



Impact of feedbacks on Chihuahuan desert grasslands: Transience and metastability

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[1] A simplistic model of grass-shrub dynamics was used to investigate the role of grass demographic processes on grassland-shrubland dynamics when grasses are in competitive advantage over shrubs. The model suggests that a feedback between grass biomass and soil erosion may cause an abrupt transition to a shrubland state. The model explains how a simple change in either grass recruitment or grass mortality, presumably linked to climate change or grazing, could produce changes in Holocene flora and the conversion of grasslands to shrublands, which has been observed throughout the southwestern U.S. in the past 150 years.

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1. Introduction

[2] Arid and semiarid regions cover more than 40% of the Earth's land surface. Broad-scale land degradation in these regions (i.e., desertification) directly impacts ca. 250 million people in the developing world and could potentially impact the 2.5 billion people who live in dry lands worldwide [Reynolds *et al.*, 2007]. Desertification is also increasingly recognized as an important element of global change. For instance, changes in vegetation structure and albedo accompanying desertification can significantly impact regional climate with feedbacks to ecosystem dynamics [Taylor *et al.*, 2002]; and desertification has been shown to impact animal biodiversity [Bestelmeyer, 2005]. Atmospheric dust with its myriad impacts [Kaufman *et al.*, 2005; Kellogg and Griffin, 2006; Okin *et al.*, 2004] is produced in deserts worldwide and is increased with desertification [Gillette and Pitchford, 2004; Moulin and Chiapello, 2006]. A report by Seager *et al.* [2007] predicts increasingly arid conditions in the next decades in the southwestern U.S., southern Europe, the Mediterranean, and the Middle East, which will contribute to desertification.

[3] One of the major forms of desertification worldwide is the invasion of shrubs into former perennial grasslands in an abrupt, and potentially irreversible, transition [Allred, 1996; Archer *et al.*, 1995; Schlesinger *et al.*, 1990]. Abrupt changes are often thought to be indicative of transitions between alternative stable states [Westoby *et al.*, 1989] and to arise as a result of positive feedbacks [Wilson and Agnew, 1992]. A grass-fire feedback is often invoked to explain the

rapid shift to a shrubland state under the assumption that shrubs outcompete grasses [Van Auken, 2000]. The competitive advantage of shrubs may have arisen relative recently due to CO₂ fertilization [Polley, 1997], warming [Idso, 1992], or changes in precipitation patterns [Brown *et al.*, 1997]. Or, shrubs may have always been in competitive advantage but were limited by seed dispersal, particularly through the agency of Native Americans, who were significant shrub seed predators [Fredrickson *et al.*, 2006]. Several recent papers have shown that the grass-fire feedback does result in bistable dynamics when shrubs outcompete grasses [Anderies *et al.*, 2002; D'Odorico *et al.*, 2006].

[4] The shift to the alternative stable shrub state required two factors: a feedback that creates the alternative stable state, and a driver that initiates the shift from one state to the other. In the case of the grass-fire feedback, fire suppression induced by grazing acts as the driver of the state change, and the fire-induced shrub mortality acts as the feedback. This feedback is thought to occur because fires kill shrub seedlings, and fires can only be sustained with significant grass biomass acting as a continuous stratum of fuel. With increased grazing, it is argued, fire became less frequent, allowing more shrubs to survive to maturity. In this model, because shrubs are in competitive advantage relative to grasses, the greater shrub biomass that occurred after the cessation/reduction of wildfire would have further limited grass biomass and the incidence of wildfire, thus completing the feedback loop. In a system where grasses maintain a competitive advantage over shrubs, the grass-fire feedback would not be able to explain the existence of the shrubland state as a stable state of the system.

[5] However, other feedbacks have been suggested to be responsible for the bistable dynamics of Chihuahuan Desert grasslands. In particular, Schlesinger *et al.* [1990] suggested that soil erosion was a key contributor to shrub encroachment. In this case, the loss of grass cover, due for example to overgrazing, is followed by loss and redistribution of soil resources from plant interspaces to areas beneath shrub canopies, creating semi-permanent fertile islands. Many

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experimental studies have investigated the importance of this grass-erosion feedback, with the consensus that erosion by wind and water is capable of removing soil resources required for plant growth and propagation [Li *et al.*, 2007, 2008; Okin *et al.*, 2001; Parsons *et al.*, 2003; Schlesinger *et al.*, 1999, 2000; Wainwright *et al.*, 2000]. In this case, the transition to the shrub state could have been induced by changes, namely a decrease, in the reproduction rates of grasses.

[6] Paleodata argue for the predominant role of climate in the decrease of the reproduction rates of grasses prior to the arrival of European settlers. For example, during the first millennium C.E. shrub cover in the Chihuahuan Desert was high relative to the middle Holocene when lowlands in the region were grass-dominated [Van Devender and Spaulding, 1979]. The shift from grass to shrub domination during the first millennium C.E., cannot be explained by livestock grazing. Instead, a climate-related change in plant recruitment must have been responsible for this prehistoric change in physiognomy. The paleoclimatic record indicates anomalously warm periods during the first millennium C.E. (the Medieval Warm Period), and the dominance of shrubs during this time might have been related to warmer climate [Bradley *et al.*, 2003; Stine, 1994]. The conversion of Chihuahuan desert shrublands back to grasslands has been attributed by Neilson [1986] to the Little Ice Age. Grass establishment during the cooler, moister conditions of this period must have outpaced mortality enough to reestablish Chihuahuan desert grasslands. After the Little Ice Age, climatic conditions became warmer and drier. Higher grass mortality in conjunction with limited recruitment likely opened the door for dominance of xerophytic shrubs such as *Larrea* and *Prosopis*, even before the arrival of European settlers and their cattle.

[7] The purpose of this report is to investigate, from a modeling perspective, the ability of the grass-erosion feedback to induce bistability in Chihuahuan Desert grasslands, especially when grasses are in competitive advantage with regard to shrubs. We use this modeling framework to speculate on the possible state of the Chihuahuan Desert landscape just prior to the European colonization. We argue that bistability could have been a key feature of grass-shrub dynamics even without invoking the existence of a competitive advantage for shrubs or a grass-fire feedback. In the presence of the grass-fire feedback and the grass-erosion feedback, bistability is a likely feature of these ecosystems regardless of whether grasses or shrubs are in competitive advantage with regard to the other. We argue further that, in the presence of the grass-erosion feedback, demographic changes linked to climate may have been partially responsible for the susceptibility of grasslands to shrub invasion even if grasses had retained their competitive advantage over shrubs.

2. Model Description

[8] Our model considers growth of existing plants, rate of establishment of individuals from seed, vegetative reproduction, and plant mortality. Under the assumption that grasses have a competitive advantage over shrubs, we model the dynamics of grass biomass, G [mass/area],

independently of those of shrubs. We express the temporal variability in G as

$$\frac{dG}{dt} = \alpha G \left(1 - \frac{G}{C_G} \right) - k_G G \quad (1)$$

[9] The first term on the right-hand side of equation (1) uses a logistic model to express the increase in the number of grass plant individuals because of successful recruitment. The choice of the logistic model presumes that the rate of reproduction is proportional to the existing grass biomass and to the available resources. With the logistic model, the overall reproduction rate is relatively low for both low and high values of G , because of low seed and stolon production or resource limitations, respectively. At intermediate values of G , there is ample seed/stolon production as well as ample soil resources to allow a relatively high reproduction rate in the model. The carrying capacity, C_G [mass/area], represents the maximum sustainable grass biomass allowed by the available resources. The reproduction coefficient α [time⁻¹], accounts for vegetative and seed reproduction, and can be expressed as the sum of two terms, α_v and α_s for vegetative and seed reproduction, respectively. For instance, the effect of a decrease in the rate of grass vegetative reproduction can be accounted for through a decrease in the parameter α_v . The second term in equation (1) accounts for the reduction of grass biomass associated with climate fluctuations, diseases, or disturbances such as grazing. A key aspect of grass response to grazing is the fact that defoliation results in curtailment of root growth/activity and hence reduces the ability of the grass plants to obtain soil resources [Briske and Richards, 1995]. Grass biomass reduction occurs at rates proportional to existing biomass, with parameter k_G [time⁻¹].

[10] The dynamics of shrub biomass, S [mass/area], are modeled as the result of a logistic growth and mortality.

$$\frac{dS}{dt} = \beta S \left(1 - \frac{(G+S)}{C_S} \right) - k_s S \quad (2)$$

where mortality rate of shrubs is given by $k_s S$ where k_s [time⁻¹] is the fraction of shrub biomass that dies in a given year. Mortality of shrubs in the model can result from either fire or prolonged drought. C_S [mass/area] is the carrying capacity for shrubs, β [time⁻¹] determines the rate of shrub biomass growth due to shrub establishment and growth. This rate is proportional to the existing shrub biomass, S , and to the resources left available by grasses and the existing shrub biomass. This formulation ensures asymmetric competition whereby grasses have a competitive advantage over shrubs. This formulation also assumes that grass and shrub biomass have the same resource demand. A [unitless] multiplicative term could be introduced in the numerator of the second term in parentheses in front of S or G to express the resource use of one relative to the other. However, the addition of this term would not alter the emergence of bistability in the system, and would only effect the equilibrium shrub biomass given a specific grass state.

[11] If the carrying capacity of grasses, C_G in equation (1), is kept constant, then any change in the grass/shrub ratio due

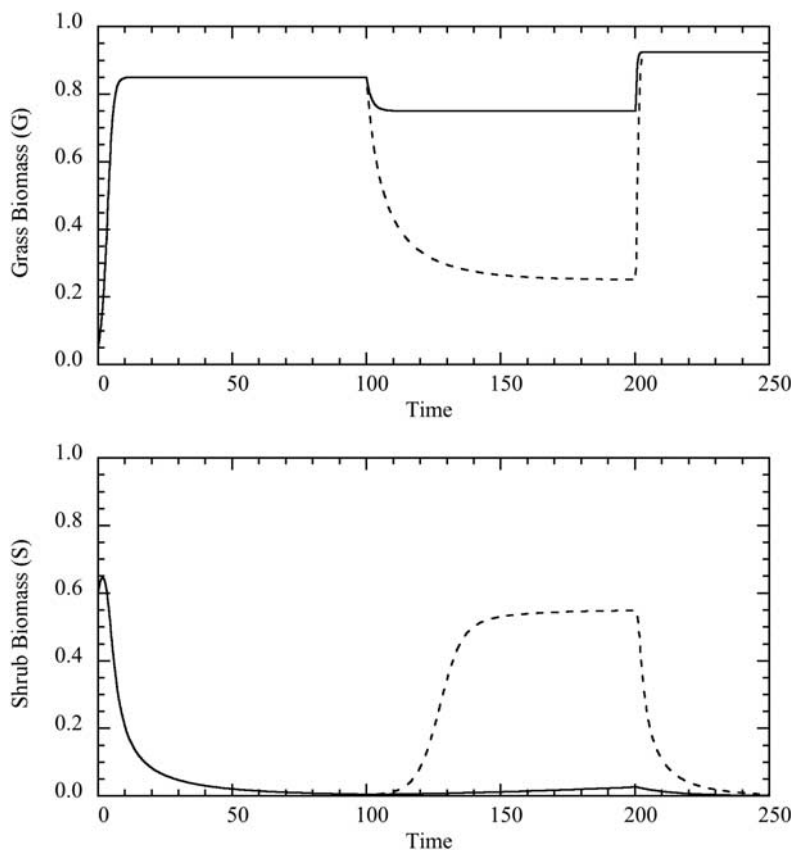


Figure 1. Time series of (top) grass biomass and (bottom) shrub biomass ($C_G = 1$; $k_G = 0.15$; $C_S = 1$; $\beta = 0.5$; $k_S = 0.1$). Originally, α is set to 1.0. At time $t = 100$, α is reduced to 0.6 (solid line) or 0.2 (dashed line). At time $t = 200$, α is set to 2.0. Results are identical whether the fire feedback is turned on ($c > 0$) or off ($c = 0$).

to changes in the grass reproduction rate, α , or mortality rate, k_G , are entirely reversible (see section 3 and Figure 1). That is to say, if the reproduction rate of the grasses decreases or the mortality rate increases at one time and then recovers later, the system will revert to the original values for grass and shrub biomass. In short, under these conditions, the system does not exhibit the existence of alternative stable states that are believed to be common in rangeland systems [e.g., *Bestelmeyer et al.*, 2003, 2004; *Briske et al.*, 2005; *Stringham et al.*, 2003; *Westoby et al.*, 1989].

[12] The model system is therefore unable to model bistable dynamics unless a positive feedback exists between grass vegetation and its environment, limiting resources, and/or disturbance regime. Two major feedbacks may exist in dryland grasslands: (1) between grass vegetation and soil resources [e.g., *Schlesinger et al.*, 1990] and (2) between grass biomass and fire regime [*Anderies et al.*, 2002; *van Langevelde et al.*, 2003]. In the first case, the loss of grass is associated with increased rates of erosion, loss of nutrient-rich topsoil, increased runoff and reductions in water holding capacity as well as loss of other soil resources, resulting in a decrease in the carrying capacity of grass species. In the second case, the loss of grass biomass results in a reduction in fuel load and the consequent reduction in fire frequency/intensity favors shrub dominance. In this

paper, we initially account only for the first mechanism, which is commonly recognized as one of the contributing factors to land degradation in the Chihuahuan Desert [e.g., *Li et al.*, 2007; *Schlesinger et al.*, 1990] and then add the impact of fire-vegetation feedbacks [*Anderies et al.*, 2002; *van Langevelde et al.*, 2003]. It is clear that a change in competitive advantage that came to favor shrubs would result in the invasion of shrubs into grasslands. Thus, we do not consider this mechanism for shrub encroachment in our model.

[13] To express the positive feedback between grass cover and soil resources, we express the carrying capacity of the grass, C_G , as an increasing function of G as shown in Figure 2, i.e., with C_G converging asymptotically to a maximum value for large values of G , when factors independent of grass biomass become limiting. Thus, we normalize C_G with respect to this maximum value and express it as

$$C_G = G^2(a - G) + bG = -G^3 + aG^2 + bG. \quad (3)$$

with a and b being two parameters determining the shape of the $C_G(G)$ curve. With this formulation of C_G , low values of C_G are produced by low values of G due to the loss of surface soil resources with sparse grass cover. Low values

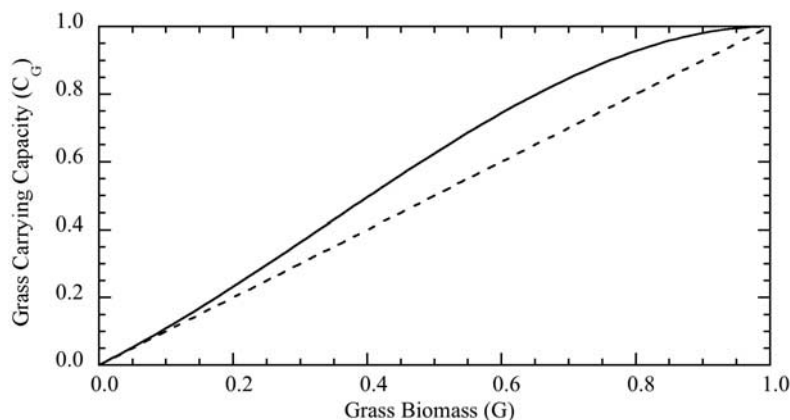


Figure 2. Dependence between grass carrying capacity and grass biomass expressed by equation (3), calculated with $a = b = 1$. The dashed line is $G = C_G$.

of C_G , in turn, result in reduced rates of grass establishment due to reduced soil resources.

[14] To express the interaction between grass and fires, we next express the mortality (or “harvest”) term, k_S , in equation (4) as proportional to the grass biomass, to account for the dependence of shrub mortality on grass-based fuel load,

$$k_S = cG + d \quad (4)$$

with c accounting for the strength of the fire-vegetation interaction, and d representing the rate of fire-independent shrub mortality. Thus, higher amounts of grass biomass are associated with more frequent and intense fires [e.g., Brooks *et al.*, 2004; Van Wilgen *et al.*, 2004], hence with stronger disturbance on shrub vegetation.

3. Results

[15] Figure 1 shows an example of time series obtained from the solution of equations (1) and (2), in the absence of any positive feedback between grass growth and removal of soil nutrients. In this case, C_G is set to a constant value of 1. Both equations for grass and shrub growth produce only one stable equilibrium state $G_{st} = C_G (1 - k_G/\alpha)$ and $S_{st} = \max(C_S (1 - k_S/\beta) - G_{st}, 0)$ respectively. A decrease in the rate of grass reproduction (i.e., in α) results in a decrease in G_{st} and in the consequent increase in S_{st} . Thus, decreases in α cause grass (shrub) biomass to decrease (increase) in time converging to its new asymptotic value. These transients are shown in Figure 1 subsequent to a 40% and 80% decrease (at time $t = 100$) in the reproduction coefficient, α . In this case, the transition to a new steady state is reversible, and when at time $t = 200$, the value of α is changed to 2.0, the grass returns to another, higher state.

[16] As noted, changes in grass biomass and the emergence of multiple stable states can be created by erosion-induced losses in soil resources resulting from the role of grasses in mitigating erosion [e.g., Gillette and Pitchford, 2004; Wainwright *et al.*, 2000]. To investigate the effect of this feedback, we account for the decrease in the carrying capacity of grasses with decreasing grass covers and express

C_G as a function of G (equation (3) and Figure 2). This dependence induces bistability in the dynamics of G , with $G = 0$ and grass dominance being both stable states of the system. Figure 3 (top) shows an example of bistable grass dynamics: depending on the initial conditions G converges to two different stable states. As a result of the bistability in grass biomass, the shrub dynamics are also bistable as shown in Figure 3 (bottom). We stress that this bistability of grass dynamics is entirely due to the positive feedback between grass biomass and soil erosion expressed by equation (3), while the bistability in shrub dynamics arises as an effect of grass bistability and of the effect of grasses, on shrubs expressed in equation (2).

[17] A decrease in the reproduction rate has an interesting impact on the dynamics of grass and shrub biomass as suggested by the 50% decrease in the reproduction coefficient, α , in Figure 3. This decrease shifts a grass-dominated system to the stable shrub-dominated state with no grass biomass. Because of the stability of this state, a subsequent reestablishment of conditions favorable to grass reproduction could not drive the system to a grass-dominated state until the state with $G = 0$ is destabilized.

[18] To further investigate the effect of reproduction rates on the bistability of grass dynamics we determined the stable and unstable states of G as a function of α/k (Figure 4). It was found that a threshold exists for α/k (i.e., the ratio of recruitment to mortality) below which there is no stable grass dominance. In these conditions the system has only one stable state at $G = 0$ (shrub dominance). If α/k does not decrease below this threshold value, the system does not shift to the $G = 0$ state, though grass dominance loses its resilience, i.e., smaller disturbances are needed to determine the abrupt and irreversible loss of grass vegetation and the consequent shrub encroachment.

[19] The vegetation-fire interactions (equation (4)) does not qualitatively modify the bistable properties of the system modeled by equations (1)–(4) (not shown). In fact, as long as grasses are assumed to be in competitive advantage over shrubs, the vegetation-fire interactions cannot affect grass dynamics, and rather operates only through shrub dynamics (equation (2)). In this case, the dynamics of grasses remain unaffected by the feedback with fires, while

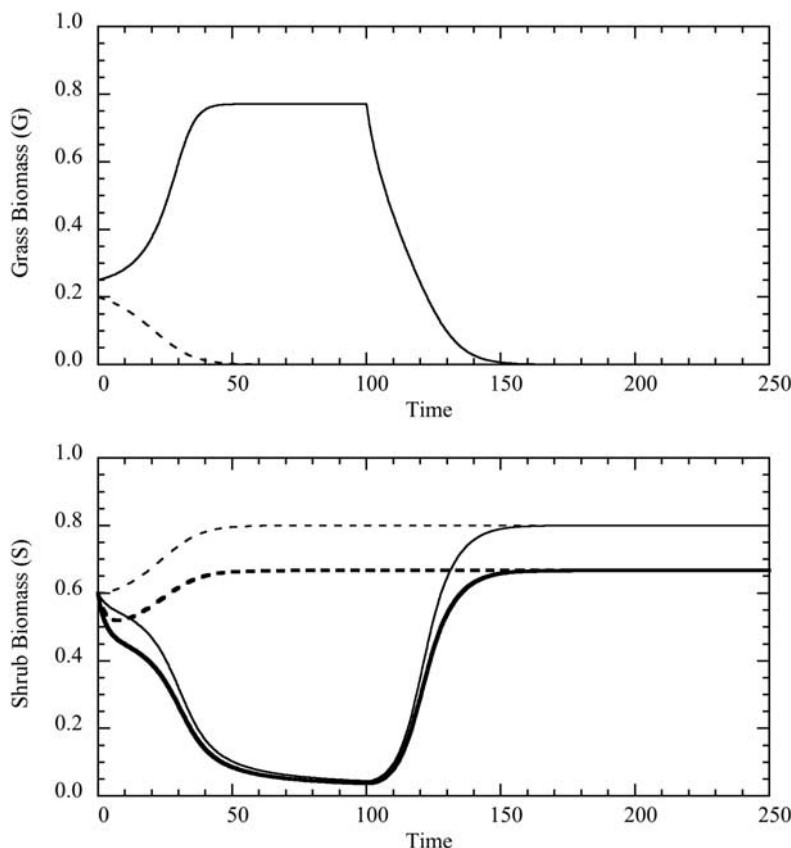


Figure 3. Time series of (top) grass and (bottom) shrub biomass obtained with two different initial conditions ($k_G = 0.15$; $C_S = 1$; $\beta = 0.5$; $k_S = 0.1$) and with C_G dependent on G as in Figure 2. Originally, the reproduction coefficient, α , is set to 1.0. At time $t = 100$, α decreases to 0.5. At time $t = 200$, α increases to 2.0. For grass biomass, results are identical whether the fire feedback is turned on ($c > 0$) or off ($c = 0$). For shrub biomass, results differ slightly whether the fire feedback is turned on ($c > 0$; thick lines) or off ($c = 0$; thin lines).

fire-induced disturbance of woody vegetation is more frequent and intense in the presence of an abundant grass cover. The emergence of bistability in the presence of vegetation-erosion feedbacks (equation (3)) in a system with state-dependent fire regimes (equation (4)) is induced by the nonlinearity associated with equation (3) (i.e., the effect of grass-soil erosion feedbacks) as discussed for the case of Figure 3 (bottom), rather than by the effect of fire dependence on grass biomass. So, while the vegetation-fire interactions are able to exacerbate the effects of the decline in grass establishment leading to an abrupt shift to the state $G = 0$, the effects of these fire-vegetation interactions are not important when G is in advantage with respect to S .

[20] The situation is different when shrubs are in competitive advantage: in this case a decline in G leads to an increase in S and to a decrease in fire pressure due to a reduction in grass fuel biomass [D'Odorico *et al.*, 2006]. So, if shrubs are in competitive advantage, a reduction in the rate of shrub disturbance by fires leads to the encroachment of woody vegetation at the expense of grasses. In this case the dynamics of S depend on G through equation (4), while those of G depend on the abundance, S , of the dominant species. This type of dynamics has been investigated by other authors [Anderies *et al.*, 2002; D'Odorico *et al.*, 2006;

van Langevelde *et al.*, 2003], who showed the possible emergence of alternative stable states (grassland and shrubland) when fire dynamics are either modeled as a nonlinear

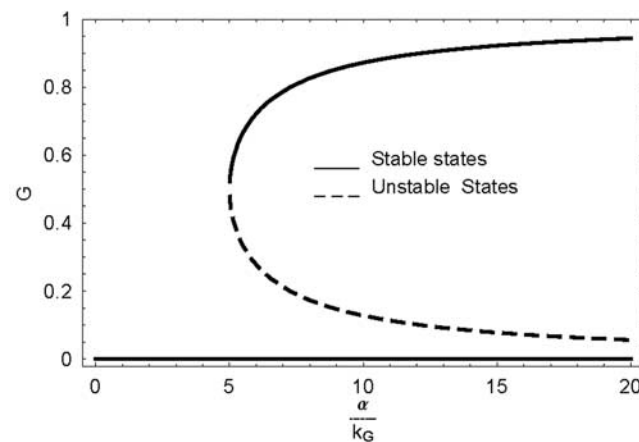


Figure 4. Stable and unstable states of the system for different values of α/k_G calculated with C_G dependent on G as in Figure 2.

deterministic function or as a linear random function of the state variables.

4. Discussion

[21] The conversion of grasslands to shrublands has been observed worldwide, but its reversibility has been a matter of some question. Aggressive “brush management” involving the use of herbicides and mechanical treatments to reduce shrub cover and reinstate grass dominance was widely practiced in the US and Australia in the 1940s–1980s [Bovey, 2001; Scifres, 1980; Valentine, 1989]. While such practices were effective for short periods of time (5–10 years) shrubs quickly reestablished dominance. Such observations suggested that (1) grasslands and shrublands were alternate stable states, distinguished by differences in soil properties, seed bank, vegetative regenerative potential, and disturbance regimes; (2) once grasslands were sufficiently altered (e.g., by grazing, cessation of fire, soil erosion) and a critical threshold exceeded, succession would propel the site into the shrubland domain; and (3) once in the shrubland domain, reversion to the grassland state would be highly unlikely [Archer, 1989]. While there is substantial observational evidence consistent with this scenario, there is surprisingly little quantitative evidence. Furthermore, while there is a long history [e.g., May, 1977] and much recent discussion on the nature of thresholds portending abrupt change in ecosystems, there is some debate as to its practicality [e.g., Groffman *et al.*, 2006]. How far and under what circumstances can a grassland site be pushed before entering into the shrubland domain? What changes in ecosystem properties and feedbacks are involved in this state transition?

[22] *D’Odorico et al.* [2006] have shown that the feedback between fire and vegetation, in which higher grass biomass provides more fuel for fires that kill shrub seedlings, can give rise to bistability in systems where shrubs would otherwise have an innate competitive advantage. The model presented here investigates the impact of plant establishment, plant mortality, and abiotic transport on the conversion of grasslands to shrublands in the Chihuahuan Desert under the assumption that grasses outcompete shrubs for resources. Our results show that in the presence of a positive feedback, presumably the well-studied vegetation-erosion feedback [Li *et al.*, 2007, 2008; Okin *et al.*, 2006; Parsons *et al.*, 1996, 2003; Wainwright *et al.*, 2002], bistability emerges even when grasses are advantaged relative to shrubs. It is not necessary to invoke changes in the competitive advantage between shrubs and grasses [Brown *et al.*, 1997; Idso, 1992; Sala *et al.*, 1997], nor is it necessary to assume that shrubs outcompete grasses and are limited only by seed dispersal. Our model suggests that so long as grasses in the Chihuahuan Desert were reproductively viable and replacing themselves subsequent to mortality, desert grassland communities would have been resistant to shrub encroachment; and that a key component of this resistance to structural change is the ability of grasses to stabilize soils. Thus, we argue that abiotic transport is a key component in the conversion of grasslands to shrublands, as laid out conceptually by Archer [1989] and Schlesinger *et al.* [1990]. The emergence of the alternative, shrub-dominated stable state and the presence of bistability, which

are direct consequences of the vegetation-erosion feedback, indicate that the model system has only limited resilience with respect to grass establishment and mortality.

[23] In the southwestern U.S., the feedback between soil resources, erosion, and vegetation has been well established [Okin *et al.*, 2006; Schlesinger *et al.*, 1990; Thurow, 1991; Wainwright *et al.*, 2002], and importance of the fire-grass feedback has also been highlighted [Archer, 1995; D’Odorico *et al.*, 2006; Van Auken, 2000]. The strength of these feedbacks is likely system-dependent and a function of geophysical susceptibility to abiotic transport and species adaptation to fire. In some semiarid grasslands, such as the South African Karoo, the balance between grasses and shrubs has shifted back and forth in the recent past [Hoffman *et al.*, 1995]. This reversibility suggests the vegetation-erosion and vegetation-fire feedbacks may be weak or absent in this region. A major challenge facing ecologists is to provide land managers with information that can guide their decisions on where to focus their efforts and limited resources in heterogeneous landscapes (i.e., concentrate resources on landscapes where it is reasonable to expect grasslands may be reinstated; avoid areas likely to remain as shrublands regardless of management inputs). We propose that systematic assessments of vegetation-erosion and vegetation-fire feedbacks would provide a promising theoretical foundation upon which to base such decisions.

[24] So, in what condition did European settlers of the Chihuahuan Desert find the rangelands into which they had moved? A decrease in the reproductive rate of grasses following the Little Ice Age could have two possible implications depending on the magnitude of climate change. Small, climate-induced declines in reproductive rates would have decreased grassland resilience making these systems more vulnerable to other disturbance, such as livestock grazing. Graphically, this change would appear in Figure 4 as a movement along the top solid line from the right toward the threshold on the left. As one moves along this path, the disturbance required to trigger the shift to the alternative shrub-dominated state would diminish (e.g., the system would become increasingly sensitive to grazing or additional climate change). In this case, at the time of European settlement, Chihuahuan Desert grasslands may have been in a metastable state. Alternatively, large climate-induced declines in reproductive rates would have destabilized the grassland state such that the system was already in transition to the shrub-dominated state at the time of settlement. This transition would occur at the timescale of decades to centuries and would have been controlled by the relative magnitudes of the rates of reproduction and mortality. Graphically, this corresponds to a decrease in the ratio of α/k_G below the threshold point where there is only one stable state that is dominated by shrubs. In this case, the system would have been unstable and in a transient state at the time of European settlement. Grazing disturbance by the livestock introduced by the new settlers would have accelerated a climate-induced displacement of grasses by shrubs that was already underway.

5. Conclusions

[25] The historically dominant perennial grass species in the Chihuahuan Desert (*Bo eriopoda*, black grama grass)

does not readily reproduce under the current climate conditions. This begs the question of how this plant could have dominated the extensive grasslands present in the Chihuahuan Desert at the time of European settlement. We present here a simplistic model of grass-shrub dynamics to investigate the relative roles of grass reproduction and mortality on grassland-shrubland dynamics when grasses are in competitive advantage over shrubs. The model predicts that for Chihuahuan Desert systems, a feedback between grass biomass and soil erosion can induce the irreversible and abrupt transition from a grassland to a shrubland state. This feedback may vary in strength in grasslands elsewhere with important implications for state reversibility. Because of its conceptual nature, the model is not intended to predict the timing and rate of shrub encroachment. Even so, the model captures many fundamental aspects of the dynamics in semiarid grasslands and is relatively conservative in its assumptions about interspecific competition (i.e., assumes that grasses are in competitive advantage relative to shrubs). As such, it provides a tool for qualitatively understanding ecosystem state transitions and the potential role of interacting biotic and abiotic processes in driving state changes. The model can be used to generate explicit hypotheses about alternative mechanisms capable of triggering the transition of grasslands to shrublands. For instance, we hypothesize that changes in grass reproduction put the system into either a metastable or transient state at the time of European settlement. This hypothesis must be tested in the real world with appropriate tools. We suggest that investigation of controls on grass establishment and mortality in field experiments would be productive avenues of research to investigate this hypothesis. In addition, paleo, historical and modern ecological studies that document reproductive rates of important grass species could provide key evidence for evaluating this hypothesis.

[26] Our assumption that grasses are in competitive advantage relative to shrubs arose from the desire to make the most conservative assumption to explain the grassland-shrubland dynamics. We believed that this assumption was the most likely to yield grass-dominated states and thus serve as the basis of a *reductio ad absurdum* argument on the competitive advantage of shrubs and the importance of the fire-vegetation feedback. In fact, with the inclusion of a commonly invoked [e.g., Archer, 1989; Peters et al., 2006; Schlesinger et al., 1990] and experimentally validated [e.g., Li et al., 2007; Okin et al., 2001; Schlesinger et al., 1996] vegetation-erosion feedback, our model shows that even in cases when grasses are in competitive advantage, small changes in either their recruitment or mortality can result in the conversion of a grassland to a shrubland.

[27] Thus, we are left with an argument in the familiar *v* *elimination* form: (1) either shrubs or grasses are in competitive advantage, (2) if shrubs are in competitive advantage, then the system exhibits bistable dynamics due to fire-vegetation feedbacks [D'Odorico et al., 2006], and (3) if grasses are in competitive advantage, then the system exhibits bistable dynamics due to erosion-vegetation feedbacks (this study). We conclude, therefore, that the system exhibits bistable dynamics, no matter which life form has the competitive advantage. Furthermore, both assumptions lead to bistable dynamics in which the shrub state, once entered, is highly persistent. We therefore conclude that the

present shrub-dominated state is essentially permanent until the climate changes to favor grass establishment over mortality. This change, should it occur, would both circumvent the vegetation-erosion feedback and provide the quantity and continuity of fine fuel needed to reestablish a vegetation-fire feedback. Paleodata suggest this conversion is possible [Van Devender and Spaulding, 1979]. However, given that mean temperatures in the southwestern U.S. are predicted to increase, and that droughts are predicted to become more common [Seager et al., 2007], the prospects for climate changes that will favor grass establishment in the foreseeable future are dim.

[28] In the meantime, our model suggests that there might be fruitful avenues of research into slowing or even reversing shrub encroachment. Because bistable dynamics arose in our model only when there was a feedback between vegetation cover and abiotic transport, we hypothesize that management techniques that effectively dampen this feedback (e.g., retard erosion) may allow land managers to avert undesirable transitions on susceptible or at-risk rangelands and position shrub systems for a grassland transition.

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References

- Allred, K. W. (1996), Vegetative changes in New Mexico rangelands, in *New Mexico's Natural Heritage: Biological Diversity in the Land of Enchantment*, edited by E. A. Herrera and L. F. Huenneke, pp. 168–231, N. M. Acad. of Sci., Albuquerque, NM.
- Anderies, J. M., et al. (2002), Grazing management, resilience, and the dynamics of a fire-driven rangeland system, *Ecosystems*, 5(1), 23–44.
- Archer, S. (1989), Have southern Texas savannas been converted to woodlands in recent history?, *Am. Nat.*, 134(4), 545–561.
- Archer, S. R. (1995), Herbivore mediation of grass-woody plant interactions, *Trop. Grasslands*, 29, 218–235.
- Archer, S., et al. (1995), Mechanisms of shrubland expansion: Land use, climate or CO₂, *Clim. Change*, 29(1), 91–99.
- Bestelmeyer, B. T. (2005), Does desertification diminish biodiversity? Enhancement of ant diversity by shrub invasion in south-western USA, *Diversity Distrib.*, 11(1), 45–55.
- Bestelmeyer, B. T., et al. (2003), Development and use of state-and-transition models for rangelands, *J. Range Manage.*, 56(2), 114–126.
- Bestelmeyer, B. T., et al. (2004), Land management in the American Southwest: A state-and-transition approach to ecosystem complexity, *Environ. Manage.*, 34(1), 38–51.
- Bovey, R. W. (2001), *Woody Plants and Woody Plant Management: Ecology, Safety, and Environmental Impact*, Marcel Dekker, New York.
- Bradley, R. S., et al. (2003), Climate in medieval time, *Science*, 302(5644), 404–405.
- Briske, D. D., and J. H. Richards (1995), Plant responses to defoliation: A physiological, morphological, and demographic evaluation, in *Wildland Plants: Physiological Ecology and Developmental Morphology*, edited by D. J. Bedunah and R. E. Sosebee, pp. 635–710, Soc. for Range Manage., Denver, Colo.
- Briske, D. D., et al. (2005), State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives, *Rangeland Ecol. Manage.*, 58(1), 1–10.
- Brooks, M. L., et al. (2004), Effects of invasive alien plants on fire regimes, *Bioscience*, 54(7), 677–688.
- Brown, J. H., et al. (1997), Reorganization of an arid ecosystem in response to recent climate change, *Proc. Natl. Acad. Sci. U.S.A.*, 94, 9729–9733.
- D'Odorico, P., et al. (2006), A probabilistic analysis of fire-induced tree-grass coexistence in savannas, *Am. Nat.*, 167(3), E79–E87.
- Fredrickson, E. L., et al. (2006), Mesquite recruitment in the Chihuahuan desert: Historic and prehistoric patterns with long-term impacts, *J. Arid Environ.*, 65(2), 285–295.
- Gillette, D. A., and A. M. Pithcford (2004), Sand flux in the northern Chihuahuan desert, New Mexico, USA, and the influence of mesquite-dominated landscapes, *J. Geophys. Res.*, 109, F01003, doi:10.1029/2003JF000025.

- Groffman, P., et al. (2006), Ecological thresholds: The key to successful environmental management or an important concept with no practical application?, *Ecosystems*, 9, 1–13.
- Hoffman, M. T., et al. (1995), Desertification of the eastern Karoo, South Africa: Conflicting paleoecological, historical, and soil isotopic evidence, *Environ. Monit. Assess.*, 37(1-3), 159–177.
- Idso, S. B. (1992), Shrubland expansion in the American Southwest, *Clim. Change*, 22, 85–86.
- Kaufman, Y. J., et al. (2005), The effect of smoke, dust, and pollution aerosol on shallow cloud development over the Atlantic Ocean, *Proc. Natl. Acad. Sci. U.S.A.*, 102(32), 11,207–11,212.
- Kellogg, C. A., and D. W. Griffin (2006), Aerobiology and the global transport of desert dust, *Trends Ecol. Evol.*, 21(11), 638–644.
- Li, J., et al. (2007), Quantitative assessment of wind erosion and soil nutrient loss in desert grasslands of southern New Mexico, USA, *Biogeochemistry*, 85(3), 317–332.
- Li, J., et al. (2008), Effects of wind erosion on the spatial heterogeneity of soil nutrients in two desert grassland communities, *Biogeochemistry*, 88(1), 73–88.
- May, R. M. (1977), Thresholds and breakpoints in ecosystems with a multiplicity of stable states, *Nature*, 269, 471–477.
- Moulin, C., and I. Chiapello (2006), Impact of human-induced desertification on the intensification of Sahel dust emission and export over the last decades, *Geophys. Res. Lett.*, 33, L18808, doi:10.1029/2006GL025923.
- Neilson, R. P. (1986), High-resolution climatic analysis and Southwest biogeography, *Science*, 232, 27–34.
- Okin, G. S., et al. (2001), Degradation of sandy arid shrubland environments: Observations, process modelling, and management implications, *J. Arid Environ.*, 47(2), 123–144.
- Okin, G. S., et al. (2004), The impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems, *Global Biogeochem. Cycles*, 18, GB2005, doi:10.1029/2003GB002145.
- Okin, G. S., et al. (2006), Multiscale controls on and consequences of aeolian processes in landscape change in arid and semiarid environments, *J. Arid Environ.*, 65, 253–275.
- Parsons, A. J., et al. (1996), Responses of interrill runoff and erosion rates to vegetation change in southern Arizona, *Geomorphology*, 14(4), 311–317.
- Parsons, A. J., et al. (2003), The role of overland flow in sediment and nitrogen budgets of mesquite dunefields, southern New Mexico, *J. Arid Environ.*, 53(1), 61–71.
- Peters, D. P. C., et al. (2006), Disentangling complex landscapes: New insights to forecasting arid and semiarid system dynamics, *Bioscience*, 56, 491–501.
- Polley, H. W. (1997), Implications of rising atmospheric carbon dioxide concentration for rangelands, *J. Range Manage.*, 50(6), 562–577.
- Reynolds, J. F., et al. (2007), Global desertification: Building a science for dryland development, *Science*, 316(5826), 847–851.
- Sala, O. E., et al. (1997), Plant functional types in temperate semi-arid regions, in *Plant Functional Types, Int. Geosphere-Biosphere Programme Book Ser.*, vol. 1, edited by T. M. Smith et al., pp. 217–233, Cambridge Univ. Press, New York.
- Schlesinger, W. H., et al. (1990), Biological feedbacks in global desertification, *Science*, 247, 1043–1048.
- Schlesinger, W. H., et al. (1996), On the spatial pattern of soil nutrients in desert ecosystems, *Ecology*, 77(2), 364–374.
- Schlesinger, W. H., et al. (1999), Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico. I: Rainfall simulation experiments, *Biogeochemistry*, 45, 21–34.
- Schlesinger, W. H., et al. (2000), Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico. II: Field plots, *Biogeochemistry*, 49, 69–86.
- Scifres, C. J. (1980), *Brush Management: Principles and Practices for Texas and the Southwest*, Tex. A&M Univ., College Station, Tex.
- Seager, R., et al. (2007), Model projections of an imminent transition to a more arid climate in southwestern North America, *Science*, 16(5828), 1181–1184.
- Stine, S. (1994), Extreme and persistent drought in California and Patagonia during medieval time, *Nature*, 369(6481), 546–549.
- Stringham, T. K., et al. (2003), State and transition modeling: An ecological process approach, *J. Range Manage.*, 56(2), 106–113.
- Taylor, C. M., et al. (2002), The influence of land use change on climate in the Sahel, *J. Clim.*, 15(24), 3615–3629.
- Thurrow, T. L. (1991), Hydrology and erosion, in *Grazing Management: An Ecological Perspective*, edited by R. K. Heitschmidt and J. W. Stuth, pp. 141–160, Timber Press, Portland, Oreg.
- Valentine, J. F. (1989), *Range Development and Improvements*, Academic Press, New York.
- Van Auken, O. W. (2000), Shrub invasions of North American semiarid grasslands, *Annu. Rev. Ecol. Syst.*, 31, 197–215.
- Van Devender, T. R. and W. G. Spaulding (1979), Development of vegetation and climate in the southwestern United States, *Science*, 204, 701–710.
- van Langevelde, F., et al. (2003), Effects of fire and herbivory on the stability of savanna ecosystems, *Ecology*, 84(2), 337–350.
- Van Wilgen, B. W., et al. (2004), Response of savanna fire regimes to changing fire-management policies in a large African national park, *Conserv. Biol.*, 18(6), 1533–1540.
- Wainwright, J., et al. (2000), Plot-scale studies of vegetation, overland flow and erosion interactions: Case studies from Arizona and New Mexico, *Hydrol. Processes*, 14(16–17), 2921–2943.
- Wainwright, J., et al. (2002), Hydrology-Vegetation interactions in areas of discontinuous flow on a semi-arid Bajada, southern New Mexico, *J. Arid Environ.*, 51(3), 319–338.
- Westoby, M., et al. (1989), Range management on the basis of a model which does not seek to establish equilibrium, *J. Arid Environ.*, 17(2), 235–239.
- Wilson, J. B., and A. D. Q. Agnew (1992), Positive-feedback switches in plant communities, *Adv. Ecol. Res.*, 23, 263–336.

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