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Toward ecologically-based invasive plant management on rangeland

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Land managers typically use herbicides, biological controls, fire, grazing, and revegetation to manage and restore rangeland dominated by invasive plants. Without careful planning and implementation, these tools may temporarily control the weeds but may ultimately have minimal influence on ecological processes, fail over the long term, and lead to weed reinvasion. This can result from the lack of a broad ecological perspective. Successional management provides a process-based framework for weed ecologists to develop and test integrated weed management strategies and for land managers to organize implementation of these strategies in a way that adequately addresses ecological processes. This framework offers land managers practical methods for modifying ecological processes to direct plant community composition away from invasive species and toward desired plant assemblages. To date, successional management has not gained widespread application because, in part, it has not been conceptually linked to other successional models. Therefore, we illustrate how other successional models can be incorporated within the framework. Incorporating other prevailing successional models will further elucidate ecological processes, offer additional management strategies, and widen the possibilities for ecologically based management of rangeland weeds. Approaching management of weed-infested rangeland through this process-based framework will enable managers to implement strategies that maximize the likelihood of success because these methods will be integrated based on ecological principles. Successional management should be adjusted as we gain a better understanding of the factors that drive succession.

Key words: Ecological processes, invasion, restoration, succession, weeds.

Plant ecologists have studied temporal and spatial changes in plant community composition for more than a century and a half. Thoreau (1860) used the term "succession" to describe temporal changes in plant community composition, and observations by Clements (1916; 1936) and Gleason (1917) appear to be responsible for the term's general acceptance. During the past century, the concept of succession has included a new and troublesome factor—nonindigenous, invasive species. Nonindigenous plant invasions can dramatically change the rate and direction of succession (Billings 1990); the structure, organization, and function of ecosystems (D'Antonio and Vitousek 1992; Lacey et al. 1989; Olson 1999a; Whisenant 1990); and the aesthetic, ecological, and economic value of rangelands (DiTomaso 2000).

When successional trajectories are changed by the presence of invasive plants, management focuses on killing the weeds with traditional control methods, such as herbicides, biocontrols, or mechanical control, with limited regard to the underlying processes that contributed to the invasion (Sheley and Krueger-Mangold 2003). This approach often results in reinvasion or invasion by an equally undesirable nonindigenous species. To achieve sustainable management, managers need to address fundamental ecological processes and how they promote the establishment and persistence of invasive plants (Sheley and Krueger-Mangold 2003).

Successional management has been proposed as a way to develop ecologically based management strategies for invasive plants (Pickett et al. 1987; Sheley et al. 1996). Numerous models that explain mechanisms responsible for plant community change through time and space have been developed throughout the 20th century, but none of them have been included in successional management. The purpose of this article is to illustrate how to integrate other mechanistic successional models into the successional management framework to improve our understanding of plant community dynamics.

Successional Management Framework

Pickett et al. (1987) proposed a hierarchical successional management framework that lends itself well to understanding processes influencing plant community dynamics. The first level of the hierarchy identifies three general causes of succession: site availability, species availability, and species performance (Table 1). For invasion to occur, safe sites for the invader need to be present. Second, invader propagules need to occupy those sites. Third, the invading species must perform successfully in the new sites. These general causes underlie all cases of plant community change and can guide our search for a better understanding of succession and its management (Pickett et al. 1987). Ecological processes that influence the three causes of succession form the second level of the hierarchy (Table 1). We have clarified the second level of the hierarchy by including the term "components" in addition to "processes"; many of the factors within the second hierarchical level are not ecological processes, per se, but encompass crucial components that are the consequence of and catalysts for ecological processes. The third and final level of the hierarchy details site-specific, modifying factors that alter the processes and components and, in turn, influence successional dynamics (Table 1). Knowledge about the

TABLE 1. Causes of succession, contributing processes and components, and modifying factors (modified from Pickett et al. 1987).

Causes of succession	Processes and components	Modifying factors
Site availability	Disturbance	Size, severity, time intervals, patchiness, predisturbance history
Species availability	Dispersal	Dispersal mechanisms and landscape features
	Propagule pool	Land use, disturbance interval, species life history
Species performance	Resource supply	Soil, topography, climate, site history, microbes, litter retention
	Ecophysiology	Germination requirements, assimilation rates, growth rates, genetic differentiation
	Life history	Allocation, reproduction timing and degree
	Stress	Climate, site-history, prior occupants, herbivory, natural enemies
	Inteference	Competition, herbivory, allelopathy, resource availability, predators

modifying factors can help in identifying strategies and methods for shifting successional trajectories in desired directions.

Luken (1990) applied the successional management framework to natural resource management. He used management-oriented vernacular to describe the three causes of succession: designed disturbance, controlled colonization, and controlled species performance. Successional management was modified specifically for nonindigenous plant invasions by Sheley et al. (1996) and Sheley and Krueger-Mangold (2003). They argued that plant communities dominated by invasive plants could likely be restored by strategically addressing the three causes of succession. Since being proposed for natural resource and invasive plant management, successional management has also been proposed for restoring damaged wildlands (Whisenant 1999).

Successional management has been tested for invasive plant management over the past several years. The potential efficacy of biocontrol was evaluated with successional management by understanding how natural enemies affect the processes and components of dispersal, stress, and interference of target and nontarget plants (Sheley and Rinella 2001). Restoring rangeland infested with invasive plants became more effective as the causes of succession were increasingly addressed (R. L. Sheley, J. S. Jacobs, and J. J. Svejcar, unpublished data). Augmentative restoration of weed-infested rangeland included applying successional management by assessing the current state of processes associated with the three causes of succession. When processes were found to be damaged, they were amended in an effort to restore native grasses and forbs (Bard et al. 2004).

The adoption of successional management has been hampered because we lack a thorough understanding of the factors that modify the processes and components directing succession. Within the framework, the causes, processes, and components of succession are presented, but very little mechanistic detail is discussed. The framework does not allow for varying degrees of importance and functionality of different processes and components from site to site. For example, the most influential process at one site may not be the most influential at another; additionally, the degree to which an ecological process has been altered may vary across a landscape (Bard et al. 2004). A more comprehensive understanding and a better assessment of the relative importance and the degree each process and component is functioning at a site would strengthen the framework and increase its usefulness for management and restoration of weed-infested rangeland.

The successional management framework could be strengthened by integrating other mechanistic successional models into a more robust, unified framework that clarifies the details and relative importance of processes and components from site to site. Successional management provides an encompassing perspective on plant community dynamics, whereas other prevailing successional models provide detailed mechanisms of plant community change. Together, successional management and other successional models may be useful for implementing ecologically based, invasive plant management. The succession management framework can be refined and improved as our understanding of other successional models improves.

Processes and Components

An in-depth understanding of ecological processes and their modifying factors is essential if the successional management framework is to move from theory to application for invasive plant management. We acknowledge that successional management has weaknesses, and we do not claim to fill in all the gaps between its theory and application. Instead, we hope to move toward clarification of complex processes and components by illustrating how additional successional models may be considered within the context of the framework. We challenge other ecologists and land managers to continue filling knowledge gaps between successional management theory and application by thinking beyond our current toolbox and developing and testing strategies that are founded on the ecological processes that may be most influential in their particular situation.

Disturbance

Disturbance is defined as a relatively discrete event in time that disrupts ecosystem, community, or population structure and changes the resources, substrate availability, or physical environment (White and Pickett 1985). Disturbance is commonly viewed as contributing to weed invasion (Lozon and MacIsaac 1997) and, therefore, viewed negatively by land managers. Rangeland is typically managed to prevent natural disturbance, but this can potentially increase the severity of a natural disturbance when it does occur. For example, historic fire suppression resulted in increased fuel loads and high intensity wild fires that are believed to have contributed to the expansion of cheatgrass (*Bromus tectorum* L.) in the Great Basin (Whisenant 1990).

Disturbance is considered in the tolerance model of succession (Connell and Slatyer 1977) and the fluctuating resource availability theory (Davis et al. 2000). The tolerance model proposes that as succession proceeds, species tolerant of highly stressful environmental conditions, such as low

TABLE 2. Causes of succession, contributing processes and components, and modifying factors in the expanded successional management framework (modified from Pickett et al. 1987). Successional models and relevant citations are listed in italics under processes. Bold-faced modifying factors are additional modifying factors proposed in text.

Causes of succession	Processes and components	Modifying factors
Site availability	Disturbance *Tolerance (Connell and Slatyer 1977); Fluctuating Resource Availability (Davis et al. 2000)*	Size, severity, time intervals, patchiness, predisturbance history, **shallow tillage, grazing with multiple types of livestock**
Species availability	Dispersal *Inhibition (Connell and Slatyer 1977); Initial Floristic Composition (Egler 1954)*	Dispersal mechanisms and landscape features, **dispersal vectors, seedbed preparation, seeding in phases**
	Propagule pool *Inhibition, Initial Floristic Composition*	Land use, disturbance interval, species life history, **assessment of propagule pool, seed coating**
Species performance	Resource supply *Facilitation (Connell and Slatyer 1977); Resource Ratio Hypothesis (Tilman 1977, 1982, 1984, 1988)*	Soil, topography, climate, site history, microbes, litter retention, **soil resource assessment, soil impoverishment, *R****
	Ecophysiology *Vital Attributes (Noble and Slatyer 1980)*	Germination requirements, assimilation rates, growth rates, genetic differentiation, **comparison between native and introduced environments, seed priming**
	Life history *Tolerance* K- *and* r-*strategists (MacArthur 1962)*	Allocation, reproduction timing and degree, **sensitivity analysis**
	Stress *Tolerance, C-S-R (Grime 1979); Community Assembly Theory (Diamond 1975)*	Climate, site-history, prior occupants, herbivory, natural enemies, **identifying abiotic and biotic filters, seeding species-rich mixtures**
	Interference *Inhibition*	Competition, herbivory, allelopathy, resource availability, predators, other level interactions, **cover crops, assisted succession**

nutrient, water, and light availability, replace species with low tolerance of those conditions. When disturbance frequency remains low, those species that tolerate stressful conditions continue to dominate. Once disturbance occurs, the system becomes characterized by less-stressful conditions in terms of resource availability, and this may initiate a change in plant community composition.

The fluctuating resource availability theory states that disturbance may cause a decline in resource use by plants or an increase in resource supply rates through plant decomposition, thus leading to an increase in resource availability and increasing susceptibility to invasion (Davis et al. 2000). For example, fire can result in a decline in resource use by killing existing vegetation while simultaneously causing a resource flux by depositing nutrient-rich ash and increasing light penetration to the soil surface (Wright and Bailey 1982).

Implications for Successional Management

Rangeland managers may profit by viewing disturbance as an opportunity to shift plant community composition toward a more desired state (Westoby et al. 1989). Rangeland infested by near-monocultures of nonindigenous plants that appear to be tolerant of current conditions may have to be disturbed to increase resource availability for desirable species (Cox and Anderson 2004). This is sometimes accomplished with herbicides, plowing, fire, and chaining (Sheley and Petroff 1999). We encourage the further evaluation of shallow tillage and grazing with multiple classes of livestock to modify the process of disturbance in a useful manner (Table 2).

Shallow tillage with a disc, spring-toothed harrow, or other implement may be appropriate for management of some nonindigenous, invasive species growing on relatively flat, arable sites. Shallow tillage every 3 wk until the soil freezes in the fall, for one to two growing seasons, has been used to manage leafy spurge (*Euphorbia esula* L.) (Dersheid et al. 1960, 1963; Lym and Messersmith 1993). Dalmatian toadflax [*Linaria dalmatica* (L.) Mill.] was controlled by tilling every 7 to 10 d during two successive growing seasons (Parker and Peabody 1983). Shallow tillage not only impedes the performance of some weeds but also prepares seedbeds and increases resource availability for desired species (Cox and Anderson 2004; Sheley et al. 2005).

The specificity and intensity of disturbance may be controlled by grazing with multiple types of livestock. Certain classes of livestock preferentially graze specific plant lifeforms—sheep usually prefer forbs over grasses and shrubs, whereas cows often preferentially graze grasses, and goats often prefer shrubs (Olson 1999b). If rangeland is heavily grazed by cattle, grasses are at a disadvantage for acquiring water and nutrients compared with forbs, making improperly grazed grasslands more susceptible to invasion by annual grasses and nonindigenous forbs (DiTomaso 2000). By manipulating timing and intensity of grazing, managers can control patterns of defoliation to place a target plant at a competitive disadvantage relative to other plants in the community (Frost and Launchbaugh 2003). In grazed systems, inherent diet selections have assisted in shifting species composition of native plant communities (Bowns and Bagley 1986). Knowledge gaps exist concerning multispecies grazing and weed management; therefore, we propose further testing of this strategy within the successional management framework. We hypothesize that grazing with multiple types of livestock may equalize disturbance across plant growth forms and increase invasion resistance.

Dispersal

The inhibition (Connell and Slatyer 1977) and initial floristic composition (Egler 1954) models of succession rely heavily on the process of dispersal because they imply that any species can establish and reproduce as long as its propagules are available at the site. Once established, a species persists by acquiring and accumulating available resources, thereby inhibiting the invasion of subsequent species until the next disturbance occurs. Invasive plants like spotted knapweed (*Centaurea maculosa* Lam.) can disperse to a recently disturbed site, acquire available resources, hinder the establishment of more desirable species, and arrest successional dynamics (Blicker et al. 2002; Chicoine et al. 1985). The models of inhibition and initial floristic composition imply that rangeland dominated by invasive plants is likely to remain in its current state unless propagules of different species are introduced through restoration activities.

Implications for Successional Management

Ecologists and land managers need a better understanding of weed seed dispersal vectors across landscapes, followed by focused management on those areas likely to experience an influx of seeds, especially following a disturbance. Dispersal before and immediately following disturbance is critical because those species that distribute their propagules across the disturbed area may remain dominant. For example, extensive stands of cheatgrass alter organic matter on the soil surface and fire-return intervals to favor continued cheatgrass dominance (Evans et al. 1970, Whisenant 1990). Roads, trails, streams and rivers, and winter feeding areas for livestock and wildlife are often highly disturbed and traveled by humans, livestock, and wildlife and, thus, should be carefully monitored for new weed infestations and managed for weed control (Forcella and Harvey 1983; Tyser and Key 1988) (Table 2).

In contrast to the prevention of weed seed dispersal, dispersal of desirable species during restoration of weed-infested rangeland may be more easily modified and controlled. Dispersal of desirable species can be modified through seedbed preparation and seeding methods (Table 2). Chambers (2000) modified soil surface characteristics to examine the effects on seed entrapment and retention and subsequent seedling emergence and survival on sagebrush steppe in Wyoming. She found that large depressions (50 cm wide by 10 cm deep) trapped and retained the most seeds and resulted in the highest seedling emergence compared with smaller depressions. When restoring weed-infested rangeland, we should consider how to best prepare the seed bed and the best seeding method to favor establishment of desirable species and hamper reestablishment of weedy species. For example, we hypothesize that large-seeded species like bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey] and bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh.) A. Löve] will establish best on a seedbed that has similarly sized holes, indentations, and crevices. The relationship between seedbed characteristics and seed morphology is an area of research that needs further investigation.

The sequence, rate, and frequency of dispersal events can have large effects on community composition (Booth and Swanton 2002). Rangeland restoration often fails because climatic conditions, especially precipitation events, are not consistently conducive to species establishment (Bleak and Keller 1974). Increasing dispersal frequency by seeding in phases throughout multiple seasons or years will increase the seeds' chances of encountering environmental conditions that are most conducive to seedling establishment and survival (Table 2). For example, it may be beneficial to refrain from seeding until weather patterns suggest a high potential for establishment. When reseeding perennial grasses following western juniper (*Juniperus occidentalis* spp. *occidentalis* Hook.) control on rangeland in central Oregon, establishment was best when total precipitation for November through January exceeded 12.5 cm and in which none of the 3 mo individually were below 4.3 cm (Eddleman 2002). The potential for a second phase of planting in February or March, after seeding the previous fall, would allow an evaluation of available winter moisture and might increase the probabilities for successful restoration.

Propagule Pool

As with dispersal, the inhibition (Connell and Slatyer 1977) and initial floristic composition (Egler 1954) models of succession imply that a species can establish and reproduce if its propagules are available. Invasive species often have very large and long-lived seed banks compared with native species because of a combination of high seed production and dormancy (Radosevich et al. 1997). Many invasive species are known to exhibit somatic polymorphism or the ability to produce seeds of differing morphologies, dormancy, and germination requirements (Harper 1977). This is generally viewed as a mechanism to enhance survival across differing habitats and environmental conditions.

Desirable species may be found in the propagules pool in much lower proportions compared with invasive species after decades of invasive plant dominance (Navie et al. 2004). If so, then introduction of desirable species is necessary, often at high seeding rates to compete with the large number of weed seeds (Velagala et al. 1997). In addition, evidence suggests weedy species are less likely to reinvade a plant community when the community already contains species in a similar functional guild (Fargione et al. 2003; Pokorny 2002).

Implications for Successional Management

Immediately following disturbance, managers should assess the composition of the propagule pool to determine whether seeding is necessary (Poulsen et al. 1999) (Table 2). If above-ground cover of desirable species is less than 20%, propagule availability of desired species is probably low and reintroduction of their propagules is necessary (Goodwin et al. 2006). Reinvasion may be hindered if the remaining vegetation and propagule pool contain multiple functional guilds (Carpinelli 2000; Symstad 2000). Furthermore, the presence of species-rich functional guilds similar to the weed being managed may hinder reinvasion. For example, Pokorny (2002) found that invasion by the forb, spotted knapweed, was minimized by the presence of other native forbs, more so than any other functional group. If desirable functional guilds are rare or missing, revegetation of these guilds is necessary. Application of broadleaf herbicides may eliminate the functional guilds that are most similar to invasive forbs, thereby promoting reinvasion. Choosing an herbicide

and applying it at the appropriate rate and time can minimize damage to nontarget forbs (Sheley and Denny 2006).

Establishing desirable species is difficult and often unsuccessful. Introduction and establishment of desirable species may be enhanced by seed coating (Table 2). Seed coating can be used to treat desired species with compounds that decrease susceptibility to pests and pathogens and alleviate abiotic stress. Alfalfa (*Medicago sativa* L.) seeds treated with peat and lime produced significantly greater plant emergence and plant survival than noncoated seeds in field trials (Walsh and Turk 1988) and were especially helpful for alfalfa establishment under conditions of limited moisture (Turk 1983). Seed-coating technology can be especially useful in arid and semiarid environments and warrants further investigation.

Resource Supply Rate

As succession progresses, resource supply varies as a response to changes in soil physical characteristics, soil nutrient and water content, soil microbial populations, and litter accumulation (Wardle 2002a). Facilitation, a successional model first proposed by Clements (1916) and later expanded upon by Connell and Slatyer (1977), occurs when early successional species increase nutrient supply rates, increase litter and decomposition rates, decrease light penetration to the soil surface, and shift composition of the plant and microbial community (Wardle 2002b).

Another successional model based on resource supply, the resource ratio hypothesis, states that succession is a result of species' unique requirements for essential resources, especially soil nutrients (Tilman 1982, 1988). According to this hypothesis, late-successional species are better competitors for soil nutrients and moisture than early successional species. As succession progresses, a species attains dominance when ratios of essential soil resources result in its maximum population growth rate relative to competing species. Tilman (1982) postulated that the outcome of competition at limited resource supply rates could be predicted by a species' R^*, the amount of a resource necessary for a species to maintain a stable population within a habitat. A resource supply rate higher than R^* leads to an increase in population size; any value lower than R^* leads to a decrease in population size. The resource ratio hypothesis predicts that a species with a lower R^* will competitively displace a species with a higher R^*, under equilibrium conditions (Tilman 1982, 1984, 1988).

Implications for Successional Management

Before attempting to restore weed-infested rangeland, soil resource availability should be assessed to determine what amendments are necessary for establishing a more desirable plant community (Bard 2004) (Table 2). Studies indicate that invasive species generally prefer environments with high resource supply rates, especially for nitrogen (N) (Blumenthal et al. 2003; Burke and Grime 1996; Huenneke et al. 1990; Maron and Connors 1996). Soil impoverishment, which is the addition of carbon to soil to increase soil microbial populations, which, in turn, decrease soil N by sequestration, has been proposed as a method for managing weeds (Morgan 1994) (Table 2). Carbon additions have been used to shift plant communities to late-successional stages (McLendon and Redente 1991; Paschke et al. 2000) and to decrease performance of invasive species (Blumenthal et al. 2003; Herron et al. 2001).

Species' R^*s may provide insight into the effectiveness of management strategies (Table 2). For example, Brockington (2003) proposed using spotted knapweed's estimated R^* to assess whether a biocontrol agent was effectively reducing the plant's ability to uptake soil nutrients, thereby, decreasing its competitiveness. In addition, knowledge of species' R^* for various limiting resources can be used to predict the outcome of plant community dynamics, to identify areas susceptible to invasion based on patterns of resource availability and invasive species' R^*s, and to alter resource availability to direct plant community dynamics toward a desired state.

Ecophysiology

Noble and Slatyer (1980) referred to ecophysiological traits as "vital attributes." Vital attributes include traits that enable persistence through a disturbance, that permit establishment and maturation after a disturbance, and that inhibit other species. Ecophysiological traits, such as germination requirements, nutrient-assimilation rates, growth rates, and genetic differentiation, might help predict which species will dominate in a plant community under various environmental conditions (Pickett 1982).

Implications for Successional Management

Comparisons between an invasive species' native and introduced environment might explain biotic and abiotic conditions responsible for invasive behavior (Callaway and Aschehoug 2000; Hierro and Callaway 2003) (Table 2). Some invasive plants may use mechanisms that are not present in the communities they invade and, thereby, disrupt inherent, coevolved interactions among native species, the so-called "novel weapons" hypothesis (Callaway and Aschehoug 2000; Callaway et al. 2005). For example, nonindigenous, invasive forbs may be better host plants for arbuscular mycorrhizae and develop more extensive hyphal networks than native rangeland grasses (Zabinski et al. 2002). Further research into a species' ecophysiology and community dynamics within a species' native environment may help develop ecologically based management in the invaded ecosystem.

Many invasive annual grasses and forbs have faster germination rates than natives (DiTomaso 1999; Miller et al. 1999; Mosely et al. 1999; Rice 1999; Sheley et al. 1999a). Seed-priming has increased germination rates of natives (Hardegree 1994 and 1996; Hardegree et al. 2002). Priming native seeds before planting into infested rangeland may ensure resource preemption and a positive feedback between growth and resource uptake (Radosevich et al. 1997), thereby, leading to greater restoration success (Table 2). Although seed-priming has been traditionally used in horticultural settings, research into the feasibility of seed priming for large weed infestations on rangelands has been initiated (CIPM 2005) and warrants further investigation.

Life History

Life history describes phenological, physiological, and behavioral traits employed by a species as it passes from seed to adulthood. The tolerance model of succession states that

mechanisms responsible for the location of a species on a successional trajectory are associated with life history (Connell and Slatyer 1977). Early successional species that grow quickly and produce large seed masts are eliminated in the absence of disturbance because they allocate resources to reproduction and dispersal rather than to competitive plant structures (*r*-strategists; MacArthur 1962). In contrast, late-successional species dominate later because they grow more slowly, are longer-lived, and allocate resources to below-ground growth rather than seeds, allowing them to be more tolerant of stressful environmental conditions like drought and low-nutrient supply rates (*K*-strategists; MacArthur 1962). Even though invasive plants have been categorized as *r*-strategists (Bazzaz 1986), many appear to also possess some *K*-strategist traits, such as drought tolerance (Radosevich et al. 1997).

Implications for Successional Management

Examining the life history of invasive plants and performing sensitivity analyses has been proposed as a means of identifying vulnerable phases and key processes that regulate population dynamics (Jacobs and Sheley 1998; Kriticos et al. 1999; Maxwell et al. 1988; Sagar and Mortimer 1976) (Table 2). A sensitivity analysis on the life history of cheatgrass and yellow starthistle (*Centaurea solstitialis* L.) suggested the most-effective management for cheatgrass would focus on decreasing adult survivorship or seed production, whereas the most-effective management for yellow starthistle would center on reducing the number of juvenile plants transitioning to adults (Sheley and Larson 1994). Information like this helps managers decide the optimum time to administer control strategies.

Although it may be cumbersome to perform sensitivity analyses on every invasive plant, we can perform sensitivity analyses on invasive species' functional groups that have been categorized based on genus, phenology, habitat preference, or other traits. Placing invasive plants into key functional groups and performing sensitivity analyses will identify life-history stages most susceptible to management (Table 2). Once these life-history stages are identified, we can focus our management on modifying the process or component that has the most influence on the life-history stage. For example, if the highest sensitivity values for cheatgrass (i.e., annual grass) are associated with adult survivorship and seed production (Sheley and Larson 1994), management strategies should focus on limiting dispersal and reducing the propagule pool.

Stress

Competitive-stress tolerant-ruderal (C-S-R) theory (Grime 1979) focuses on stress, in addition to disturbance and competition. From a continuum of low-to-high stress, disturbance, and competition, three evolutionary strategies are apparent: ruderals, stress tolerators, and competitors. Stress tolerators are those species that persist under conditions of high stress, low disturbance, and minimal competition.

According to community assembly rules, stress tolerators persist because they are able to pass through various filters, i.e., conditions that cause stress (Diamond 1975). Booth and Swanton (2002) applied community assembly theory to weed communities and arrived at three types of filters or stressful conditions that limit which species dominate along the successional trajectory: geographic, environmental, and internal. Geographic filters act as barriers to dispersal, (e.g., oceans and mountain ranges); environmental filters function as stressful environmental conditions, such as drought, floods, or shade; and internal filters eliminate those species that cannot successfully compete with neighboring plants because of a stressful plant–plant interaction, like allelopathy, predation, or parasitism (Booth and Swanton 2002).

Implications for Successional Management

Effective rangeland weed management requires the identification of abiotic and biotic filters or stressors that are influential in permitting invasion (Table 2). Weed prevention programs must identify and use geographic and environmental filters against propagule movement and establishment to enhance existing barriers and create new barriers to invasive plants. By identifying avenues of introduction into landscapes susceptible to invasion, we will more effectively contain existing infestations and prevent new infestations. Establishing supplementary filters through management strategies like treating the periphery of existing infestations with herbicides, using weed-free hay and topsoil, limiting disturbance and improper grazing, and monitoring to identify and control invasive plants will increase the effectiveness of prevention-based strategies (Sheley et al. 1999b).

Filters to dispersal and establishment also exist when attempting to establish desired species during restoration. We suggest that one method to overcome environmental and internal filters for establishing desired species is to seed with species-rich mixes vs. mixes with only two or three species (Table 2). Species-rich seed mixes have a higher chance of containing species that successfully survive stressful environmental conditions in a given year to increase establishment of desirable species. Half (2004) found that seeding a mix of six species resulted in seedling densities equal to or better than seedling densities of each species seeded in monoculture. Furthermore, species-rich seed mixes may address internal dynamics by ensuring complementary functional guilds that increase invasion resistance (Carpinelli et al. 2004; Pokorny 2002; Symstad 2000).

Interference

Interference refers to the reduction of fitness of neighboring plants from various mechanisms. Interference mechanisms include competition, allelopathy, herbivory, resource availability, predators, and other trophic-level interactions (Pickett et al. 1987). The inhibition model focuses on interference mechanisms that limit the growth and reproduction of one species in the presence of another to the extent that new species are prevented from establishing (Connell and Slatyer 1977). For example, the success of some *Centaurea* species is believed to stem partly from the allelopathic compounds they exude (Callaway and Aschehoug 2000; Fletcher and Renny 1963; Hierro and Callaway 2003).

Competition strongly influences plant community dynamics (Grime 1979; Tilman 1982; Grace and Tilman 2003). A review of studies that investigated mechanisms by which invasive plants alter community structure showed that 85% of the studies documented strong competitive effects

of the invasive species on growth, reproduction, and resource allocation of native residents (Levine et al. 2003). Competition for resources between nonindigenous and native plants can occur during many life stages (Hamilton et al. 1999). Invasive annual grasses effectively competed with seedlings and multi-aged adults of the native bunchgrass, purple needlegrass (*Nassella pulchra* A. Hitchc.), suggesting potential for their long-term dominance in the absence of management (Hamilton et al. 1999).

Implications for Successional Management

When restoring weed-infested rangeland, we propose the addition of cover crops to shift interference mechanisms, primarily competition, in favor of desirable, native species (Table 2). Cover crops are short-lived species that are seeded with the main crop to assist in its establishment (Hartwig and Ammon 2002). Cover crops decrease water runoff and soil erosion (Hartwig 1988), add organic material to the soil (Hartwig and Ammon 2002), and sequester N (Corak et al. 1991). Cover crops have been used primarily in cropping systems (Hartwig and Ammon 2002), but their benefits may be similar during restoration of invasive plant-infested rangelands. For example, Herron et al. (2001) found that the addition of annual rye (*Secale cereale* L.) to a mixture of spotted knapweed and bluebunch wheatgrass lowered soil N and increased the competitiveness of bluebunch wheatgrass by 10-fold relative to spotted knapweed.

Interference from nonindigenous annual grasses can limit restoration of native communities. Assisted succession, the initial sowing of competitive, introduced grasses followed by a subsequent seeding of native species, may provide more interference with invasive annual grasses than seeding initially with late successional native species (Jones 1997; Roundy et al. 1997) (Table 2). Establishment of crested wheatgrass to decrease annual grass cover and return ecosystem function has been shown to later increase establishment of native bunchgrasses and shrubs in cheatgrass–infested rangeland (Cox and Anderson 2004). Assisted succession can be more costly, but the benefit of a successful restoration project that reestablishes a healthy ecosystem far outweighs the expense.

Conclusion

Our expanded successional management framework illustrates how other successional models can be incorporated to further elucidate ecological processes and provide a perspective for organizing process-based management strategies. The model supports the development of testable hypotheses about plant community change, specifically the invasion of nonindigenous species, and can be updated and improved as new successional theories are developed and tested. The incorporation of additional mechanistic models of succession offers a more ecologically based perspective on current management strategies, increases the probability of the framework being applied effectively, and challenges ecologists and practitioners to develop new strategies for managing invasive plants. Furthermore, by linking ecologically based process models to successional management, we can infer where the models need modification. In other words, integrating other models that explain plant community dynamics into the framework can help test whether the models are appropriate.

This expanded successional management model warrants further testing and application to rangelands invaded by nonindigenous plants. We believe that by considering successional management collectively with other process-based models of plant community dynamics, we can approach invasive plant management with a higher likelihood of developing effective, ecologically based management strategies. Furthermore, the succession management framework can be refined and improved as our understanding of other successional models improves.

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