

Incorporating Plant Mortality and Recruitment Into Rangeland Management and Assessment

Tony Svejcar,¹ Jeremy James,² Stuart Hardegree,³ and Roger Sheley¹

Authors are ¹Research Leader and Weed Ecologist, USDA–Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA; ²Director and Extension Rangeland Specialist, UC Sierra Foothill Research and Extension Center, Browns Valley, CA 95918, USA; and ³Plant Physiologist, USDA–Agricultural Research Service, Northwest Watershed Research Center, Boise, ID 83712, USA.

Abstract

Rangeland management is largely focused on managing vegetation change. Objectives may include managing against change if the desired vegetation is in place, or attempting to create a shift in vegetation if the desired plant community is not present. There is a rich body of research documenting influences of disturbance and management on rangeland vegetation. However, in many cases the information is largely observational and does not identify mechanisms driving change. We propose using the regeneration niche concept to more effectively predict when vegetation change is possible and to suggest successional direction. Simply stated, as plants die and leave gaps in the community, recruitment of new individuals will dictate successional direction. Recruitment requires that propagules are present, that the propagules find safe sites in which to establish, and that the seedlings and young plants are able to compete with existing vegetation and survive. In many rangeland communities, perennial bunchgrasses are a key to stability and invasion resistance. Existing literature shows that most rangeland bunchgrasses have average life spans of 10 yr or less, so periodic recruitment is necessary to maintain communities in which they are a major component. Disturbance can influence plant population dynamics, and we suggest classifying disturbances based on how they influence mortality and recruitment. We also suggest that more emphasis be placed on the concept of critical transitions and less on the degree of disturbance per se. In other words, a small disturbance at the wrong point in community composition (low plant density and high gap size for example) can cause a transition, whereas major disturbance in a high condition community may yield little risk of transition. We suggest that a focus on mortality and recruitment will provide a mechanistic approach for predicting vegetation change and making management decisions. We refer to this approach as recruitment-based management.

Key Words: disturbance, plant succession, recruitment, state-and-transition models, thresholds

INTRODUCTION

A substantial portion of rangeland management is focused on vegetation change. Many biotic and abiotic factors influence this process, and the complex nature of rangeland management can create a large array of management options, potential vegetation outcomes, and modifying factors. Much of the research on vegetation change involves measurements of plant community composition over time, after a disturbance or application of a management treatment. Most management knowledge is similarly acquired by observing changes, but often without data collection. In both research and management contexts, the conclusions apply to the specific conditions under which the observations were made. A disadvantage of using this type of knowledge is the lack of a mechanistic basis and thus limited predictive ability (Svejcar and Sheley 1995). Without a mechanistic understanding, it will be difficult to assess how a slight shift in driving factors might impact vegetation dynamics. The lack of predictive ability is a major shortcoming of vegetation management in general.

One approach to improving our ability to predict vegetation change revolves around population dynamics and life history

analysis. Although we have limited information on the life span of perennial rangeland plant species, it is clear that many herbaceous species do not live more than a couple of decades (Wright and Van Dyne 1976; West et al. 1979; Lauenroth and Adler 2008). When plants die, they create gaps in communities which can be filled by existing dominant species or by new or rare species. This relatively simple concept was termed the “regeneration niche” by Grubb (1977), and is a critical phase from the standpoint of plant community change or resilience. There is mortality associated with a species’ life span, but there is also mortality associated with both natural and human-caused disturbance. These disturbances can be relatively short duration (e.g., fires, insect and disease outbreaks, seasonal drought), or long duration (e.g., climatic shifts, chronic heavy grazing, alien species invasions). We are much more effective at evaluating the impacts of short-term disturbances on vegetation change than those of long-term disturbances. Vegetation shifts associated with the more subtle and long-term disturbances can be difficult to detect, especially in the early stages.

In a stable plant community, recruitment of new individuals is roughly equal to mortality, whereas replacement by other species indicates a community shift. Plant species have a variety of reproductive strategies associated with different life histories (e.g., Grime 2002). Many of the strategies are a result of ecological trade-offs—where allocation to one function results in a corresponding decrease to other functions (Fenner and Thompson 2005). For example, some plants have very rapid growth rates, but do not compete well for soil resources (Grime

Correspondence: Tony Svejcar, USDA–ARS, 67826-A Hwy 205, Burns, OR 97720, USA.
Email: Tony.Svejcar@ars.usda.gov or Tony.Svejcar@oregonstate.edu

Manuscript received 24 June 2013; manuscript accepted 31 May 2014.

© 2014 The Society for Range Management

2002). These trade-offs contribute to the broad array of species in any given environment. Additionally, characteristics of adult plants might or might not exist in the juvenile life history stage of the same species (Facelli 2008), and there is currently no system for classifying seedlings from a functional perspective (Leck and Outred 2008). The literature on seedling characteristics and natural recruitment in rangeland systems is fairly limited. A clearer understanding of natural recruitment and life history characteristics will assist in predicting vegetation change and selecting appropriate management actions.

The regeneration niche concept also holds promise for strengthening our assessment of transitions in state-and-transition models (STMs). This approach, which was first introduced by Westoby et al. (1989), has been widely adopted for describing vegetation dynamics on rangelands. As currently applied, STMs allow for relatively reversible community shifts contained within a stable state, but much less reversible shifts among stable states (e.g., Bestelmeyer et al. 2003; Stringham et al. 2003). Recent literature has focused on defining transitions or thresholds (Briske et al. 2006) and incorporating ecological resilience explicitly into the STM framework (Briske et al. 2008). Since the introduction of STMs over 20 yr ago, the thresholds and transitions among states have probably created more controversy than any other aspect of the model. We suggest that a focus on mortality and recruitment will provide a means of more clearly identifying likely transitions among states.

Our goals in this paper are to: 1) develop a clear linkage between regeneration niche (mortality/recruitment) and vegetation change; 2) provide suggestions for incorporating this linkage into management, assessment, and research; and 3) provide several examples of recruitment-based management. Our discussion focuses on bunchgrass-dominated rangelands, where recruitment is primarily from seed.

DISCUSSION

Vegetation Change

Plant ecologists have a long history of studying succession, defined as temporal changes in plant community composition (Krueger-Mangold et al. 2006). The rangeland management profession is largely based on understanding and managing changes in plant composition. A clear understanding of how a variety of factors interact with management is critical to the decision-making process. Pickett et al. (1987) identified three general causes of succession: species availability, site availability, and species performance. If recruitment is to occur, propagules of the species must be present, safe sites must be available to the propagules for establishment, and the species must perform well enough to survive over time. These concepts are consistent with the regeneration niche, but provide details on the conditions under which recruitment occurs. Krueger-Mangold et al. (2006) list some of the processes and modifying factors for the three general causes of succession.

Plant Recruitment as a Driver of Vegetation Change

There are many mechanisms used by plants to regenerate populations (Grime 2002). The two primary methods of

providing new propagules are vegetative reproduction (such as rhizomes or stolons), or sexual reproduction via seed. Bunchgrasses are generally assumed to reproduce via seed, although there is evidence that over time, some bunches can break up and migrate apart (Liston et al. 2003). For this discussion, we focus on individuals and communities that reproduce predominantly from seed. In general, the importance of recruitment is inversely proportional to a species' life span (Eriksson and Ehrlén 2008). In other words, short-lived species need to be replaced with new individuals more frequently than long-lived individuals. The recruitment process requires production of viable seeds and then the steps outlined in Figure 1, culminating in an established adult.

Unfortunately, there is little information on life expectancy of herbaceous rangeland species. Some woody rangeland plants can be aged using growth ring analysis (e.g., Schultz et al. 1990; Wall et al. 2001; Ziegenhagen and Miller 2009), but similar techniques are not available for herbaceous species. As Lauenroth and Adler (2008) note: "One of the few ways to determine demographic parameters for populations of herbaceous plants is by long-term mapping of individuals in permanent plots... The difficulty of the data collection and analysis are reasons why such analyses are rare." It is possible to reconstruct past history with most woody plants, but with herbaceous species, it is necessary to collect data as establishment and mortality occur. Unfortunately, this means that long-term data sets suitable for evaluating demography of herbaceous species must have been initiated decades ago.

To understand the importance of periodic recruitment, it is useful to have some indication of life span. Because of the patience required to actually quantify this parameter, there are limited studies, and the three we will focus on were initiated between 1915 and 1932. West et al. (1979) presented demographic data on sagebrush steppe species from southeastern Idaho; measurements were taken from 1930 to 1956 and then in 1973. If we average ungrazed grasses, these authors found high first-year mortality (58%), an average life span of 6.7 yr for plants >1 yr of age, and maximum observed longevity of about 34 yr. Lauenroth and Adler (2008) presented demographic data for southern mixed-grass prairie in western Kansas during 1932 to 1972. If we again average values for grasses (11 species), the first year mortality is 56% and maximum observed life-span averages about 28 yr (range=5 to 39). In both cases, the length of time necessary for data collection might constrain life-span estimates. Lauenroth and Adler (2008) suggest their life-span estimates for short-lived species were accurate but that their estimates for long-lived species were likely low. Wright and Van Dyne (1976) analyzed data on desert grassland species from southern New Mexico collected during 1915 to 1968. For the seven major grass species they studied, maximum life span ranged from 6.9 to 27.5 yr. Mean life span for individual plants living at least 1 yr varied from 2.8 yr to 3.9 yr for the seven species. Thus, species with long maximum life spans also had relatively higher mortality rates of young plants than species with shorter life spans, which explains why mean life span only varied by a year among the seven species, whereas maximum life span varied by over 20 yr. Life-span estimates for forbs are uncommon, although Lauenroth and Adler (2008) had estimates for 29 forbs from western Kansas, and in general forbs were shorter-

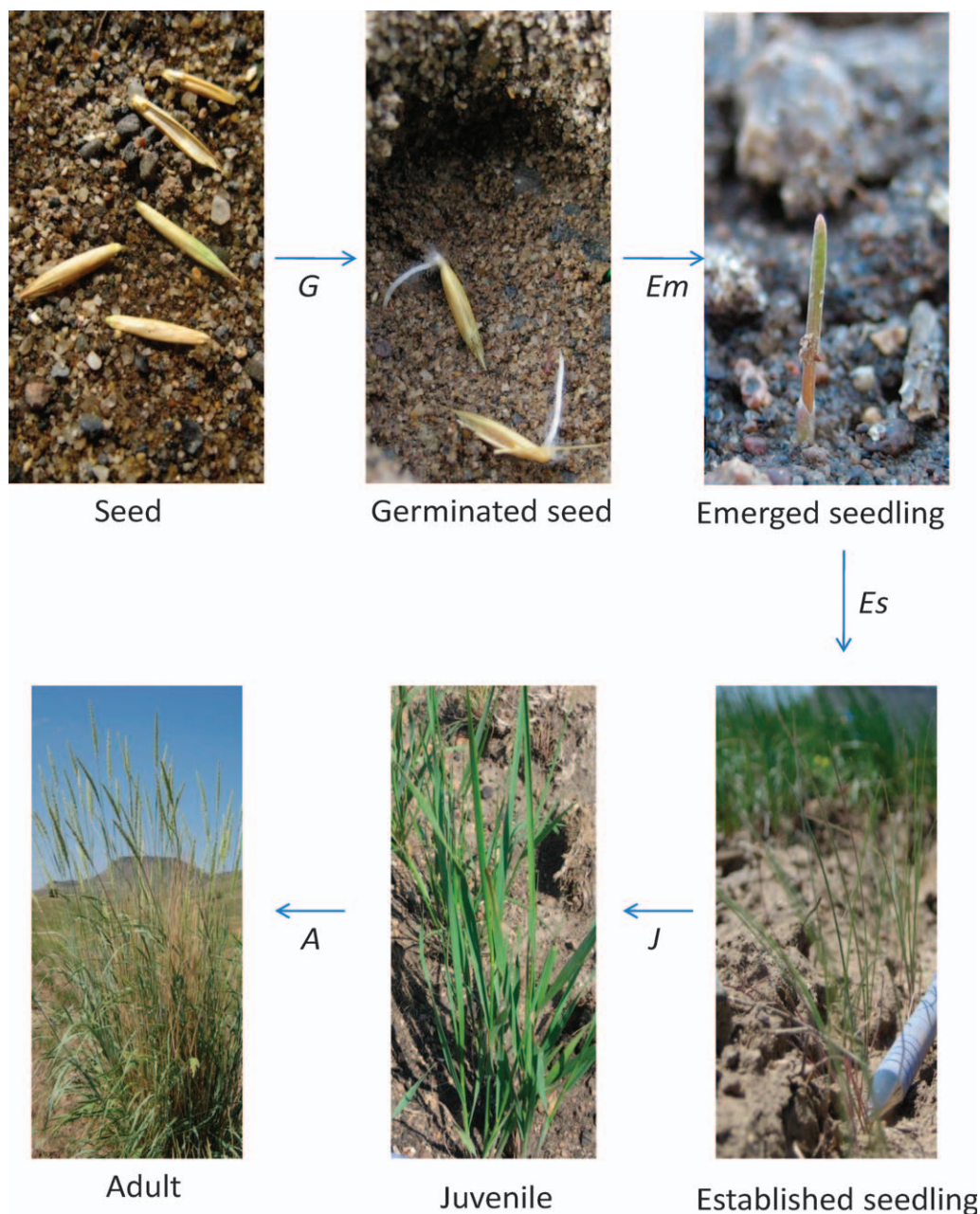


Figure 1. Pictorial representation of the life stages of a rangeland bunchgrass. The transitions follow the outline provided by James et al. (2011): G indicates germination; Em , seedling emergence; Es , seedling establishment; J , juvenile stage; and A , adult stage.

lived than grasses (maximum life spans averaged 10.4 yr for the 29 forbs and 28.2 yr for the 11 grasses in their data set). Regardless of individual species characteristics, it appears clear that frequent recruitment will be necessary to maintain many of these grassland species.

Research from Australia and South Africa also supports the view that recruitment is essential in the maintenance of rangeland plant communities. O'Connor (1991) put forward the hypothesis that local extinction of palatable bunchgrasses can occur in South African grasslands. He based this hypothesis on the fact that the bunchgrass of interest had a life span of about 10 yr and seed bank persistence of 2–3 yr. Thus, a major disruption in recruitment would put bunchgrass populations at

risk. O'Connor suggested that the combination of drought and heavy grazing can simultaneously increase bunchgrass mortality and reduce recruitment. Similarly, research from Australia shows that mortality of bunchgrasses increased rapidly as defoliation increased beyond 50% of biomass (Hacker et al. 2006). In addition, nongrazed bunchgrasses experienced mortality if 3-mo rainfall totals dropped below 75 mm (Hodgkinson and Miller 2005). In this study, results were highly species-dependent; 10-yr survivorship of mixed-age cohorts ranged from less than 10% to about 75%, depending on bunchgrass species.

Demographic characteristics are easier to assess for non-sprouting woody rangeland species. Examples of maximum

life spans for woody rangeland species from the western United States would include: 127 yr (mean age=58 yr) for bitterbrush, 38 yr (mean age=20 yr) for sagebrush, and 61 yr (mean age=14 yr) for rabbitbrush (Adams 1975); 1 350 yr (age structure varied among stands) for curlleaf mahogany (Schultz et al. 1990); and up to 1 600 yr (again age varies dramatically with stand) for western juniper (Miller et al. 2005). Age structure of woody plants depends on past disturbance history (such as fire), but in general, life spans for woody plants tend to be much longer than those recorded for grasses or forbs.

Because of the long sampling periods needed to quantify the demographics of perennial plant populations, new knowledge in this area will be acquired slowly. However, it might be possible to synthesize existing knowledge, identify logical species groupings, and evaluate factors that assist or impede seedling establishment and thus recruitment. Demographic characteristics can be useful for classifying ecological groups, and developing a better understanding of life history/habitat relationships (Silvertown et al. 1993). As habitats, and potentially climates, change, it would be helpful to be able to predict which species are favored or disfavored based on life history characteristics. The same can be said for predicting the impacts of management practices on vegetation. Any major change in the relationship between average longevity and recruitment rates will change vegetation composition (West et al. 1979). There are both biotic and abiotic factors that can influence recruitment. The presence of adult plants can have either positive or negative consequences on recruitment. Gomez-Aparicio (2009) conducted a metaanalysis of published studies which manipulated plant interactions for restoration of degraded terrestrial vegetation. She found that inhibition by neighbor plants is common in early successional herbaceous communities, and facilitation is typical for communities dominated by shrubs and trees. In a shortgrass steppe, Aguilera and Lauenroth (1995) demonstrated that establishment of dominant grasses required disturbances that generated gaps in the native vegetation. Zimmermann et al. (2008) drew similar conclusions working in semiarid savanna in Namibia. Other biotic factors that affect recruitment include soil pathogens, seed predation, and seedling herbivory (Burdon and Shattock 1980; Moles and Westoby 2004). There is also a host of abiotic factors that influence recruitment—drought, temperature, and soil characteristics are among the more general categories (Winkel et al. 1991; Moles and Westoby 2004; Boyd and Davies 2010).

We conclude that rangeland grasses and forbs are probably shorter-lived than many vegetation scientists and managers have assumed. This is just a general observation based on the lack of discussion of recruitment to maintain existing communities. If all rangeland species were long lived, then periodic recruitment would be less important in directing vegetation change. The maintenance of existing communities or states is tied directly to replacement of existing species, and transitions occur when recruitment involves alternative species. Disturbances can play a major role in vegetation dynamics, but we are not aware of approaches that classify disturbances based on their impacts on plant population dynamics. Such an approach would provide a clearer link between a particular disturbance and its impact on plant community change.

Defining Disturbance

The term “disturbance” includes a wide variety of factors, many of which influence mortality and recruitment. As with many ecological concepts, there is a variety of definitions and conceptual approaches associated with disturbance. We will briefly describe some of the prevailing definitions and then present a conceptual basis that ties this concept more directly to mortality and recruitment.

One of the major conceptual divides in defining disturbance has to do with treatment of historical disturbance regimes. This is what White and Jentsch (2001) refer to as “relative” and “absolute” definitions. Relative disturbances would be those outside the normal range for a given ecosystem. For example, fires are a normal part of many grassland and shrub-steppe ecosystems, so elimination of fire would actually be considered a disturbance (White and Jentsch 2001). This is a difficult concept for many of us to adopt. And there are at least two major problems associated with the relative definition of disturbance; it assumes that: 1) past disturbance history is clearly defined, and 2) conditions are constant enough that the ecosystem is still favored by the historical disturbance regime. The difficulty in defining past disturbance regimes for many rangelands arises from long intervals between disturbances (e.g., long fire-return intervals), coupled with large year-to-year weather variability. There are also long climatic cycles that can influence disturbance regimes. Swetnam and Betancourt (1998) noted that fires in the southwestern United States are associated with periods of high amplitude in the Southern Oscillation, which produce rapid switching from wet to dry years. Must large-scale climatic patterns be factored into historical disturbance regimes? This would clearly be a complicating factor. We also know that atmospheric CO₂ has been steadily increasing, and this influences plant growth. Given the positive responses of some invasive species to rising CO₂ (e.g., Ziska et al. 2005), can we assume past disturbance regimes will necessarily provide a predictable outcome (Davies et al. 2009)?

In contrast, the absolute definition does not make reference to historical events; a disturbance is a disturbance, regardless of past patterns. There is still the issue of what exactly constitutes a disturbance. There are two general definitions that overlap under most conditions. White and Pickett (1985) define disturbance as “a relatively discrete event in time that disrupts the ecosystem, community or population structure and changes the resources, substrate availability or physical environment.” Grime (2002) defines disturbance as “the mechanisms which limit the plant biomass by causing its partial or total destruction.” Normally the disturbances defined by White and Pickett (1985) will also limit plant biomass, but not always. The time frame is also a point of confusion in developing a clear definition. Most authors have adopted the discrete event view of disturbance, often weeks or less (White and Jentsch 2001). So in this case, a one-time heavy defoliation over a short period would be a disturbance, but long-term overgrazing would not be considered a disturbance. Similarly, 2 mo with no precipitation might be viewed as a disturbance from drought, but several consecutive years of low rainfall would not be considered a disturbance. If we used Grime’s (2002) definition, both these circumstances would result in loss of plant biomass, and thus both could be considered a disturbance.

Because of the role disturbance plays in vegetation change, it is important to have a clear definition and conceptual basis for discussing this issue. Much of rangeland management is focused on the plant community level, so we choose that level on which to focus. Many of the disturbances we discuss in this profession are longer in duration than weeks. Although we like the White and Pickett (1985) definition, many factors we discuss as disturbance on rangelands are of longer duration, and are a better fit to Grime's (2002) definition. Overgrazing, multiyear droughts, and consecutive years of insect and rodent population explosions are all of a longer-term nature than are discrete events. For the purposes of our discussion on recruitment, we will separate disturbances into two major categories: 1) acute disturbances, which occur within one growing season or less; and 2) chronic disturbances, which last more than one growing season (Fig. 2). This approach provides a functional basis for assessing impacts of disturbance on mortality and recruitment. For example, an acute disturbance can have immediate impacts on mortality, whereas a chronic disturbance (or stress) might simply impact life span.

Global change can create additional complications with regard to definitions of disturbance. Smith et al. (2009) developed an approach to incorporating global change into a more traditional disturbance-based framework. Although there is no question that continued resource alterations (increased atmospheric CO₂ or nitrogen deposition for example) can reorder plant communities, we chose not to address this point in our disturbance discussion. We view disturbances as factors that have a start and end point, even if multiple years are involved. In the case of atmospheric CO₂ or nitrogen deposition, the changes will likely be continuous and only in one direction—atmospheric CO₂ is not likely to decline any time soon. From our point of view, global change could reset the baseline for a community and these changes will be important to understand, but we chose not to include global change in our discussion of disturbance.

Resilience, Tipping Points, and Critical Transitions

Identifying ecological thresholds and factors that confer community resilience has created a good deal of controversy in the rangeland management profession. These concepts are important for management and assessment, and we argue that they tie back directly to the regeneration niche and thus mortality and recruitment. Because transitions involve changes in species, mortality and recruitment would necessarily provide the underlying mechanism.

There has been substantial interest in incorporating resilience into both STMs (e.g., Briske et al. 2008) and into invasive plant management (e.g., Sheley et al. 2006). The question is: Can a plant community or state resist change in the face of disturbance or encroachment by undesirable species? A variety of terms and concepts have been applied to ecological stability and thus resilience (Grimm and Wissel 1997). The simplest definition is probably the ability to return to the reference state after temporary disturbance (Grimm and Wissel 1997). Many of the stated definitions have to do with the energy or degree of disruption needed to change a system, and are more conceptual than practical from a management standpoint. As Briske et al. (2008) state, "assessment of state resilience represents an ecologically robust approach to ecosystem management, but does not readily lend itself to application." We agree that resilience has been a challenging concept to apply to management, but suggest there are opportunities for both conceptual and practical improvement.

Resilience is often viewed in terms of degree of disturbance. For example, a particular state might be resistant to short-term drought, but not multiyear drought, or to fire followed by some other disturbance. This disturbance-centric thought process misses the fact that response to disturbance might depend on the condition of a particular state. This is the general concept behind "at-risk" plant community phases; however, the fact that disturbance impacts can vary by community phase is not always captured in STMs. A conceptual example of changes in resilience is presented by Briske et al. (2006), where a

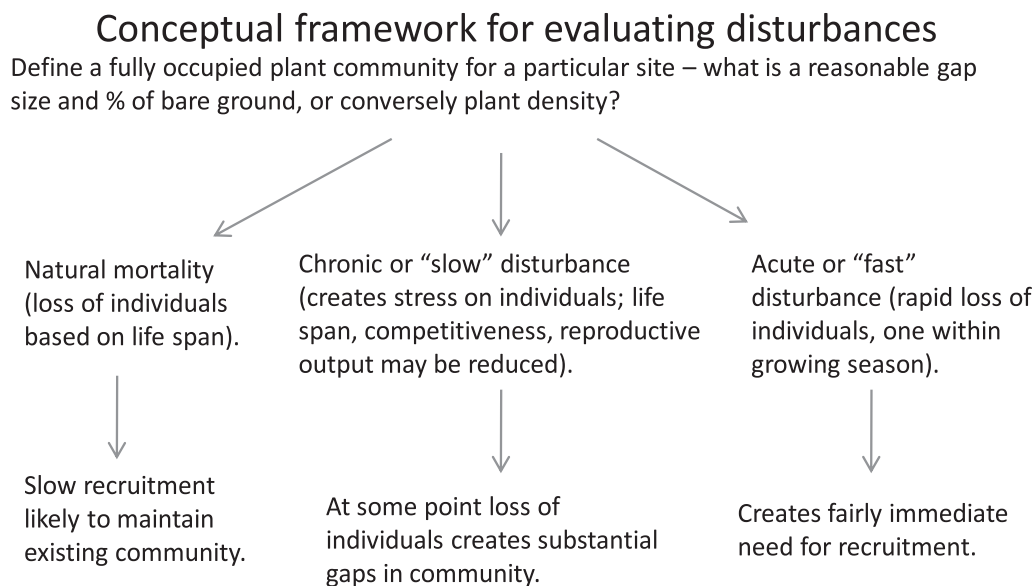


Figure 2. Conceptual framework for classifying disturbances based on their potential impacts on mortality and recruitment. Disturbances might or might not have an effect on mortality and recruitment, but if they do, the dynamics resulting from chronic or acute disturbance will usually be quite different.

prethreshold state progresses through the following stages: structural shifts → species losses → functional changes → extinction of prethreshold properties. The sagebrush steppe provides a tangible example of these stages: shrub/bunchgrass community with high bunchgrass density (prethreshold state) → loss of some bunchgrasses, large gap sizes (structural change) → invasive annual grasses increase, reduced density, and in some cases loss, of herbaceous natives (species losses) → initial fire removes stability provided by shrubs and further opens community to dominance by annuals (functional changes) → recurring fire cycle created by dominance of fire-prone annual grasses (extinction of prethreshold properties). The impact of a given disturbance is very different at the various stages of threshold progression. One reason the response to disturbance changes is that species availability and species performance shift along the threshold progressions. Although disturbance often receives a good deal of attention, it is important to recognize that all three of these factors—disturbance, species availability, and species performance influence succession (Sheley et al. 1996). Disturbance and resilience should be considered in a systems context.

The concepts of criticality and critical transitions have recently garnered attention in the ecological literature (Burkett et al. 2005; Pascual and Guichard 2005; Scheffer et al. 2009; Dakos et al. 2011). On the surface, these discussions appear very similar to the ongoing debates about resilience and state transitions. However, several important points have emerged from the more recent literature. Criticality is defined as the point at which a system is poised to transition (Pascual and Guichard 2005), which sounds similar to an at-risk community. However, there is an important concept attached to the definition of criticality—that at these critical points, small changes in an underlying process can result in a large shift in state. Pascual and Guichard (2005) use as examples wind-disturbed forests and intertidal mussel beds. In the forest example, with only a slight increase in gap size there was a rapid collapse in area of trees; and small changes in predator efficiency or wave force can cause collapse of the mussel bed. This general phenomenon can occur in a wide variety of situations, including human medicine, epidemiology, global finance, and demography (Scheffer et al. 2009). This concept can explain why we often miss these critical transitions; we can watch changes occur over time with no transition, and suddenly a small change results in a dramatic shift. An example on rangelands would be populations of some weed species. The weed might occupy an area for decades at relatively low population levels, and then expand dramatically over short periods of time.

The concept of critical thresholds or tipping points is potentially useful in rangeland management, but how does one define and identify these points? Dakos et al. (2011) postulated that any system close to a critical transition would be slow to recover from disturbance, a phenomenon they termed “critical slowing down.” This concept might provide a means of testing characteristics of a plant community that is approaching a critical transition point. For example, is there a particular cover level or density of perennial vegetation below which the risk of weed invasion increases? Could the threshold stages outlined earlier for sagebrush steppe each be tested for disturbance response? We suggest that resilience and critical

thresholds could be defined based on mortality and recruitment: how much disturbance is required to induce mortality, and once plants die, are they replaced by existing species or by species that can signal a state change.

Recruitment-Based Management

The rangeland management profession has its roots in restoring degraded rangelands. Implicit in this effort is the establishment of desirable species where they existed only in low densities. Even the early grazing management literature discussed the need for recruitment. For example, in Hormay and Talbot's (1961) introduction of their grazing system, they identified three issues that required attention: restoring plant vigor, ensuring development and ripening of seed, and ensuring establishment of seedlings. The first volume of *Journal of Range Management* includes an article which focused on death loss, seedling establishment, and plant ages of sagebrush over a 31-yr period (Lommasson 1948). In field discussions with land managers and other scientists, this topic often arises, yet we have no formal framework for incorporating plant recruitment into the planning process.

We concluded previously that rangeland bunchgrasses and forbs are probably shorter-lived than many managers and scientists have assumed. Recruitment is generally discussed in the context of restoring rather than maintaining rangeland plant populations. State-and-transition models provide an effective means of capturing the possible plant communities on a particular ecological site, but would benefit from both a better system of identifying movement toward thresholds and measureable parameters that predispose a site to crossing a critical threshold. We suggest that Grubb's (1977) concept of the regeneration niche is a good starting point. A visual representation of this concept appears in Figure 3. Simply put, if a gap is created in a community, how is that gap filled? Young et al. (2005) go a step further and define a series of ontogenetic niches: reproductive, dispersal, recruitment or establishment (similar to Grubb's regeneration niche), and adult.

The effectiveness of high-seral native bunchgrasses in maintenance of sagebrush steppe rangeland has been well-documented (Davies et al. 2011), and analogous situations exist in many other rangeland types. For example, Fair et al. (1999) presented a 38-yr record demonstrating that openings created by mortality were filled by recruitment in a stable mixed-prairie community. We suggest that bunchgrass density, or conversely, gap size between bunchgrasses, provides a logical starting point in assessing resilience or distance from a critical transition. A disturbance at a high density of bunchgrasses might have low probability of causing a transition, whereas a similar disturbance at a low bunchgrass density might result in a high probability of state change. Testing the concept of critical slowing down across a variety of community phases and rangeland types would help identify the utility of this concept.

The thought process associated with recruitment-based management need not be complicated. Some basic steps to consider are listed below:

- Plant communities should be viewed as dynamic with mortality and recruitment as the driving forces behind vegetation change. As rudimentary as this concept seems, it is often not a major consideration in rangeland management.

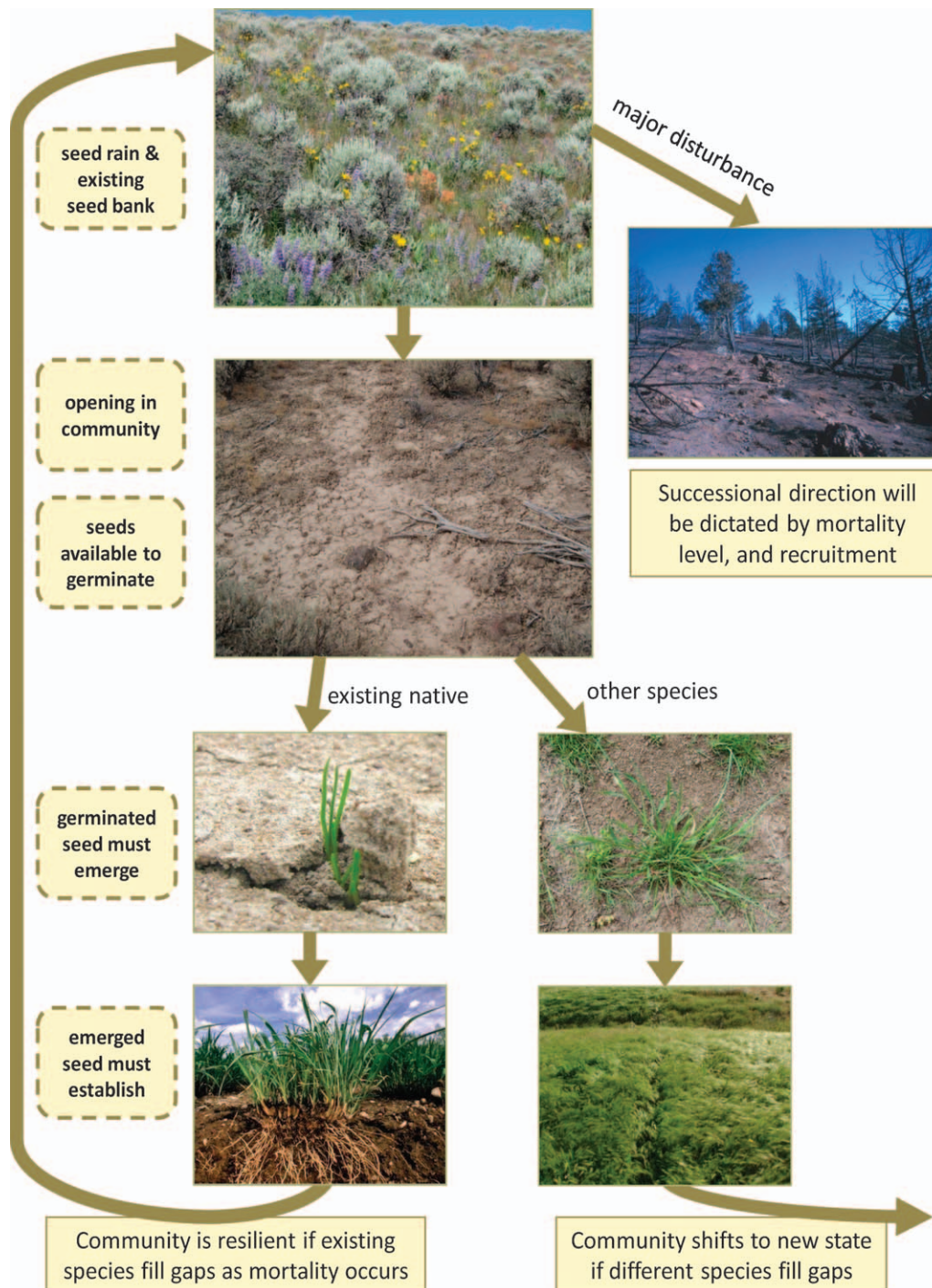


Figure 3. Representation of the regeneration niche concept under two different sets of conditions.

- The reason might be that we seldom document either dead bunchgrasses or seedlings.
- Assess existing knowledge of life spans and response to disturbance of dominant species. Although life-span data for bunchgrasses might be limited, there is good evidence that many species have average life spans of about a decade. The Australian work cited earlier (Hodgkinson and Miller 2005; Hacker et al. 2006) provides good examples of how disturbances (or stress) influence mortality.
 - Assess the current status of the community in question from a recruitment standpoint. Are there significant gaps in the community? Gaps can provide ideal monitoring locations to assess recruitment. Pictures might be sufficient for evaluating gap dynamics over time. GPS-tagged photographs would be helpful in this regard.
 - If there are gaps in a community, recruitment will require propagules, so an evaluation of seed rain and seed bank dynamics would be helpful. Seed banks often do not reflect current vegetation, largely because of variable seed produc-

tion and longevity among species. Early seral species tend to produce more seed and have longer-lived seed than later seral species. Current seed rain might be an important source of propagules.

- Seedling establishment faces many hurdles in most rangeland environments. If gaps have developed within a community, what are the characteristics of the gaps? Is the soil likely to crust? Are there visible safe sites where seeds are more likely to establish?
- Do sequences of events line up in a way that favors recruitment? If, for example, seed longevity of a desired species is 2–3 yr, then a good-seed production year would need to be followed within several years by a good seedling-establishment year. How do disturbances, propagule availability, and establishment weather line up? Sequences of events are difficult to study, but could be critical in determining species composition of rangelands. Time series data or pictures might be critical for evaluating episodic events such as recruitment and mortality.

Examples of Recruitment-Based Management

Southern African Grassland. Perennial grasslands in southern Africa are subject to both periodic drought and heavy grazing. O'Connor (1991) hypothesized that this combination of stresses could cause local extinction of palatable grass species. The mechanism for extinction includes both limited seed production and seedling establishment in response to the dual stresses and a relatively short-lived seed bank. The grassland species can experience high levels of mortality from either drought or heavy grazing, but neither stress alone causes extinction (Fig. 4). Because the seed bank for the palatable grasses is short-lived, “persistence” of propagules is ensured by the seed rain of adult plants. In this setting, seed dispersal of palatable grasses is relatively limited. Based on life-history analysis, O'Connor (1991) argues that his hypothesis of local extinction is well-supported by empirical studies of vegetation trend. The probability of local extinction is greater in more arid rangeland where frequency and duration of droughts are greater.

Management implications for the southern African grasslands are that reduced grazing pressure during some wet years is necessary to maintain the palatable grasses as part of the community. Alternatively, loss of the grasses could indicate the transition to a new state, which O'Connor (1991) refers to as “a number of different possible end points.” A third implication, which O'Connor (1991) offers as a test of successional pathways, is to provide seeds of palatable perennial grasses in recently abandoned fields. Assuming favorable rainfall and reduced grazing pressure, adding a seed source would test the hypothesis that local extinction was the cause of the state change and provide a means of crossing back over the threshold.

Western US Mountain Big Sagebrush. Mountain big sagebrush (*Artemisia tridentata* Nutt. subsp. *vaseyana* [Rydb.] Beetle) is a nonsprouting shrub species that is susceptible to mortality from wildfire and thus must recover from seed. Because this species is important from a habitat perspective, managers often attempt to artificially re-establish mountain big sagebrush after wildfires. Unfortunately, success rates tend to be relatively low (Dalzell 2004) and costs can be high. Seeds of mountain

big sagebrush are relatively short-lived and most seeds lose viability 24 mo after reaching the soil surface (Wijayratne and Pyke 2009). After examining a series of wildfires in this community type, Ziegenhagen and Miller (2009) determined that sites having favorable conditions for recruitment of mountain big sagebrush seedlings the first 2 yr after fire were likely to recover to preburn levels of shrub cover within 20–30 yr. Because sagebrush seed dispersal is limited, if shrub establishment did not occur during the first several years post-fire, shrub cover remained low decades later. Historically, fire had significant impacts on this community, with fire return intervals ranging from 10–15 yr, depending on site productivity (Miller and Rose 1999). At slightly lower elevations, Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle and A. Young) communities, high grass density can limit recruitment of shrubs (Boyd and Svejcar 2011).

Management implications for Mountain big sagebrush communities are two-fold: 1) if favorable weather allows for sagebrush seedling establishment the first 2 yr after a fire, resources would be wasted on reseeding; and 2) if reseeding is not an option, lack of seedlings 2 yr (or growing seasons) after a fire would suggest transition to a more grass-dominated community, at least for several decades (Fig. 4). A high density of bunchgrasses might increase the length of time required for shrub recruitment.

We use these examples to illustrate the value of recruitment in evaluating management actions and potential transitions between states. There is also a separation in these examples between acute and chronic disturbances (Fig. 2). The separation is conceptually important: the first 2 yr after fire are critical because of sagebrush seed longevity, whereas management decisions in the South African grassland might be more influenced by weather in a particular year.

Research Needs

There has been substantial research on both mortality and recruitment of rangeland plants. However, much of the work has not been synthesized and there are still substantial gaps in knowledge. The topics to be considered below largely follow the thought process we suggested earlier for recruitment-based management.

- *Life span and mortality.* What are expected life spans of various species, and how are they influenced by climate, management, and disturbance?
- *Community gaps.* Openings or gaps in plant communities are generally required for successful recruitment (Aguilera and Lauenroth 1995; Fair et al. 1999; Zimmerman et al. 2008). A better understanding of the relationship between gaps and community change would help in assessing state transitions.
- *Seed banks, seed rain, and dispersal.* Seed banks often do not reflect current vegetation on a site (Koniak and Everett 1982; Edwards and Crawley 1999; Allen and Nowak 2008), and current seed rain could be critical for maintaining a species or plant community (O'Connor 1991; Edwards and Crawley 1999). Yet there is relatively little information on production of viable seed under natural rangeland conditions, or how that production is influenced by weather, management, or disturbance.

Examples of recruitment-based assessment

Factors which influence resilience, or probability of state change.	<u>Extinction-prone grassland</u>	<u>Mountain big sagebrush after fire</u>
1. Seed bank, seed rain, other propagules.	Heavy grazing combined with drought reduces or eliminates seed rain; palatable grasses are both defoliated and exposed to drought; seed bank is short lived, and eventually depleted.	Sagebrush shrubs removed by fire; seed rain interrupted; seed bank for shrub recovery viable for about 2 years.
2. Seed dispersal of target species.	Limited.	Limited.
3. Establishment windows.	Non drought years with light grazing.	First 2 years following fire.
4. Opportunities and risks.	-Palatable grassland species experience high mortality with either drought or heavy grazing, but neither alone causes extinction. -Local extinction may cause state change to less palatable, less productive community type.	-Favorable weather during the first 2 years after fire will eliminate the need for costly reseeding efforts. -If fire causes mortality of grasses and shrubs, weedy species may invade.
5. Management implications.	Reduce grazing pressure during favorable years to allow seed rain and seeding establishment.	During first 2 years after fire, observe weather conditions and seedling establishment before expending resources on reseeding.

Figure 4. Tabular summary of recruitment-based management.

- *Seedbeds and seedling establishment.* Much of the research on seedbeds has been associated with rangeland reseeding efforts. Over two decades ago, Call and Roundy (1991) stated, “A more mechanistic research approach is needed to better understand factors governing germination, seedling establishment, and plant community development in natural and synthetic systems to guide revegetation toward biological diversity.” As with seed production, an understanding of factors which limit seedling establishment will be needed to predict succession.
- *Sequences and timing of events.* Sequences or exact timing of events (such as seed inputs, disturbances, weather patterns, and management actions) could be critical in determining vegetation persistence or change (Westoby et al. 1989; O’Connor 1991; Edwards and Crawley 1999). This is a difficult subject to study, but one which requires attention.
- *Disturbance and transitions.* There is a need for more emphasis on the interaction between disturbances and plant population dynamics. The work by Dakos et al. (2011)

provides one conceptual basis for evaluating transition—is there a critical “slowing down” at some point in community composition? In other words, can we identify points at which a community is slow to recover, and does this situation indicate the community is at risk of a transition?

State-and-Transition Models

Many of the concepts presented in this paper are consistent with current STM methods and approaches. A focus on the regeneration niche and mortality/recruitment simply provides the mechanisms responsible for either community shifts or transitions among stable states. A better understanding of the factors that influence mortality and recruitment will improve our ability to predict vegetation change. The two examples presented earlier (Fig. 4) demonstrate how disturbance and weather interact. It will not be possible to experimentally test all possible combinations of disturbance, weather, and management, but a sound mechanistic basis will improve our ability

to predict outcomes. Warning signals for undesirable transitions should allow managers to focus resources on higher priority areas.

Westoby et al. (1989) discussed opportunities and hazards associated with different stable states. This approach, to some extent, has been lost in subsequent STM discussions. Some opportunities might require specific sequences of years or combinations of weather and management. And the opportunities can generally be tied directly to recruitment of desirable species. The hazards might be tied to events which cause mortality of desired species and allow recruitment of species we would rather not have. In summary, we believe that more focus on mortality, recruitment, and clearer definitions for disturbance and critical transitions will improve the value of STMs for making management decisions.

MANAGEMENT IMPLICATIONS

Rangeland management has always had a strong focus on vegetation change and succession. However, there is a need to move beyond describing changes after the fact and improve our predictive ability. The regeneration niche concept provides a framework within which the underlying basis for vegetation change can be evaluated. We suggest that a focus on plant mortality and recruitment will help managers anticipate and explain vegetation changes. Such an approach provides a basis for classifying disturbances, weather events, and management practices. For example, some disturbances have an immediate effect on plant survival (such as fire), whereas others can affect life span but not cause immediate death (heavy grazing, extended drought). This approach will require a synthesis of existing scientific literature and a good deal of gap-filling research on rangeland plant population dynamics. Bunchgrass density is emerging as a critical parameter for evaluating recovery and invasion-resistance of sagebrush-steppe rangelands after disturbance (Davies et al. 2011).

As a starting point, we suggest the following steps for developing recruitment-based management:

- Use a dynamic mortality/regeneration lens when viewing a plant community. Are there clues about community change over a 5–10 yr time horizon?
- Assemble existing knowledge about life history and resilience of critical plant species. How are they affected by weather, disturbance, and management?
- Incorporate measurements of mortality and recruitment into monitoring programs. Fixed-location plot photos could be useful in this regard if individual plants can be identified.
- Document vegetation gaps and potential sources of propagules to fill gaps.
- Evaluate recruitment potential of gaps, e.g., safe sites and soil surface characteristics.
- Identify sequences of events that might be necessary for recruitment. For example, on arid rangelands, several consecutive wet years might be necessary to allow both adequate seed production and seedling establishment.

For several of the steps, there is existing scientific literature, but clearly a focused research effort is required to fill knowledge gaps. This knowledge will also assist in document-

ing factors which drive transitions among stable states and thus make State-and-Transition Models more predictive.

ACKNOWLEDGMENTS

The authors would like to thank Drs. Joel Brown and Chad Boyd for comments on an earlier version of the manuscript. We thank many of our coworkers for the discussions which led to this manuscript.

LITERATURE CITED

- ADAMS, A. W. 1975. A brief history of juniper and shrub populations in southern Oregon. Corvallis, OR, USA: Oregon State Wildlife Commission. Wildlife Research Report #6, 33 p.
- AGUILERA, M. O., AND W. K. LAUENROTH. 1995. Influence of gap disturbances and type of microsites on seedling establishment in *Bouteloua gracilis*. *Journal of Ecology* 83:87–97.
- ALLEN, E. A., AND R. S. NOWAK. 2008. Effect of pinyon-juniper tree cover on the soil seed bank. *Rangeland Ecology & Management* 61:63–73.
- BESTELMEYER, B. T., J. R. BROWN, K. M. HAVSTAD, R. ALEXANDER, G. CHAVEZ, AND J. E. HERRICK. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114–126.
- BOYD, C. S., AND K. W. DAVIES. 2010. Shrub microsite influences post-fire perennial grass establishment. *Rangeland Ecology & Management* 63:248–252.
- BOYD, C. S., AND T. J. SVEJCAR. 2011. The influence of plant removal on succession in Wyoming big sagebrush. *Journal of Arid Environments* 75:734–741.
- BRISKE, D. D., B. T. BESTELMEYER, T. K. STRINGHAM, AND P. L. SHAVER. 2008. Recommendations for development of resilience-based state-and-transition models. *Rangeland Ecology & Management* 61:359–367.
- BRISKE, D. D., S. D. FUHLENDORF, AND F. E. SMEINS. 2006. A unified framework for assessment and application of ecological thresholds. *Rangeland Ecology & Management* 59:225–236.
- BURDON, J. J., AND R. C. SHATTOCK. 1980. Disease in plant communities. *Applied Biology* 5:145–219.
- BURKETT, V. R., D. A. WILCOX, R. STOTTLEMYER, W. BARROW, D. FAGRE, J. BARON, J. PRICE, J. NIELSEN, C. D. ALLEN, D. L. PETERSON, G. RUGGERONE, AND T. DOYLE. 2005. Nonlinear dynamics in ecosystem response to climatic change: case studies and policy implications. *Ecological Complexity* 2:357–394.
- CALL, C. A., AND B. A. ROUNDY. 1991. Perspectives and processes in revegetation of arid and semiarid rangelands. *Journal of Range Management* 44:543–549.
- DAKOS, V., S. KÉFI, M. RIETKERK, E. H. VAN NES, AND M. SCHEFFER. 2011. Slowing down in spatially patterned ecosystems at the brink of collapse. *American Naturalist* 177:6: E153–E166.
- DALZELL, C. R. 2004. Post-fire establishment of vegetation communities following reseedling on Southern Idaho's Snake River Plain [thesis]. Boise, ID, USA: Boise State University. 112 p.
- DAVIES, K. W., C. S. BOYD, J. L. BECK, J. D. BATES, T. J. SVEJCAR, AND M. A. GREGG. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144:2573–2584.
- DAVIES, K. W., T. J. SVEJCAR, AND J. D. BATES. 2009. Interaction of historical and nonhistorical disturbances maintains native plant communities. *Ecological Applications*, 19:1536–1545.
- EDWARDS, G. R., AND M. J. CRAWLEY. 1999. Herbivores, seed banks, and seedling recruitment in mesic grasslands. *Journal of Ecology* 87:423–435.
- ERIKSSON, O., AND J. EHRLÉN. 2008. Seedling recruitment and population ecology. In: M. A. Leck, V. T. Parker, and R. L. Simpson [EDS.]. Seedling ecology and evolution. Cambridge, UK: Cambridge University Press. p. 239–254.
- FACELLI, J. M. 2008. Specialized strategies I: seedlings in stressful environmental. In: M. A. Leck, V. T. Parker, and R. L. Simpson [EDS.]. Seedling ecology and evolution. Cambridge, UK: Cambridge University Press. p. 56–78.
- FAIR, J., W. K. LAUENROTH, AND D. P. COFFIN. 1999. Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals. *Journal of Ecology* 87:233–243.

- FENNER, M., AND K. THOMPSON. 2005. The ecology of seeds. Cambridge UK: Cambridge University Press. 260 p.
- GOMEZ-APARICIO, L. 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology* 97:1202–1214.
- GRIME, J. P. 2002. Plant strategies, vegetation processes, and ecosystem properties. New York, NY, USA: John Wiley & Sons. 417 p.
- GRIMM, V., AND C. WISSEL. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109:323–334.
- GRUBB, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52:107–145.
- HACKER, R. B., K. C. HODGKINSON, G. J. MELVILLE, J. BEAN, AND S. P. CLIPPERTON. 2006. Death model for tussock perennial grasses: thresholds for grazing-induced mortality of mulga Mitchell grass (*Thyridolepis mitchelliana*). *The Rangeland Journal* 28:105–114.
- HODGKINSON, K. C., AND W. J. MILLER. 2005. Death model for tussock perennial grasses: a rainfall threshold for survival and evidence for landscape control of death in drought. *The Rangeland Journal* 27:105–115.
- HORMAY, A. L., AND M. W. TALBOT. 1961. Rest-rotation grazing... a new management system for perennial bunchgrass ranges. Berkeley, CA, USA: US Department of Agriculture, Forest Service. Production Research Report, No. 51. Pacific Southwest Forest and Range Experiment Station. 43 p.
- JAMES, J. J., T. J. SVEJCAR, AND M. J. RINELLA. 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. *Journal of Applied Ecology* 48:961–969.
- KONIAK, S., AND R. L. EVERETT. 1982. Seed reserves in soils of successional stages of pinyon woodlands. *American Midland Naturalist* 108:295–303.
- KRUEGER-MANGOLD, J. M., R. L. SHELEY, AND T. J. SVEJCAR. 2006. Toward ecologically-based invasive plant management on rangeland. *Weed Science* 54:597–605.
- LAUENROTH, W. K., AND P. B. ADLER. 2008. Demography of perennial grassland plants: survival, life expectancy and life span. *Journal of Ecology* 96:1023–1032.
- LECK, M. A., AND H. A. OUTRED. 2008. Seedling natural history. In: M. A. Leck, V. T. Parker, and R. L. Simpson [EDS.]. Seedling ecology and evolution. Cambridge, UK: Cambridge University Press. p. 17–55.
- LISTON, A., B. L. WILSON, W. A. ROBINSON, P. S. DOESCHER, N. R. HARRIS, AND T. SVEJCAR. 2003. The relative importance of sexual reproduction versus clonal spread in an aridland bunchgrass. *Oecologia* 137:216–225.
- LOMMASSON, T. 1948. Succession in sagebrush. *Journal of Range Management* 1:19–21.
- MILLER, R. F., J. D. BATES, T. J. SVEJCAR, F. B. PIERSON, AND L. E. EDDLEMAN. 2005. Biology, ecology, and management of western juniper. Corvallis, OR, USA: Oregon State University Agricultural Experiment Station. Technical Bulletin 152. 77 p.
- MILLER, R. F., AND J. A. ROSE. 1999. Fire history and western juniper encroachment in sagebrush steppe. *Journal of Range Management* 52:550–559.
- MOLES, A. T., AND M. WESTOBY. 2004. What do seedlings die from and what are the implications for evolution of seed size? *Oikos* 106:193–199.
- O'CONNOR, T. G. 1991. Local extinction in perennial grasslands: a life-history approach. *American Naturalist* 137:753–773.
- PASCUAL, M., AND F. GUICHARD. 2005. Criticality and disturbance in spatial ecological systems. *Trends in Ecology and Evolution* 20:88–95.
- PICKETT, S. T. A., S. L. COLLINS, AND J. J. ARMESTO. 1987. Models, mechanisms and pathways of succession. *Botanical Review* 53:335–371.
- SCHAEFFER, M., J. BASCOMPTÉ, W. A. BROCK, V. BROVKIN, S. R. CARPENTER, V. DAKOS, H. HELD, E. H. VAN NES, M. RIETKERK, AND G. SUGIHARA. 2009. Early-warning signals for critical transitions. *Nature* 461:53–59.
- SCHULTZ, B. W., P. T. TUELLER, AND R. J. TAUSCH. 1990. Ecology of curlleaf mahogany in western and central Nevada: community and population structure. *Journal of Range Management* 43:13–19.
- SHELEY, R. L., J. M. MANGOLD, AND J. L. ANDERSON. 2006. Potential for successional theory to guide restoration of invasive-plant-dominated rangelands. *Ecological Monographs* 76:365–379.
- SHELEY, R. L., T. J. SVEJCAR, AND B. D. MAXWELL. 1996. A theoretical framework for developing successional weed management strategies on rangeland. *Weed Technology* 10:766–773.
- SILVERTOWN, J., M. FRANCO, I. PISANTY, AND A. MENDOZA. 1993. Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81:465–476.
- SMITH, M. D., A. K. KNAPP, AND S. L. COLLINS. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90:3279–3289.
- STRINGHAM, T. K., W. C. KRUEGER, AND P. L. SHAVER. 2003. State and transition modeling: an ecological process approach. *Journal of Range Management* 56:106–113.
- SVEJCAR, T. J., AND R. L. SHELEY. 1995. A conceptual framework for integrating natural resource management and research. In: N. E. West [ED.]. Proceedings of the Fifth International Rangeland Congress. Denver, CO, USA: Society for Range Management. p. 547–548.
- SWETNAM, T. W., AND J. L. BETANCOURT. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate* 11:3128–3146.
- WALL, T. G., R. F. MILLER, AND T. J. SVEJCAR. 2001. Juniper encroachment into aspen in the northwest Great Basin. *Journal of Range Management* 54:691–698.
- WEST, N. E., K. H. REA, AND R. O. HARNISS. 1979. Plant demographic studies in sagebrush–grass communities of southeastern Idaho. *Ecology* 60:376–388.
- WESTOBY, M., B. WALKER, AND I. NOYMEIR. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.
- WHITE, P. S., AND A. JENTSCH. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* 62:399–450.
- WHITE, P. S., AND S. T. A. PICKETT. 1985. Natural disturbance and patch dynamics. In: S. T. A. Pickett and P. S. White [EDS.]. The ecology of natural disturbance and patch dynamics. Orlando, FL, USA: Academic Press. p. 3–13.
- WIJAYATNE, U. C., AND D. A. PYKE. 2009. Investigating seed longevity of big sagebrush (*Artemisia tridentata*). Reston, VA, USA: US Geological Survey Open File Report 2009-1146. 26 p.
- WINKEL, V. K., B. A. ROUNDY, AND J. R. COX. 1991. Influence of seedbed microsite characteristics on grass seedling emergence. *Journal of Range Management* 44:210–214.
- WRIGHT, R. G., AND G. M. VAN DYNE. 1976. Environmental factors influencing semidesert grassland perennial grass demography. *Southwestern Naturalist* 21:259–274.
- YOUNG, T. P., D. A. PETERSEN, AND J. J. CLARY. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology Letters* 8:662–673.
- ZIEGENHAGEN, L. L., AND R. F. MILLER. 2009. Postfire recovery of two shrubs in the interiors of large burns in the intermountain west, USA. *Western North American Naturalist* 69:195–205.
- ZIMMERMANN, J., S. I. HIGGINS, V. GRIMM, J. HOFFMANN, T. MUNKEMULLER, AND A. LINSTADTER. 2008. Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability. *Journal of Ecology* 96:1033–1044.
- ZISKA, L. H., J. B. REEVES, AND B. BLANK. 2005. The impact of recent increases in atmospheric CO₂ on biomass production and vegetative retention of cheatgrass (*Bromus tectorum*): implications for fire disturbance. *Global Change Biology* 11:1325–1332.