

Scale-Dependent Feedbacks Between Patch Size and Plant Reproduction in Desert Grassland

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ABSTRACT

Theoretical models suggest that scale-dependent feedbacks between plant reproductive success and plant patch size govern transitions from highly to sparsely vegetated states in drylands, yet there is scant empirical evidence for these mechanisms. Scale-dependent feedback models suggest that an optimal patch size exists for growth and reproduction of plants and that a threshold patch organization exists below which positive feedbacks between vegetation and resources can break down, leading to critical transitions. We examined the relationship between patch size and plant reproduction using an experiment in a Chihuahuan Desert grassland. We tested the hypothesis that reproductive effort and success of a dominant grass

(*Bouteloua eriopoda*) would vary predictably with patch size. We found that focal plants in medium-sized patches featured higher rates of grass reproductive success than when plants occupied either large patch interiors or small patches. These patterns support the existence of scale-dependent feedbacks in Chihuahuan Desert grasslands and indicate an optimal patch size for reproductive effort and success in *B. eriopoda*. We discuss the implications of these results for detecting ecological thresholds in desert grasslands.

Key words: critical threshold; desertification; dryland; state transition; *Bouteloua eriopoda*; Chihuahuan Desert; resilience; patch size; feedbacks.

INTRODUCTION

The transformation of drylands from comparatively productive to degraded states is projected to worsen

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with increasing human population and climate change (Reynolds and others 2007). Transitions to degraded states can occur with little warning and, once initiated, are difficult or impossible to reverse (Stafford Smith and others 2007; Bestelmeyer and others 2011). To manage drylands sustainably, it is important to understand the mechanisms underlying transitions to degraded states. One proposed approach for detecting incipient state transitions is to measure changes in the characteristics of plant patch-size distributions. The fragmentation of vegetation patches beyond a critical threshold is postulated to cause a breakdown of positive feedbacks

between plant patch size, resource acquisition, and plant survival and reproduction that results in a transition to a desertified state (Kéfi and others 2007; Guttal and Jayaprakash 2008; Dakos and others 2011). There are, however, few empirical studies demonstrating a relationship between patch size and feedbacks in dryland vegetation (Aguiar and others 1992; Verwijmeren and others 2013).

Scale-dependent feedback models suggest that self-organized patchiness in dryland vegetation is a consequence of the counter-acting processes of short-range facilitation and long-range competition (HilleRisLambers and others 2001; Rietkerk and Van de Koppel 2008). Facilitation (positive feedback) occurs very near to plants due to the positive effects of plants on water infiltration into the soil, interception of lateral flow, and shading that limits evaporative water loss; these processes should favor plant growth and recruitment. Over broader areas, however, resource competition for limiting soil water is manifest in an upper limit to plant cover (negative feedback) (Noy-Meir 1973; Fowler 1986).

Scale-dependent feedbacks produce the patchiness characteristic of dryland vegetation that can promote system-level resilience in response to fluctuating resource levels (Rietkerk and Van de Koppel 2008) but also make dryland vegetation vulnerable to catastrophic transitions if patch size is reduced below a critical threshold required for facilitation processes to maintain plant survival and reproduction (Ludwig and others 2005; Kéfi and others 2007). In addition, patch size may mediate the effects of environmental harshness or disturbance. Plants in smaller patches may be more susceptible to herbivory, abrasion by wind-blown material, and microclimatic stress due to elevated surface temperatures (Li and others 2007; Eldridge and others 2009; D'Odorico and others 2012). Thus, evidence for the breakdown of positive feedbacks with decreasing patch size would support the use of patch-size metrics as early warning indicators of state change.

The simultaneous action of short-range facilitation and long-range competition proposed in scale-dependent feedback models suggests that an optimal, intermediate patch size would exhibit the highest rates of plant reproduction (Figure 1). In the context of the interiors of large, dense patches, competition for limiting resources with neighboring plants would lead to lower rates of plant reproduction than medium-sized patches. The edges of large patches, however, would be more favorable sites for plant recruitment than patch interiors because plants are adjacent to interpatch areas providing

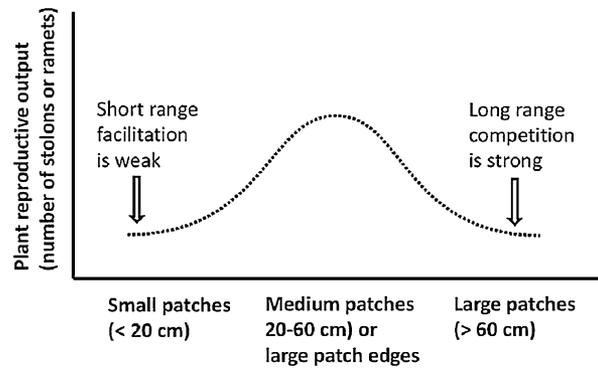


Figure 1. A conceptual diagram of the predictions from scale-dependent feedback models illustrating hypothesized relationships between patch-size classes and plant reproduction.

overland water flow. Plants in very small patches, on the other hand, would suffer from reduced facilitation and increased stress and exhibit lower reproduction than in medium-sized patches.

We tested these predictions by examining the relationship between perennial grass patch size and plant reproduction in a semiarid grassland of the Chihuahuan Desert, NM, USA. These grasslands have undergone widespread transitions to shrubland states over the past two centuries (Gibbens and others 2005). Transitions to shrubland states on sandy soils were initiated by the widespread and sudden loss of the dominant perennial grass (*Bouteloua eriopoda* Torr.) followed by colonization of shrubs (*Prosopis glandulosa* Torr.) (Bestelmeyer and others 2011; Figure 2). Heavy grazing in drought periods is believed to have caused an initial fragmentation of continuous *B. eriopoda* stands associated with a reduced patch size and increased bare ground. These changes, in turn, triggered accelerating soil degradation, shrub proliferation, and additional grass loss (Schlesinger and others 1990; Peters and others 2004). A long-term study was initiated in 1995 within a remnant grass-dominated area to examine the effects of acute, heavy grazing pressure on *B. eriopoda* loss and recovery (Bestelmeyer and others 2013). The wide variation in *B. eriopoda* patch sizes produced by the manipulations allowed us to test our predictions on a range of patch sizes within a single locality.

The results of Bestelmeyer and others (2013) indicated gradual recovery even though *B. eriopoda* patches were highly fragmented, and average patch size and cover were comparatively low immediately following the manipulation. Consequently, we also predicted that we would observe reproduction in even the smallest patches observed, that is, the smallest patches were not past a threshold in

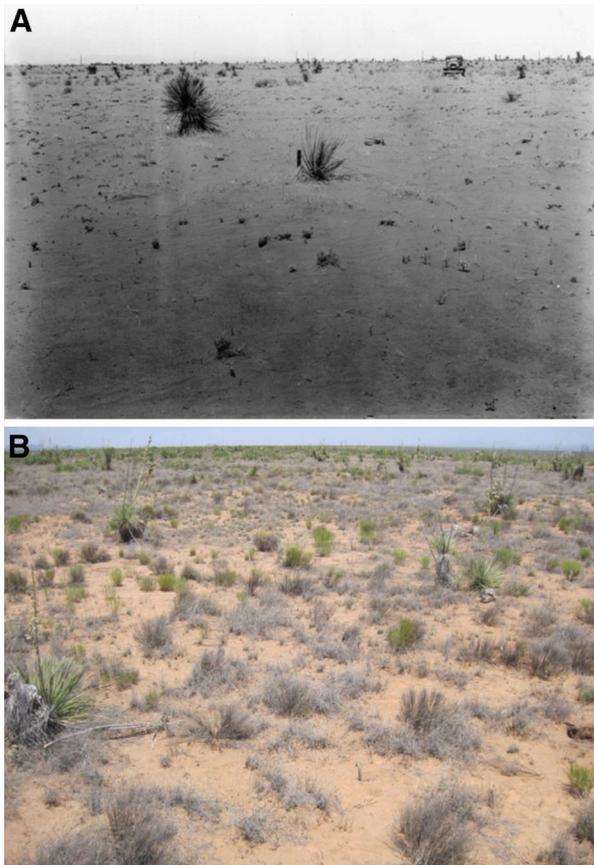


Figure 2. **A** A photograph of a denuded and eroding black grama grassland area on the Jornada Experimental Range taken in June, 1935 during a transition episode. Most such areas were subsequently transformed into mesquite shrublands. **B** A typical black grama grassland area within our study site in July 2010.

which reproduction did not occur due to environmental harshness.

METHODS

Study Area

The study area was located on the Jornada Experimental Range (JER), 37 km north of Las Cruces, New Mexico (32°35'N, 106°51'W; 1334 m a.s.l.). The JER is located within a vast system of formerly *B. eriopoda*-dominated desert grasslands extending from the southwestern United States to central Mexico (McClaran and Van Devender 1995). Soils of the study area are derived from wind-worked sandy alluvium, with a typical slope of less than 1%. Surface textures are predominantly sandy loam and are underlain by a horizon cemented by calcium carbonate at depths of 30–100 cm. Mean annual precipitation is 247 mm, half of which is received in high intensity convective thunderstorms from

July to September (<http://jornada.nmsu.edu/jornada/climate>). June–September precipitation during our study was above average during 2010 and below average in 2011 (Appendix S1). The long-term mean maximum temperature during the summer growing season (June–Sept) at the JER Headquarters based on measurements from its NOAA weather station (GHCN ID: USC00294426) is 33.6°C. Mean maximum temperature between June and September in 2010 was 33.7°C and in 2011 was 35.4°C. The study was conducted within an experimental area that produced a wide range of black grama patch sizes within a relatively small area of *B. eriopoda*-dominated grassland (Bestelmeyer and others 2013).

Patch Classification and Focal Plant Selection

A rule set for patch classification was created from analysis of classified high-resolution imagery (<10 cm ground sampling distance) obtained from the sampling site in 2009 (Laliberte and others 2007). The rule set was developed to distinguish plant environments within a patch following the observations that the smallest patches were at least 10 cm wide and that plants in areas greater than 30 cm from a patch edge were surrounded by other plants. The rule set also allowed for systematic classification of patches given the data and the preceding observations. The rule set was used to assign *B. eriopoda* patches or portions of large patches to one of four 'patch classes' (Figure 3) and to select focal *B. eriopoda* plants within patch classes. Small patches (S) were 10–20 cm from boundary to boundary in any direction. Medium patches (M) were greater than 20 cm wide in at least one dimension but did not contain any interior points greater than 30 cm from a patch edge. Large patches were all others that contained interior points greater than 30 cm from a patch edge and were divided into two distinct classes: large patch edge [L(E)] included plants not greater than 30 cm from the patch edge and large patch interior [L(I)] included plants greater than 30 cm from the patch edge. Selected patches were required to have at least 40% vegetative cover that was predominantly *B. eriopoda*. *P. glandulosa* shrubs could be no closer than 30 cm from any patch edge.

Patches were selected by first generating a large number of randomly distributed sampling points within a 6-ha area using ArcGIS 9.3 (Esri, Redlands, CA). We balanced sampling effort across twelve units of the former experimental area (Bestelmeyer and others 2013) to obtain a wide range of patch sizes and avoid clumping. We then

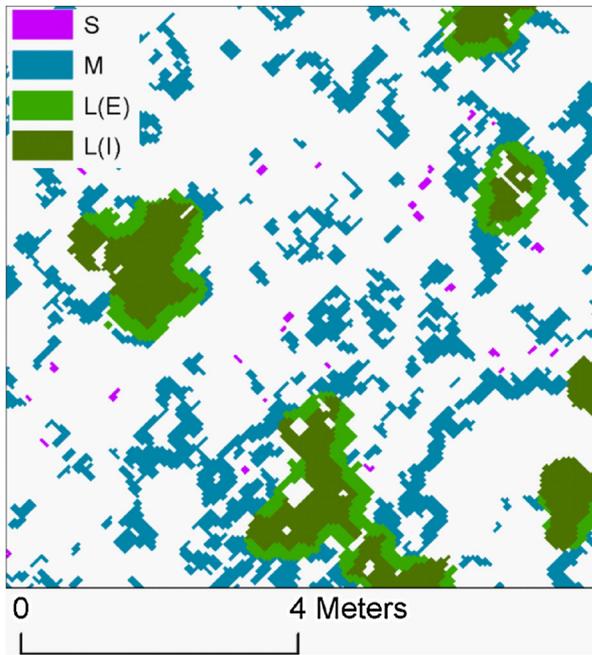


Figure 3. An example of patch classes based on a rule set applied to classified high-resolution (5 cm) aerial photography. S = small patches; M = medium; L(E) = large patch edge; L(I) = large patch interior.

visited sampling points in random order and located the nearest suitable patch using the rule set described above to obtain 36 replicates of each of the four patch classes. At each patch location, a focal *B. eriopoda* plant was randomly selected that had a 5–10 cm basal diameter.

Because wind-driven soil deposition from large bare ground areas may affect *B. eriopoda* growth and reproduction (Alvarez and others 2012), we measured fetch distances (Ludwig and others 1999) for each focal plant/microsite to use as covariates in analyses (see below). Fetch distances were measured from focal plants to a wind barrier at 241°, which is the dominant direction of erosive winds (Li and others 2007). We considered a wind barrier to be a plant with at least a 50-cm radial width, 10 cm height, and 40% internal cover. In addition, we measured the distance to the nearest *P. glandulosa* shrub with a minimum height of 50 cm, reasoning that the potential for competition for water by shrubs declines with shrub distance.

Measurements of Plant Reproduction

Plant reproductive measurements were collected on a total of 144 focal plants (4 patch classes × 36 replicates). Focal plants were mature with a basal size of 5–10 cm diameter [that is, none were seedlings or recently rooted ramets (RRs)]. We focused on

stolons and ramets because they are easily monitored, their numbers are an expression of plant reproductive effort and success, respectively, and they enable the rapid growth of plant patches that is the focus of theoretical models. Reproduction by seed was not monitored since *B. eriopoda* exhibits low seed viability and establishment success (Nelson 1934; Peters 2002; Bestelmeyer and others 2007). Plant reproductive measurements included counts of stolons, ramets, and RRs attached to the stolon. Counts were conducted for the focal plants in five sample periods (August 2010, October 2010, April 2011, October 2011, and April 2012). Stolons were counted only if they had the potential to produce ramets (that is, had well-developed ramets, incipient ramets, or swollen internodes). Ramets were counted only if they were not yet rooted but had potential to root, that is, they could not be immature (in the primary stage of formation) or dead. RR included all ramets securely rooted in the soil such that a gentle pull could not uproot them, and they were still attached to a stolon from the mother plant.

Analysis

A repeated-measures linear mixed-effects model was used to compare plant reproductive measurements at focal plants among patch classes and over different time periods (SAS V9.2; PROC MIXED; SAS Institute, Cary NC). Main effects were patch class and sampling period. A heterogeneous autoregressive covariance structure was used based on the minimum small-sample Akaike's Information Criterion (SAS Institute 2009). Data were unbalanced in some seasons due to the loss of a few patches so a Tukey–Kramer adjustment was applied in comparisons of least squares means among patch classes (Hayter 1984). Furthermore, we tested for differences among patch classes in reproductive measurements over specific time periods using contrasts (for example, a comparison of change in two patch-size classes between two sampling dates). Fetch and nearest mesquite shrub distances were included as covariables in all models.

RESULTS

Mean counts of ramets and RR for focal plants were higher in M than in L(I) and S (Table 1; Figure 4; Appendix S2). Stolons counts were marginally higher in M than L(I) ($P = 0.09$). L(E) and M did not differ in mean counts of ramets and RRs, but M had more stolons. L(E) and L(I) did not differ, but they had greater counts of stolons and ramets than S, driven by strong differences from August 2010 to April 2011. Over the relatively dry spring/summer

Table 1. Least Squares Means for Plant Attributes (Stolons, Ramets, and RRs) of Each Patch Class [Small, Medium, Large (exterior), and Large (interior)] Over All Time Periods

Attribute	Patch classes			
	Small	Medium	Large (exterior)	Large (interior)
Stolons	47.5 ± 5.6 ^c	92.7 ± 5.6 ^a	71.8 ± 5.6 ^b	74.2 ± 5.6 ^{ab}
Ramets	17.6 ± 4.3 ^c	50.4 ± 4.3 ^a	38.7 ± 4.3 ^{ab}	34.6 ± 4.3 ^b
Rooted ramets (RR)	0.8 ± 0.5 ^b	3.8 ± 0.5 ^a	2.5 ± 0.5 ^{ab}	2.1 ± 0.5 ^b

Different letters (a, b, c) indicate significant differences between patch classes for an attribute using the Tukey–Kramer adjustment ($P < 0.05$).

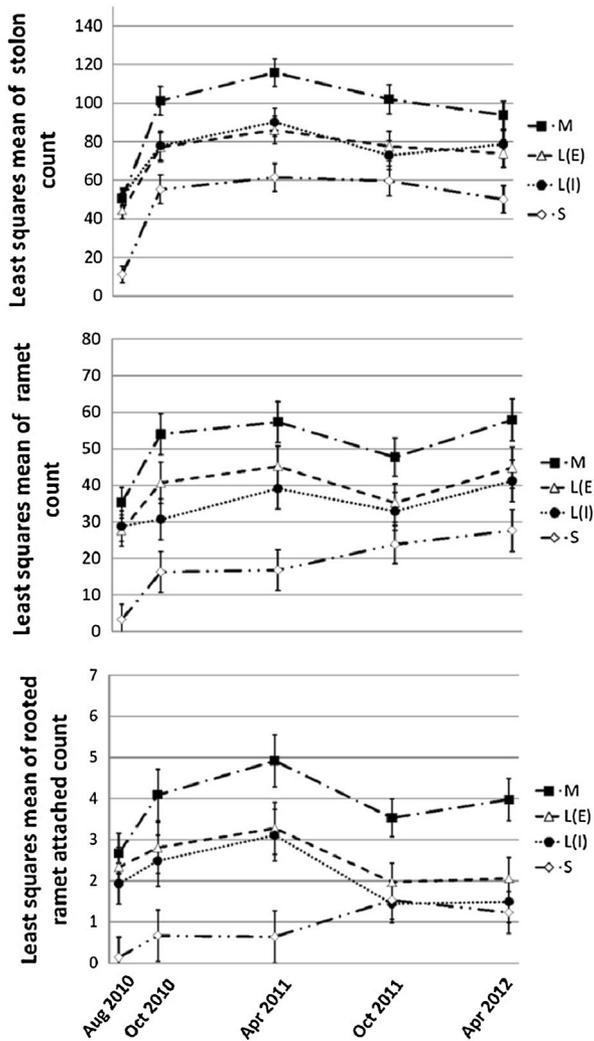


Figure 4. Least squares means and standard errors of the number of stolons, ramets, and rooted ramets attached to a stolon for focal plants of all patch classes ($n = 36$ per point). Patch class abbreviations follow Figure 3.

period from April to October 2011, counts of ramets and RR in S increased, whereas it decreased in other classes (contrast of change in S ramets vs. all others between Apr and Oct 2011 = 15.6 ± 4.4 ;

$F = 4.38$; $P = 0.0004$; contrast of RR = 2.3 ± 0.5 ; $F = 25.28$; $P < 0.0001$), after which differences between S, L(E), and L(I) were reduced. Over the April–October 2011 spring/summer period, there was an increase in RR for S, whereas decreases were observed in the other patch classes (contrast of change in S RR vs. all others over that period = 3.5 ± 0.6 ; $F = 34.50$; $P < 0.0001$). This pattern was not observed for other variables. In no case did distance to shrubs or fetch have a significant effect on plant reproductive variables.

DISCUSSION

Evidence for Scale-Dependent Feedbacks

We found that per capita reproductive effort (stolon and ramet production) and reproductive success (RRs) for the smallest patch classes were generally lower than in medium patch classes and at the edges of the largest patch classes. This pattern is consistent with patch-size mediated feedbacks and is the first such evidence in desert grasslands to our knowledge. It is also consistent with previous studies that indicate the importance of patch context for grass reproduction and growth (Aguiar and others 1992; van Wesenbeeck and others 2008). The low reproductive effort and success of plants in small patches is consistent with weakening of positive feedbacks when patch size (or plant density) is reduced, as predicted by theory (Rietkerk and van de Koppel 1997).

Although reproductive effort was greater in the large patch interiors than in the smallest patches, one measure of reproductive success was not. The early disadvantage in RR numbers experienced by plants in the smallest patches relative to those in large patch interiors had disappeared after the comparatively dry summer 2011 period, during which the number of RRs increased in small patches, yet declined in the others. This pattern may reflect differences in the competitive environment

experienced by plants in small compared to large patches as well as precipitation event sizes and duration that regulate runoff and soil moisture availability (Loik and others 2004). Densely populated plant patches (particularly in patch interiors) should have a higher concentration of roots in subsurface soils leading to greater competition for surface soil moisture (Fowler 1986). Competition for scarce soil water might provide a recruitment advantage adjacent to small patches during drought and when precipitation events are small.

Plants in the medium patch class had greater ramet production and establishment than those in large patch interiors and similar values to large patch edges. In fact, plants in medium-sized patches had an advantage over plants in smaller and larger patches in our study. This pattern likely reflects the spatial extent over which facilitation and competition processes are balanced (Manor and Shnerb 2008; von Hardenberg and others 2010), such that facilitation is important in the smallest patches and competition becomes important as plant density increases or when resource levels become strongly limiting in the largest patches (Pugnaire and others 2011). In *B. eriopoda* grasslands, grazing is known to break up patches from the largest patch sizes to medium and small patches (Paulsen and Ares 1962). Based on our results, we speculate that high grazing pressure resulting in a predominance of small patches would indicate periodic limitations in plant reproduction that, in turn, limit recovery rates (Turnbull and others 2008), whereas grazing managed to produce a predominance of medium patches would not indicate these limitations.

The patterns we observed may also be a consequence of the spatial and temporal context of the study. Although wind erosion may have important effects on the growth and survival of perennial plants in our study system (Alvarez and others 2012), we did not detect an effect of fetch length on plant reproduction, suggesting that plant protection from wind was not an important process during the study. Furthermore, the coarse surface textures and low slope of our study site might feature more rapid infiltration, lower evaporation rates, and lower rates of resource redistribution compared to fine-textured soils with greater slopes that characterize other dryland areas (Sala and others 1988; Ludwig and others 2005). Consequently, fragmentation of large patches to medium patches might produce net negative effects on reproduction in other contexts. Variations in plant adaptation, soils, and landscape context may have important consequences for the relationships between patch size and vegetation

dynamics (Maestre and Escudero 2009; Dakos and others 2011; Kéfi and others 2011).

Implications

Our results provide evidence for the operation of scale-dependent feedbacks in semi-arid grassland, in which short-range facilitation is weakened in the smallest patches, and in which long-range competition is evident in the interiors of the largest patches. Consequently, attention to patch size as an indicator of vegetation change processes (or using cover as a proxy for patch organization when the two are highly correlated) is supported by our results (Rietkerk and others 2004). The relatively high reproductive effort and success of plants in medium patch classes suggests that fragmentation resulting in medium-sized patches should not impair black grama recovery. Patch sizes less than 20 cm, on the other hand, exhibit reduced plant reproductive capacity and success. However, small patches are capable of reproduction even in drought periods when reproduction in larger patches declines. These results help explain the high resilience of black grama grasslands observed in Bestelmeyer and others (2013). The findings also indicate that the strength of patch-size mediated feedbacks may vary over time. Nonetheless, extreme fragmentation (that is, black grama occurring only in a few, widely spaced small patches) would be associated with an increased probability of local perennial grass extinction in response to severe natural disturbance, such as prolonged drought with periods of high wind, alongside additional heavy grazing pressure. Based on historical photography taken during state change episodes (Figure 2A), this scenario is likely to have led to the rapid loss of grasslands in the Chihuahuan Desert (Bestelmeyer and others 2011). A predominance of medium-sized grass patches (that is, plant patches between 20 and 60 cm) resulting from moderate grazing pressure, however, may not be a management concern due to the elevated rates of reproduction we observed.

Predictions about dryland vegetation behavior based on patch characteristics are ultimately based on assumptions about positive and negative feedback mechanisms. Although our results support scale-dependent feedback models, it is likely that the relationships between patch organization and feedbacks will vary in different ecosystems. We support the call for increasingly data-driven and mechanistic approaches to predicting transitions (Boettiger and Hastings 2013) and suggest that in

drylands, studies of patch-size plant reproduction feedback relationships in different environmental settings represent a promising empirical basis for indicator development and predictions of ecosystem change.

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