these factors can potentially elicit a change in the ratio of woody to herbaceous plants. Accordingly, climate change, intensification of grazing, elimination of fire and browsing (Hastings and Turner 1965; Grover and Musick 1990; Archer 1994; Fuhlendorf et al. 1996), atmospheric CO_2 enrichment (Idso 1992; Johnson et al. 1993), and nitrogen deposition (Köchy and Wilson 2001) have all been invoked as potential reasons for woody plant proliferation over the past century (see reviews by Archer 1994; Van Auken 2000). However, because these factors are correlative and interact across multiple spatiotemporal scales, it is neither feasible nor realistic to assess their relative importance using traditional, short-term factorial experiments. Field studies based on space-for-time substitutions and comparisons of landscapes with differing management histories have been used to assess long-term changes, but results from such studies are difficult to replicate, interpolate, or extrapolate and do not explicitly test causality. As a result, there is still considerable debate as to the relative importance of grazing, climate, and fire influences on community dynamics in drylands (O'Connor 1995; Fernandez-Gimenez and Allen-Diaz 1999; Illius and O'Connor 1999; Fuhlendorf et al. 2001). Dynamic simulation modeling is an underutilized tool that can be used to evaluate how climate or climate–disturbance interactions potentially affect tree–grass ratios and to test competing hypotheses attempting to account for woody plant increases over the past century.

Grazing, fire, and climate strongly interact to influence woody plant abundance via effects on herbaceous production and composition. High rainfall can promote

woody plant establishment, but greater herbaceous production in high rainfall years generates fine fuels and makes the system more prone to fire in subsequent dry periods (Swetnam 1988; Swetnam and Betancourt 1990; Harrington 1991). However, grazing can reduce the frequency and intensity of fire directly, by removing fine fuels and amplifying the heterogeneity of fuel continuity, and indirectly by causing a shift in plant community composition to less-productive and more-ephemeral species. Furthermore, growth of woody plants may be enhanced on grazed sites, thus enabling them to more quickly attain sizes at which they are more resistant to fire (Archer 1989, 1995). Accordingly, woody plant encroachment has been associated with grazing-induced reductions in fire frequency (Madany and West 1983; Swetnam 1988; Baisan and Swetnam 1990; Savage and Swetnam 1990). Our ability to predict the specific conditions under which woody plant encroachment might occur and the rates and dynamics of woody plant community development thus requires an integrated assessment of climate–fire–grazing interaction effects on herbaceous composition and production and woody plant growth rates.

Woody plant encroachment is a threat to sustainable livestock production in commercial enterprises and pastoral societies because of its adverse effects on herbaceous production (Scholes and Archer 1997). Habitat alterations resulting from woody plant encroachment also affect wildlife populations (Ben-Shaher 1991; Coppedge et al. 2001; Fuhlendorf et al. 2002). Prescribed burning is an important tool for maintaining grasslands and savannas (Wright and Bailey 1982); but to be effectively used, livestock grazing pressure must often be relaxed to allow fine fuels to accumulate, which requires a sacrifice of short-term revenues. Because relaxation of grazing is a cost, land managers are interested in knowing the minimum frequency with which a given management unit might need to be burned to maintain herbaceous production at a socioeconomically viable level. A knowledge of minimum prescribed fire frequencies is also of interest from the perspective of mitigating their undesirable effects on air quality. Estimating the minimum fire frequencies needed to maintain grasslands and savanna landscapes requires an integrated assessment of climate–fire–grazing interactions at decadal time scales.

Juniperus spp. (Cupressaceae) have been encroaching into grasslands and savannas in the central and western United States over the past century (Owensby et al. 1973; Bragg and Hulbert 1976; Bidwell et al. 2000; Archer et al. 2004; also see Chapter 8, this volume). Fuhlendorf et al. (1996) developed a model to examine fire frequency/intensity effects on growth and stand development of this arborescent evergreen tree. We elaborated that model to include grazing and climate influences on herbaceous composition and production and used it to address the following questions for *Juniperus* spp. in the southern Great Plains of North America: (1) What is the rate of transformation of grasslands and savannas to *Juniperus* woodlands? (2) How does the fire frequency required to maintain a savanna physiognomy change with increasing grazing pressure? (3) How do fire, grazing from domestic herbivores, and weather interact across sites with variable productivity? (4) Are shifts from grass to *Juniperus* dominance gradual, and linear; or nonlinear and characterized by abrupt thresholds? and (5) What are management

options to limit the encroachment of *Juniperus* plants into Southern Great Plains grasslands and savannas?

Study Sites

The model was parameterized for sites of contrasting productivity in the Southern Great Plains of the United States. A low-productivity site [mean annual precipitation (MAP) = 600 mm] was represented using data from the Texas Agricultural Experiment Station on the Edwards Plateau (Amos and Gehlbach 1988) near Sonora, Texas (31° N, 100° W; Smeins and Merrill 1988). A high-productivity site (MAP = 850 mm), representing tallgrass prairie landscapes, was parameterized with data from the Oklahoma State University Research Range near Stillwater (36°22′ N, 99°04′ W) (Ewing and Engle 1988). Landscapes at both sites were gently sloping (2%–4%) and heterogeneous with respect to soil depth. Both sites were historically grassland-dominated landscapes interspersed with patches of *Quercus* species, and both sites have recently experienced marked increases in *Juniperus* spp. [*J. ashei* at the Edwards Plateau site (Smeins and Merrill 1988) and *J. virginiana* at the tallgrass prairie site (Owensby et al. 1973; Bragg and Hulbert 1976; Bidwell et al. 2000)].

Model Overview

The following section briefly describes a previously developed landscape-level model that simulated the influence of fire frequency and intensity on the density and size of *J*. ashei, an evergreen, nonsprouting, arborescent, woody plant at the low-productivity site. A conceptual diagram of the model and the input and output factors are presented in Figure1. Subsequent sections then describe how that model was elaborated to examine changes in woody plant abundance under fire regimes altered by livestock (cattle) grazing on sites with contrasting aboveground primary production potentials.

Fire and Woody Plant Abundance

The STELLA (High Perfomance Systems, Inc. Hanover 1994) modeling environment was used to simulate the landscape-level influence of fire on woody plant dominance on a topoedaphically homogenous landscape over 150 years with an annual time step (Fuhlendorf et al. 1996) (see Figure 1). State variables represented the density of *J*. ashei (plants/ha). *Juniperus* plants established from seed and subsequently grew into canopy diameter size-classes (Table 1) based on known
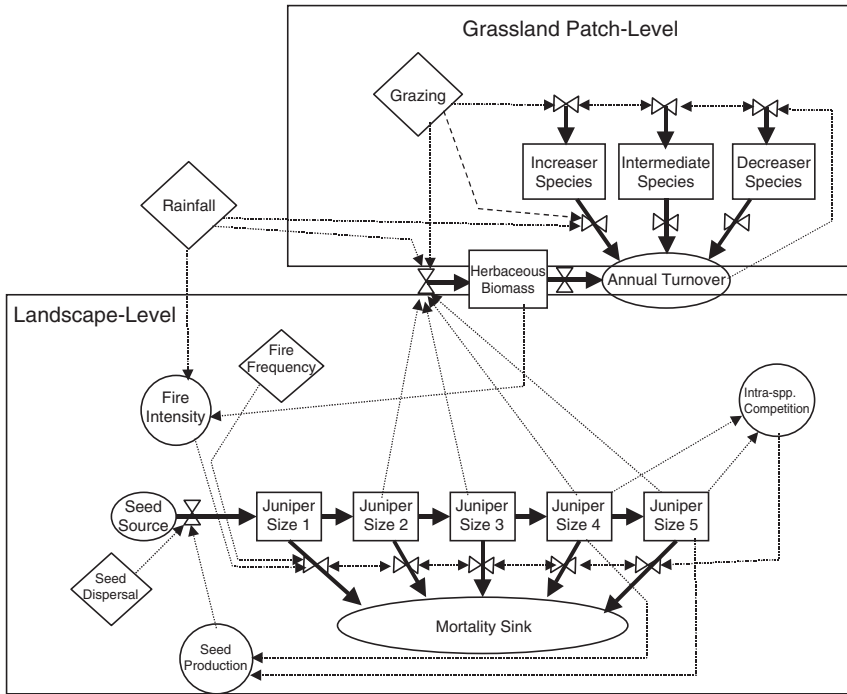
Figure 1 Multilevel conceptual model of the interactive effects of climate, grazing, and fire on tree–grass interactions. The abundance of a fire-sensitive woody plant (*Juniperus* spp.) is affected by fire intensity. Livestock grazing, rainfall, and woody plant abundance influence the composition and aboveground biomass of the herbaceous vegetation, which affects fire intensity. The model was used to ascertain what frequency of prescribed burning would be required to maintain a grassland or savanna physiognomy on high (850 mm) and low (600 mm) annual rainfall sites with contrasting livestock grazing regimes. *Solid lines* represent information transfer; *dotted lines* represent influence. (From Fuhlendorf et al. 1996)

Table 1 Mortality (%) assigned to *Juniperus* size-classes experiencing different fire intensities[a]

Size-class	Canopy diameter (m)	Fire intensity		
		Low	Medium	High
1	<0.75	20	70	99
2	0.76–1.50	20	60	99
3	1.51–3.00	10	50	80
4	3.01–6.0	0	5	30
5	>6.0	0	1	5

Fire intensity is a function of herbaceous biomass expressed relative to the maximum production under conditions of no livestock grazing (see text for explanation).
[a]See Fuhlendorf et al. (1996).

size–age relationships (Fuhlendorf 1992; Fuhlendorf et al. 1997). Trees reached seed-bearing size in diameter Class 3 and were considered mature in Class 5. Seedling establishment was a function of seed dispersal from offsite sources and onsite seed production. Seed dispersal into the area by birds and mammals (Chavez-Ramirez and Slack 1994) was simulated as stochastic events. Onsite seed production was dependent on the density of *Juniperus* plants in the three largest canopy classes. Seedling establishment was stochastic and constrained by environmental conditions (see Fuhlendorf et al. 1996).

    Juniperus mortality was density dependent and varied with tree size. *Juniperus* mortality from fire was dependent on tree size and the frequency and intensity of burning. Fire intensity, in turn, was influenced by herbaceous biomass and season (summer versus winter). As trees increased in size and density, they became more resistant to fire-induced mortality and caused a reduction in herbaceous biomass (Fuhlendorf et al. 1997), resulting in a feedback that decreased fire intensity and subsequent fire mortality. Fire-induced mortality altered tree size and density, resulting in a feedback to intraspecific tree competition. Climatic variability was not included in the *Juniperus* growth/mortality model, except as a random affect on seedling establishment.

Grazing and Fire

The *Juniperus* stand development model reviewed in the previous section was elaborated to include livestock (cattle) grazing influences on the fire regime. Livestock grazing changes both the herbaceous composition and productivity, thus altering fire frequency/intensity to potentially affect woody plant mortality. Grazing reduces herbaceous biomass both directly (through the process of forage consumption) and indirectly by causing the replacement of productive species by less productive species. State variables in the grazing submodel included total herbaceous biomass and the relative composition of three herbaceous species functional groups (S_i): those that *increase* in importance with grazing (hereafter referred to as "increasers"), those that *decrease* in importance with grazing (= "decreasers"), and an *intermediate* category representing species whose abundance peaks under moderate levels of grazing (= "intermediates") (Dyksterhuis 1949). The relative contribution to aboveground net primary production (ANPP) varies among these three functional groups as grazing increases (decreasers > intermediate > increasers) (Dyksterhuis 1949; Fuhlendorf and Smeins 1997). In our model, annual ANPP was represented as a proportion of the maximum expected to occur under no livestock grazing and favorable climatic conditions: 3500 kg/ha at the low rainfall site (Wiedenfeld and McAndrew 1968; Bryant et al. 1979; Taylor 1983; Robinson 1990; Kothmann 1968) and 6500 kg/ha at the high-productivity site (Engle et al. 1987; Gillen et al. 1998; McCollum et al. 1999). Direct effects of grazing on herbaceous biomass occurred through defoliation of grasses and was dependent on grazing intensity (heavy, moderate, or ungrazed).

Parameterization

In the original model, fire intensity was dependent on herbaceous biomass (high or low) and season of fire (winter or summer) (Fuhlendorf et al. 1996). In this study, the model was parameterized only for winter (cool season) fires, where intensity was dependent on herbaceous biomass. Summer fires were not considered because of the lack of quantitative data on herbaceous production. For the low-productivity site, fire intensities were "high" when herbaceous biomass was more than 60% of maximum potential, "medium" when herbaceous biomass was 30% to 60% of maximum, and "low" when herbaceous biomass was less than 30% of maximum. Fire intensity classes for the high-productivity site were set at greater than 40% (= high), 20% to 40% (= medium), and less than 20% (= low) of maximum herbaceous production potential. Fire-induced tree mortality was a function of tree size and fire intensity (see Table 1). Fire frequency (no fire, or fire every 2, 5, 7, 10, or 15 years) was a driving variable in the modeling experiment.

Juniperus virginiana and *J. ashei* were the woody species of interest at the high- and low-productivity sites, respectively. Time spent in the canopy diameter size-classes in Table 1 was 10, 10, 10, and 25 years, respectively, for *J. ashei* (Fuhlendorf 1992; Blomquist 1990; Fuhlendorf et al. 1996), and 8, 8, 8, and 20 years, respectively, for *J. virginiana* (Engle and Kulbeth 1992). The growth rate of *J. virginiana* at the high-productivity site was approximately 20% greater than
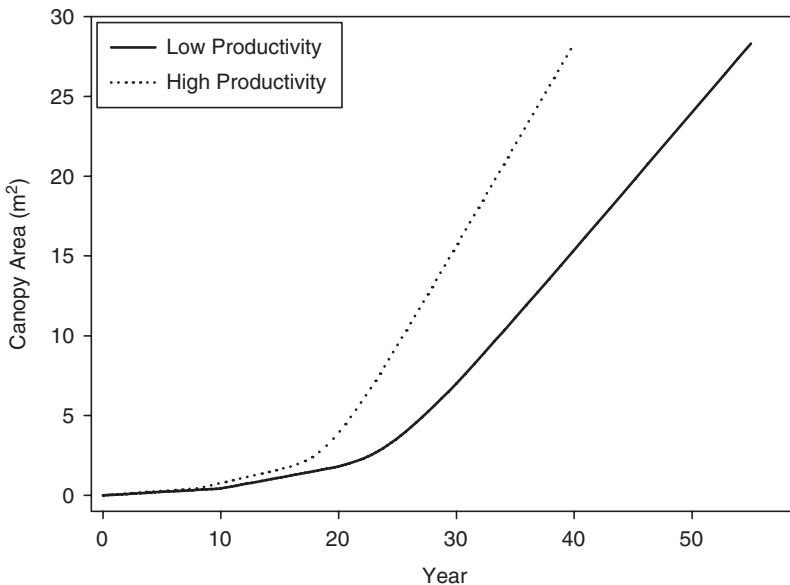

Figure 2 Rates of *Juniperus* canopy area (m²) expansion without fire on the low productivity site [*J. ashei*; mean annual precipitation (MAP), 600 mm; Fuhlendorf 1992] and the high productivity site (*J. virginiana*; MAP, 850 mm; Engle and Kulbeth 1992)

that of *J. ashei* at the low-productivity site without fire (Figure 2). Fire–grazing interactions were evaluated with 10-replicate, 150-year simulations (annual time steps).

Juniperus species are unpalatable evergreens that generally experience little herbivory (Pritz et al. 1997; Riddle et al. 1999), so it is reasonable that the influence of livestock herbivory is confined to the herbaceous component. The long-term influence of grazing on herbaceous vegetation at the low-productivity site has been well documented (see Fuhlendorf and Smeins 1997, 1998). Short-term studies at the high-productivity site indicate similar grazing influences on herbaceous productivity and composition (Cassels et al. 1995; Gillen et al. 1998). Grazing effects on floristic composition and production at both sites are reasonably described by the Dyksterhuis (1949) conceptual model. The same grazing submodel was therefore used for both sites, with variables scaled to represent relative production and composition. The model was initialized as an open savanna with herbaceous functional group (S_i; $i = 1$–3) composition representing a plant community ungrazed by livestock: increasers (S_1) = 10%, intermediates (S_2) = 20%, and decreasers (S_3) = 70%. Livestock grazing was a driving variable set as heavy continuous, moderate continuous, or ungrazed. Moderate and heavy continuous grazing represented removal of 50% and 75% of annual net primary productivity, respectively. In regions with low productivity, it is common to defer livestock grazing 1 year before a prescribed fire to accumulate fine fuel. We therefore included two additional grazing regimes to simulate this practice: moderate with 1-year rest and heavy with 1-year rest. Weather variation (W) (annual precipitation and temperature extremes) was represented as a random driving multiplier ranging from 0.01 to 2.0. In an average year ($W = 1.0$), weather would have no influence on primary production.

Changes in herbaceous composition were dependent upon the formation of gaps (G) within the grassland patches. G was influenced by W and calculated as:

$$G = \sum_{i=1}^{3} S_i^* (W^* 0.05) \tag{1}$$

where S_i was the relative composition of each herbaceous functional group. On average, this allowed for a 5% annual turnover in the relative abundance of increaser, decreaser, and intermediate grazing response groups and reflected an average longevity approximating that observed for dryland grasses (about 20 years; Canfield 1957). During wet years ($W = 0.01$ to 0.7) annual herbaceous turnover ranged from ~0 [$G = \sum_{i=1}^{3} S_i^* (0.01^* 0.05)$] to 10.5% [$G = \sum_{i=1}^{3} S_i^* (0.7^* 0.05)$]; during dry years ($W = 1.3$ to 2.0), annual turnover ranged from 19.5.

[$G = \sum_{i=1}^{3} S_i^* (1.3^* 0.05)$] to 30% [$G = \sum_{i=1}^{3} S_i^* (2.0^* 0.05)$]. When gaps formed, the funcional group composition then changed as dictated by grazing intensity (Table 2).

The relative composition of each grazing response group (S_i) was multiplied by a constant for each grazing treatment–species group combination (C_j; $j = 1, 9$) to

Table 2 Percentage (%) of herbaceous gaps occupied by various functional groups (increasers, decreasers, and invaders) under contrasting livestock grazing

Herbaceous Functional group	Grazing regime[a]		
	Heavy	Moderate	Ungrazed
Increasers	90	40	10
Intermediates	9	40	15
Decreasers	1	20	75

Gaps were created by climate-induced plant turnover (see Eq. 1).
[a]Regimes: heavy, 75% utilization; moderate, 50% utilization.
Source: Based on Fuhlendorf and Smeins (1997).

Table 3 Constants (C_j, $j = 1, 9$) used to estimate the relative herbaceous biomass in each functional group–livestock grazing regime combination

Functional group (S_i; $i = 1–3$)	Grazing regime		
	Heavy	Moderate	Ungrazed
Increasers	0.20	0.35	0.50
Intermediates	0.40	0.50	0.75
Decreasers	0.60	0.90	1.00

account for changes in primary production accompanying changes in herbaceous species (functional group) composition (Table 3). Heavy grazing resulted in communities dominated by less productive, early seral increasers, and intermediate species that were also more responsive to climatic variation than the more productive decreasers they replace (Fuhlendorf and Smeins 1997, 1998). Thus, weather variation was represented by multiplying the C_jS_i term for the increaser and intermediate species by W. To account for the influence of woody plant density on herbaceous biomass, the sum of the individual C_jS_i terms were multiplied by HB/100 (proportional reduction in herbaceous biomass for all *Juniperus* size-classes relative to the maximum that could occur in the absence of trees; Fuhlendorf et al. 1996). Herbaceous aboveground biomass (H, expressed as a percentage of the maximum possible), accounting for the combined influence of grazing, weather, and woody plant density, was thus calculated as

$$H = W(C_jS_1 + C_jS_2) + C_jS_3 * (HB/100). \qquad (2)$$

Results

Low-Productivity Site (600mm MAP)

Simulated changes in herbaceous functional group composition (Figure 3) and production (Table 4) were in general agreement with field data from the central Texas low-productivity site. In the absence of livestock grazing, the initial herbaceous vegetation, dominated by the taller, more productive species in the *decreaser* functional group, maintained its dominance. Under heavy livestock grazing,
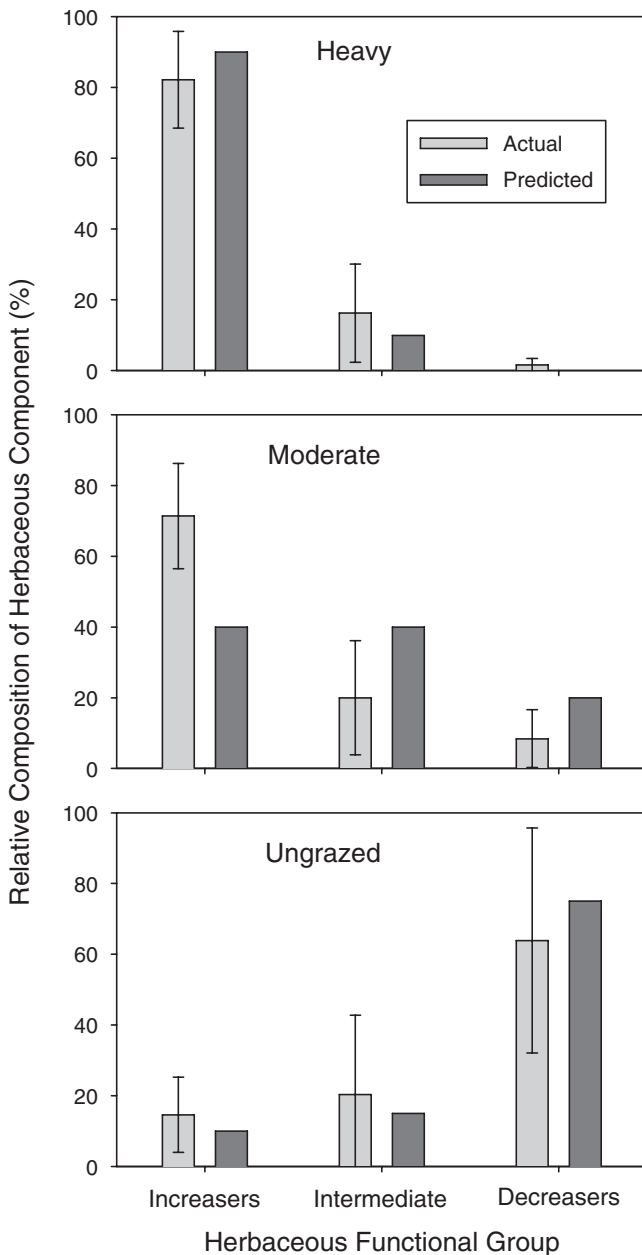
Figure 3 Mean (±SE), actual (Fuhlendorf and Smeins 1997), and predicted relative composition of herbaceous functional groups (*increasers*, *intermediates*, *decreasers*) in contrasting livestock grazing treatments (*heavy*, *moderate*, and *ungrazed*) at the low-productivity site in central Texas. For this comparison, initial conditions of the model were set to those present when livestock grazing treatments and long-term monitoring plots were installed in 1948 (heavily grazed). Results show the relative composition in 1993 (the last year of monitoring data available when this study was conducted)

Table 4 Range of predicted and actual herbaceous biomass (kg/ha) (standing biomass after grazing) on landscapes with contrasting woody cover and livestock grazing histories at the Texas A&M Sonora Research Station near Sonora, Texas

Woody cover (%)	Data source	Grazing treatment		
		Heavy	Moderate	Ungrazed
0	Model prediction	300–875 (8%–25%)	1050–2275 (30%–65%)	2800–3500
0	Bryant et al. (1979)[a]	—	1600–3200 (46%–91%)	—
20	Model Prediction	280–800 (8%–22%)	1000–2100 (29%–60%)	2600–3300 (75%–95%)
20	Kothmann (1968)	100–500 (3%–15%)	400–1100 (11%–31%)	
20	Taylor et al. (1979)	—	600–1600 (17%–45%)	—
25	Robinson (1990)	—	500–2200 (15%–63%)	
30	Model prediction	175–700 (5%–20%)	875–1575 (25%–45%)	1225–2100 (35%–60%)
30	Taylor (1983)	100–900 (3%–25%)	—	800–1600 (23%–46%)

Percent of potential maximum (3500 kg/ha) is shown in parentheses.
[a]Woody plants removed via root plowing followed by seeding with grasses.

dominance shifted to the *increaser* functional group, with species comprising the *decreaser* group becoming rare. The amount and annual variation in aboveground herbaceous biomass was influenced by grazing regime, by the density and size of *J. ashei*, and by climatic variability (Figure 4). In the absence of fire, density of the three largest *J. ashei* size-classes increased rapidly, peaking at a density of ~200 plants ha^{-1} within about 60 years (Figure 4B). At this point, density-dependent thinning occurred, causing densities to stabilize at ~100 plants ha^{-1}, regardless of grazing pressure. About 60 years into the simulation, herbaceous biomass became dynamically stable at ~10% to 40% of maximum potential on the heavily grazed and ungrazed sites, respectively (Figure 4A). With a 10-year fire frequency (and cessation of grazing for 1 year before each fire, to allow fine fuel accumulation), the herbaceous production of ungrazed and moderately grazed landscapes was maintained (Figure 4C) because fire intensity was sufficient to prevent *J. ashei* encroachment. However, on the heavily grazed site, fire intensities were reduced such that prescribed burning could not curtail *J. ashei* encroachment (Figure 4D). As a result, *Juniperus* densities increased, causing herbaceous biomass to decline (Figure 4C) to levels comparable those of the heavily grazed–no fire treatments (Figure 4A), albeit 40 to 50 years later. Temporal trends in the decline of herbaceous aboveground production accompanying grazing and *Juniperus* encroachment were nonlinear function of fire frequency mediated by rainfall (Figure 5). The variation around the mean herbaceous production values (Figure 5) and mean *J. ashei* densities (Table 5) computed from replicated simulations was typically small in herbaceous- and woody-dominated vegetation states and markedly higher in states representing transitions between these contrasting endpoints.
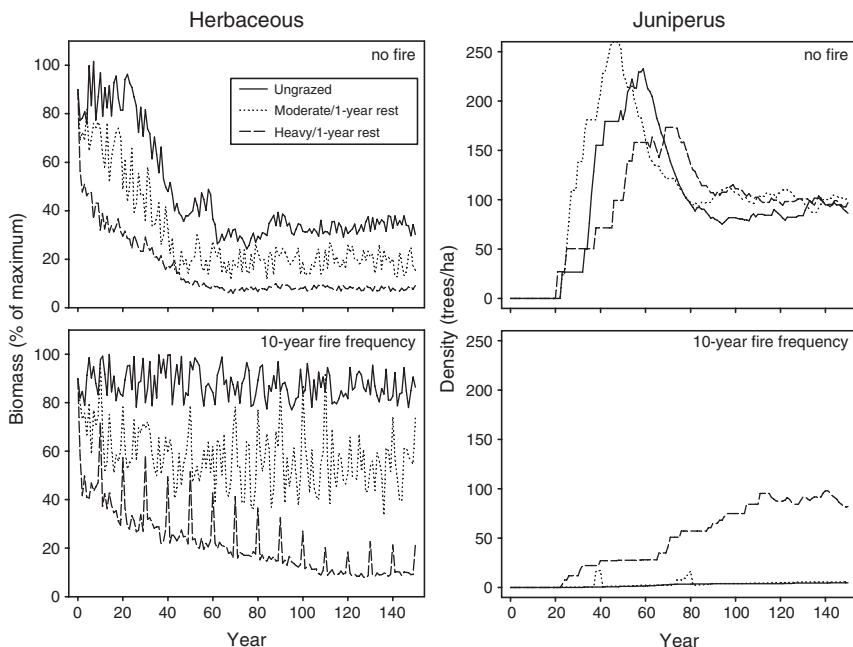
Figure 4 Simulated trends in herbaceous biomass (*left column:* top = **A**, bottom = **C**) and *Juniperus* density (*right column:* top = **B**, bottom = **D**) under three livestock grazing regimes and two fire regimes at the low rainfall site in central Texas (output representative of a single model run is shown). Herbaceous biomass is expressed as a percentage of the maximum possible; *Juniperus* density is pooled across the three largest size-classes. Annual variation in herbaceous biomass is weather related (Fuhlendorf and Smeins 1997, 1998). For burned landscapes, pastures were rested for 1 year before each fire to allow fine fuel accumulation (resulting in biomass production peaks in years with sufficient rainfall)

At the low rainfall site in central Texas, in the absence of livestock grazing (ungrazed), a fire frequency of less than 15 years was, on average, sufficient to keep *Juniperus* abundance low (<22 total trees ha^{-1}) and maintain herbaceous production at levels above 70% of maximum (see Figure 5C; see Table 5). Under moderate grazing, the critical fire return interval required to maintain grassland dominance on the low-productivity site was 5 years (see Figure 5B). With a fire frequency of 15 years, *Juniperus* woodlands consistently developed because grazing-induced reductions in fuel loads reduced fire intensity to the point where trees could consistently attain sizes resistant to fire. When grazing was curtailed the year before burning, extension of the fire return interval to 10 years enabled maintenance of a savanna physiognomy (Figure 5E).

Heavy grazing led to the formation of a closed-canopy woodland (see Table 5) with low herbaceous production (see Figure 5A). Herbaceous biomass (5%–25% of maximum) was never sufficient to carry a fire of sufficient intensity to prevent *Juniperus* establishment and growth, even in years with optimum rainfall.
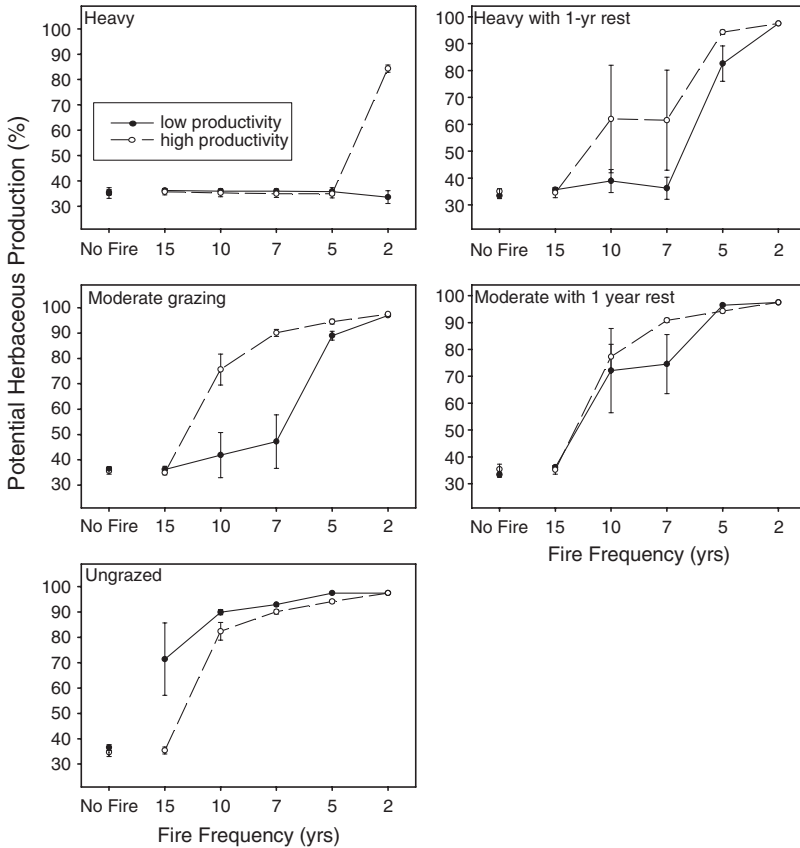
Figure 5 Potential herbaceous production at high- (MAP = 850 mm, Oklahoma) and low- (MAP = 600 mm, central Texas) productivity sites in relation to fire frequency for landscapes experiencing *Juniperus* encroachment under different livestock grazing regimes (**A** = *heavy, top left*; **B** = *moderate, middle left*; **C** = *ungrazed, bottom left*; **D** = *heavy + rest, top right*; **E** = *moderate+rest, lower right*). Potential herbaceous production is presented relative to the maximum potential in the absence of *Juniperus*. Results are means ± SD from replicated (*n* = 10) 150-year simulations

Table 5 Mean density (trees/ha) of large (canopy diameter >6 m) *Juniperus ashei* trees across all grazing treatments and fire frequencies for the low productivity site

Fire treatment	Grazing treatment				
	Ungrazed	Moderate with rest	Moderate	Heavy with rest	Heavy
No fire	70.6 (4.4)	70.2 (4.6)	70.0 (4.6)	71.8 (3.5)	72.7 (3.3)
15-year frequency	21.4 (84.1)	70.5 (3.5)	69.3 (3.6)	71.3 (2.7)	70.5 (2.6)
10-year frequency	6.9 (14.5)	20.5 (94.6)	59.4 (24.9)	66.8 (7.3)	70.6 (2.7)
7-year frequency	3.8 (13.16)	12.8 (88.3)	46.1 (34.3)	45.0 (3.2)	69.9 (2.7)
5-year frequency	0 (0)	0.9 (55.6)	7.6 (22.4)	3.9 (61.5)	70.6 (5.1)
2-year frequency	0 (0)	0 (0)	0.5 (60.0)	0 (0)	74.2 (7.1)

Coefficients of variation shown in parentheses.

Maintenance of grasslands was possible under heavy grazing but required both a high fire return interval (5 years) and 1 year of deferred grazing (Figure 5D).

High-Productivity Site (850 mm MAP)

Greater herbaceous production potential at the high rainfall Oklahoma grassland site meant greater fine fuel loads, hence greater fire intensity and higher tree (*J. virginiana*) mortality. However, *Juniperus* growth rates were also greater at the high rainfall site (see Figure 2). As a result, the relationship between grazing and fire return intervals necessary to maintain grassland dominance differed markedly from that observed for the low rainfall site. In the absence of livestock grazing, the critical fire frequency required to maintain a savanna physiognomy on the high-productivity site (10 years) was greater than that required on the low-productivity site (15 years) (Figure 5C; Figure 6). Moderate grazing had relatively little influence on the fire frequency needed to maintain a savanna on the high-productivity site (10 years), whereas moderate grazing dramatically altered the fire return interval needed to maintain savanna on the low-productivity site (15 years under no grazing versus 5 years under moderate grazing) (see Figure 5B). Indeed, for the ungrazed, moderately grazed, and moderately or heavily grazed with a rest before burning, the fire return interval required to maintain grasslands was fairly robust at about 10 years. Under heavy grazing, sufficient fuel could accumulate on the high-productivity site such that burning at 2-year intervals was still a management option for maintaining a savanna physiognomy, even without deferring grazing the year before burning (Figures 5A, 6).
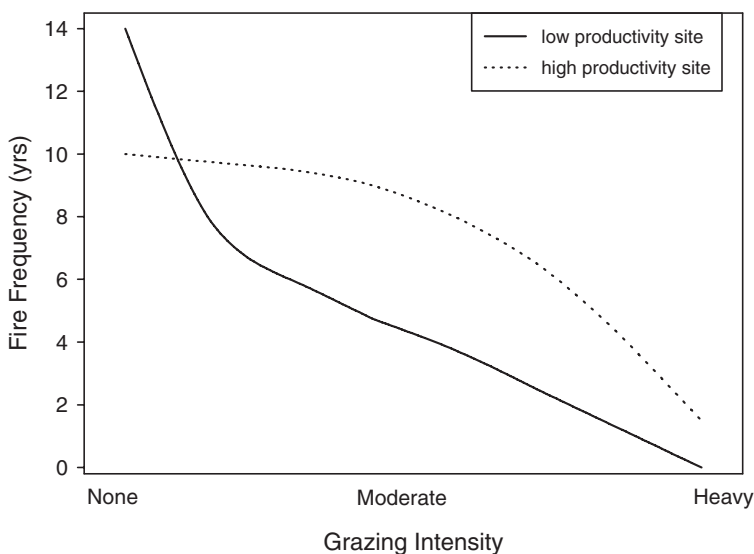

Figure 6 Theoretical presentation of fire frequency at various grazing intensities at a low-productivity site and a high-productivity site

Discussion

Long-term (45-year) analysis of permanent quadrats from the low-productivity site has documented directional trends, whereby heavy grazing resulted in short-grass-(= increasers) dominated communities of reduced productivity (Fuhlendorf and Smeins 1997, 1998). When grazing is relaxed, herbaceous composition changes and communities become dominated by more productive midheight grasses (= decreasers). Long-term directional shifts between these herbaceous states were generally linear and primarily driven by grazing; short-term dynamics embedded within the long-term changes exhibited nondirectional fluctuation associated with variability in weather and seed production. Simulated changes in species composition were representative of the long-term general patterns from the field with the assumption that fine-scaled stochasticity is removed by the large-scale nature of the model (Fuhlendorf and Smeins 1997, 1998). Predictions of relatively stable states in herbaceous composition dependent on grazing accurately depicted field data following 45 years under different grazing treatments (see Figure 3).

The balance between contrasting woody and herbaceous life forms that characterize savanna ecosystems are a function of interactions between rainfall (notably amount and seasonality), soil properties (notably texture and depth), fire, and herbivory (grazing of grasses, browsing of woody plants) (Walker 1987; Scholes and Archer 1997; Van Auken 2000). Numerous conceptual and quantitative models have attempted to addressed the nature and relative importance of these interactions (c.f. Belsky 1990; Scholes and Walker 1993; Höchberg et al. 1994; Higgins et al. 2000). These models have led to multiple hypotheses concerning the stability of grasslands and the coexistence of grasses and woody plants in savannas. Destabilization of grasslands and tree–grass interactions in savannas appears to have occurred since the mid-1800s, as evidenced by widespread reports of woody plant proliferation in these systems worldwide (see bibliography in Archer et al. 2001, 2004). As reviewed in the Introduction, causes for these changes in the life form composition of vegetation remain the subject of active debate.

In this study, we evaluated the interactive influence of fire, livestock grazing, and climatic fluctuation on the woody–herbaceous balance on sites with contrasting annual rainfall. Model predictions of changes in herbaceous aboveground production associated with grazing and *Juniperus* encroachment were accurate (see Figure 3). Pre-settlement fire frequencies are not well known in the Southern Great Plains but have been estimated at 3 to 10 years (Fuhlendorf and Engle 2001). This frequency was the combined result of natural ignitions and ignitions by First Nation peoples (Sauer 1950; Stewart 1955; Schüle 1990). Our results suggest that maintenance of pre-Anglo-European settlement grasslands and open savannas in the southern Great Plains could have been achieved with fires occurring as infrequently as 15 years. At longer fire return intervals, tree size and density increase past critical thresholds to limit potential herbaceous production to below what is needed to carry a fire that can limit *Juniperus* stand development. In the absence of fire, these grasslands can be transformed into dense, closed-canopy woodlands within 50 years without

invoking directional changes in climate, atmospheric CO_2, or nitrogen deposition. The direct effect of grazing was manifested in the composition and production of the herbaceous community, which indirectly influenced tree dynamics through its effect on fuel loads and hence fire intensity. This indirect effect of grazing on tree–grass interactions was exacerbated on low-productivity sites. Weather patterns were not important to long-term changes except when the woody–herbaceous mixture was near a critical transition threshold inflection point. Under these conditions, variation in weather produced a wide range of grass–woody plant ratios, as indicated by the large variance in mean grass production (see Figure 5).

The striking differences between high-and low-productivity sites were the result of differences in the outcome of interactions between the availability of fine fuel for fires and woody plant growth rates. Fine fuel biomass required to generate fires capable of inducing mortality of 1-m-diameter, 1-m-tall *J. ashei* and *J. virginiana* trees is about 1500 kg/ha (Wink and Wright 1973; Engle and Kulbeth 1992). This amount would be equivalent to about 25% and 40% of the maximum potential herbaceous production for the high- and low-productivity sites, respectively. When livestock grazing occurred at intensities that did not reduce fuel loads below these threshold levels, it had no bearing on the relationship between fire and woody plant density (see Figure 5). When maximum potential production was inherently low as a consequence of rainfall constraints, grazing and periodic drought were more likely to combine to reduce the probability that fuel loads would be sufficient to cause fire-induced tree mortality (see Figure 4). Therefore, the advent of moderate livestock grazing had minimal influence on the grass–woody balance at the high-productivity sites but was critical in the conversion of grasslands to woodlands through its interaction with fire on low-productivity sites. Heavy grazing reduced the effectiveness of fire in maintaining grassland dominance regardless of site productivity.

It is generally assumed that the herbaceous vegetation associated with long-term grazed sites is less effective in precluding woody plant seedling establishment than the herbaceous vegetation characterizing lightly grazed sites. Similarly, it is generally assumed that heavily grazed herbaceous plants will be less effective at competitively excluding woody plant seedlings than lightly grazed or ungrazed herbaceous plants. However, numerous field experiments have not borne out these generalizations (Archer 1995; Jurena and Archer 2003). The interpretation emerging from some of these field experiments is that herbaceous vegetation has relatively little influence on woody plant seedling establishment. As a result, it has been predicted that grazing-induced changes in herbaceous composition and production should influence woody plant recruitment via alteration of the fire regime rather than via relaxation of grass competition with tree seedlings (Archer 1995). Results from our modeling experiments support this prediction and concur with field data from the low rainfall site (Smeins and Merrill 1988; Rieneke 1996; Smeins and Fuhlendorf 1997).

Our model represented climate as a random variable that primarily influenced production and composition of the herbaceous component. Climatic fluctuations were particularly noteworthy when fire frequencies were near the threshold levels

required to prevent *Juniperus* stand development. Most variables in the model were parameterized as fixed, so random climatic fluctuations were responsible for most of the variation in herbaceous production means that were generated by averaging over 10 model runs. Variance about the herbaceous production means was substantially inflated when *Juniper* densities were at fire frequency threshold levels critical for maintaining grassland (see Figure 5). This result suggests that as landscapes near thresholds associated with fire return interval and grazing intensity their resistance to state-change may be enhanced under some weather patterns and compromised under others.

Model results illustrate how nonlinear rates of change in life form composition may occur when several factors are simultaneously evaluated. Effects of grazing or fire on a given plant functional group, when evaluated independent of each other, would likely produce very different dynamics. However, when interactions between fire, grazing, and plant functional groups are considered in concert, feedback mechanisms may result in dramatic threshold behaviors. Resource managers should be cognizant of these nonlinear dynamics and monitor conditions so that land use practices can be adjusted before critical thresholds are crossed. Our model affirms the critical role that fire plays in the conservation and management of grasslands and savannas. Increased stature and density of woody plants can be controlled with periodic fires, and this model indicates the fire frequency required to maintain grassland and savanna structure under various grazing regimes. Utilizing minimal fire frequencies and low intensities can reduce economic costs and hazards associated with prescribed fires. On highly productivity landscapes, fire can be readily integrated into traditional grazing practices and greatly enhance economic returns (Bernardo et al. 1988). On low-productivity sites, management of grazing becomes critical because of fuel limitations. The use of fire to maintain grassland dominance fuel loads is inherently constrained by low rainfall or shallow soils that require either more frequent fires or conducting the fires under more extreme environmental conditions, which increase the cost of conducting the fire and the probability of a fire escaping.

Conclusions

- Fire, grazing, and site productivity interact to regulate the relative abundance of woody and herbaceous vegetation. Weather influenced the nature of these interactions and may strengthen or dampen feedbacks. These weather effects may be particularly important when systems are near transition thresholds and may make systems either more or less vulnerable to state-change.
- Maintenance of savannas and grasslands requires prescribed burning.
- The frequency of fire needed to maintain grassland and open savanna was a positive function of woody plant growth rates.
- Shifts from grass to woody plant dominance were nonlinear and were characterized by fire frequency thresholds that varied as a function of livestock

grazing, which affected the fine fuel loads required to generate fires that impact woody plants.

- On low-productivity grassland sites, *Juniperus ashei* gained dominance in about 60 years without fire or grazing. A fire return interval of ~15 years was required to maintain an open grassland in the absence of grazing. Moderate grazing reduced the required fire return interval to ~5 years. With heavy grazing and fire, reductions in herbaceous biomass were such that fire could not be used to maintain an open grassland or savanna.
- On high-productivity sites, *Juniperus virginiana* gained dominance in ~45 years without fire or grazing. Under conditions of no or moderate grazing, a fire return interval of ~10 years was required to maintain an open grassland. With heavy grazing, a 2- to 3-year fire return interval was required to maintain an open grassland or savanna.
- Managers should be cognizant of fire–grazing–climate interactions and the nonlinear, threshold responses of vegetation to variations in their relative importance. This awareness, coupled with use of relatively simple models such as the one used in this study, would enable land use practices to be adjusted before undesirable transitions from grass to woody plant dominance occur.

Summary

The physiognomic transformation of grasslands and savannas to shrublands and woodlands has been widely reported in the world's drylands over the past century. Its causes, which are the subject of active debate, generally center around changes in climate, intensification of livestock grazing, and elimination of fire. Because these factors are correlative and interact across multiple spatiotemporal scales, quantifying their relative importance via field experimentation is difficult. We therefore conducted modeling experiments to evaluate the interactive effects of grazing, fire, and climate on tree–grass dynamics in low- and high-productivity southern Great Plains U.S. grasslands. Results from the multiscale modeling approach indicate that maintenance of pre-Anglo-European grasslands and open savannas in the southern Great Plains could have been achieved with fire return intervals of 15 years or less. In the absence of fire, succession to *Juniperus* woodland can occur on both high- and low-productivity sites, regardless of livestock grazing pressure. The livestock grazing regime (none, moderate, or heavy) did, however, affect the rates and dynamics of the physiognomic transformation and the eventual steady-state woody plant density. Our results offer guidelines for assessing the frequency and timing of prescribed burns that might be needed to maintain the grass–woody plant balance in grazed ecosystems.

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