Principles for Restoring Invasive Plant-Infested Rangeland
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Principles for restoring invasive plant-infested rangeland

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It is becoming increasingly clear that prescriptions for rangeland weed control are not sustainable because they treat the symptoms of weeds rather than their cause. Future restoration of invasive plant–infested rangeland must be based on ecological principles and concepts that provide for predictable outcomes. A generalized objective for ecologically based weed management is to develop and maintain a healthy plant community that is largely invasion resistant. Successional management based on ecological principles involves modifying the processes controlling the three general causes of succession: disturbance, colonization, and species performance. The processes controlling plant community dynamics can be modified to allow predictable successional trajectories. Successional management can lead to biomass optimization models for grazing management, spread vector analysis, and using resource availability to direct weedy plant communities toward those that are desired. Our challenge is to develop ecological principles on which management can be based.

Key words: Successional management, disturbance, colonization, species performance.

Through time, weed science has focused on weed control. Weeds have been with us since agriculture began about 10,000 years ago. Early agriculturalists used hoes and grubbing implements to control weeds (Radosevich et al. 1997). In developed countries, weed control technology has paralleled agriculture, progressing from hand tools to animal grazing to animal-powered and machine-powered implements of today.

During the 20th century, synthetic organic chemicals dominated weed management. Dinitrophenols were used extensively during the 1930s. Synthesis of 2,4-D by Pokorny (1941) and subsequent discovery of other plant growth regulators initiated the chemical age of weed control. Weed control researchers and practitioners searched for the new chemistry and the best rate and time of application. Educators and consultants provided prescriptions for weed control based on this knowledge.

After about five decades of chemical weed control, invasive plants infest an estimated 40.5 million ha in the United States (NISC 2001) and continue to spread at nearly 14% per year (Westbrooks 1998). The problem is so extensive that a presidential order directed federal agencies to manage invasive species (Clinton 1999). Similar increases are occurring on private land. We believe that herbicidal weed control prescriptions are too expensive and site specific to provide long-term effectiveness. Management that lowers the abundance of undesirable and desirable forbs may cause losses in ecological function and ultimately accelerate reinvasion (Pokorny 2002). We promote treating the cause of invasion and considering plant community dynamics, in addition to treating the symptom of weeds (Sheley et al. 1996). Using herbicides to manage invasive plants is, in some cases, analogous to using a prescription medicine to treat a foot problem caused by a biomechanical abnormality: a podiatrist can alleviate the pain by prescribing cortisone or anti-inflammatory medication (or both) or treat the cause of the pain with a shoe insert that corrects the biomechanical abnormality, therefore eliminating the pain for years. Similarly, when managing invasive plants, we can use temporary cures or try to understand and then alter the ecological mechanisms and processes that favor success.

Although herbicides were being prescribed for weed control during the 1970s, rangeland and cropland weed ecologists began to investigate the biology and ecology of plant populations in an attempt to enhance effectiveness of control techniques. Knowledge of plant traits (Baker 1974), life history (Sagar and Mortimer 1976), plant population biology (Cavers and Harper 1967), evolution, and succession (Clements 1916) contribute to our ability to control invasive plants. Invasive plant and restoration ecology are relatively new sciences that hold great promise for range and wild land weed management. These two sciences will tend to move weed management from prescriptive treatments toward the development of concepts and principles on which site-specific invasive plant management must be based. These concepts and principles will be universal rather than site specific, and they will be applied by managers educated in applied ecology. Site-specific testing and evaluation will provide landowners information for adaptive management.

Enduring invasive plant management must be based on ecological principles. Although some principles are known, new principles will focus on managing plant community dynamics to move toward a desired plant community. In many respects, managing invasive plants is analogous to building a bridge. Bridge builders could take their tools, i.e., boards, bolts, and saws, to the river and construct a bridge piece by piece using only their previous knowledge and understanding of the tools. In most cases, bridges built in such a manner would not endure. On the other hand, a bridge builder could base his or her construction on a carefully engineered plan based on concepts and principles of physics and civil engineering. In this case, the bridge would hold a predictable amount of weight and withstand expected stresses for a predictable period of time. The same is true for invasive plant management. Often, we apply our tools, such as herbicides, natural enemies, and grazing animals, without having carefully designed a strategy to influence the cause of the problem, and therefore, we treat the symptom of

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

Causes of succession	Processes	Modifying factors
Site availability	Disturbance	Size, severity, time intervals, patchiness, predisturbance history
Species availability	Dispersal	Dispersal mechanisms and landscape features
	Propagules	Land use, disturbance interval, species life history
Species performance	Resources	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, previous occupants, herbivory, natural enemies
	Interference	Competition, herbivory, allelopathy, resource availability, predators, other level interactions

weeds rather than solve the problem. In the future, invasive plant managers must understand and apply principles and concepts of ecology, the basic science behind weed management, to design and implement sustainable programs with predicable outcomes.

The purpose of this article is to discuss and provide examples of ecological concepts and principles that could be useful in engineering a sustainable invasive plant management program. We will discuss management objectives, the need for predictability, and successional theories that might lend themselves to successful invasive plant management.

Management Objectives

Historically, pest management evolved in cropping systems and focused on control. Many land managers focus weed management on controlling weeds with limited regard for the existing or desired plant community. The effectiveness of various weed management strategies depends on how land is used. Invasive plants must be considered in establishing land-use plans. Although removing weeds may be part of a restoration program, by itself an inadequate objective, especially for large-scale infestations. A generalized objective for ecologically based weed management is to develop and maintain a healthy plant community that is largely invasion resistant while meeting other land-use objectives such as forage production, wildlife habitat development, or recreation land maintenance (Sheley et al. 1996). A healthy, weed-resistant plant community consists of a diverse group of species that occupy most of the spatial and temporal niches (Tilman 1986). Diverse communities capture a large proportion of the resources in the system, which preempts resource use by weeds (Carpinelli 2000; Sheley and Larson 1996). Plant communities with representatives from various functional groups also optimize ecosystem functions and processes that regulate plant community stability. Ecologically based weed management programs must focus on establishing and maintaining desired, functional plant communities. Development and adoption of management strategies promoting desirable communities offer the highest likelihood of sustainable weed management.

Need for Predictive Capability

The ecological and economic success of range and wild land weed management programs will be evaluated based on how closely the postmanagement species or functional group composition matches the stated objectives. Ecologically based weed management requires the ability to predict community responses to natural and imposed conditions (Kedzie-Webb 1999). Without predictive capabilities, the decision to impose a particular strategy is either based on previous experience or is arbitrary. Furthermore, risk assessment of any practice, including biological control, must be based on models that provide an understanding of the plant community after implementation of the practice. An understanding of the organization, structure, and function of the postmanagement plant community is central to assessing the indirect effects of any weed management strategy because they determine the sustainability of the ecosystem. Predictive capability will require a mechanistic understanding of the ecological principles that direct a plant community's dynamics.

Mechanisms and Processes Directing Plant Community Dynamics

It has long been recognized that plant community composition changes over time (Clements 1916). Most earlier studies focused on describing those changes and relating them to plant strategies and traits to develop the ability to predict succession (Grime 2001; MacArthur 1962). More recently, ecologists have recognized that the ability to predict succession requires an understanding of the mechanisms and processes directing plant community change (Allen 1988; Louda et al. 1990; Luken 1990). Connell and Slatyer (1977) proposed three mechanisms of succession: facilitation, tolerance, and inhibition. These mechanisms include a wide variety of processes that influence succession. However, these complex models do not provide a comprehensive theoretical framework easily used for management.

Pickett et al. (1987) developed an alternative, hierarchical model of succession that includes the general causes of succession, controlling processes, and their modifying factors (Table 1). Three general causes of succession have been proposed: disturbance, colonization, and species performance (Luken 1990, Figure 1). Within the limits of our knowledge about the conditions, mechanisms, and processes controlling plant community dynamics, these three causes can be modified to predict successional transitions. We can design the disturbance regime and attempt to control colonization and species performance through management.

Successional management must be viewed as an ongoing process moving from one successional cause to the next or repeating a single cause through time. This model is driven by both naturally occurring and human-induced processes and, thus, is robust enough to incorporate almost any management decision.

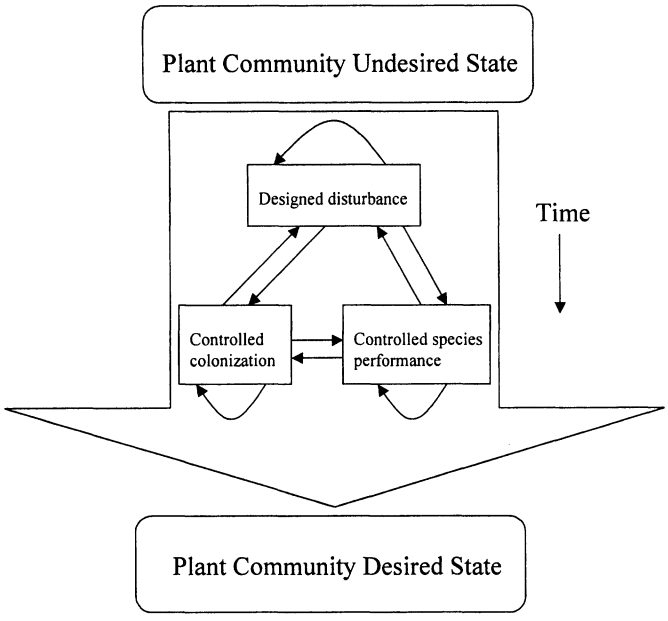

FIGURE 1. Three general causes of succession (modified from Luken 1990).

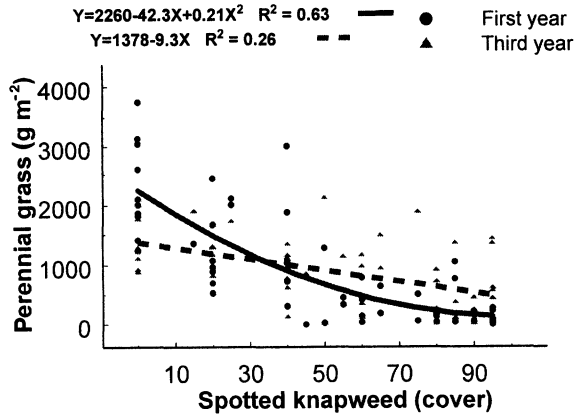

FIGURE 2. Biomass optimization model to predict indigenous perennial grass density from spotted knapweed (*Centaurea maculosa* Lam.) density after picloram treatment to optimize disturbance frequency (from Kedzie-Webb et al. 2001).

Designed Disturbance

The process of disturbance plays a central role in initiating and altering successional pathways, although a unified disturbance theory has not been developed (Pickett and White 1985). Natural disturbances, such as landslides, fire, and severe climatic conditions, initiate, retard, or accelerate succession. The size, severity, frequency, patchiness of disturbance, and predisturbance history determine the community organization and successional dynamics.

Two of the most fundamental parameters of any disturbance are size and severity. Size and severity of the disruption dictate the amount of physical space available for colonization and greatly influence timing and patterns of resource availability (Bazzaz 1983, 1984). Light and soil moisture profiles, soil nutrient content, and factors that modify the use of these resources such as air and soil temperature are affected by the extent of vegetation damage or removal (Collins et al. 1985; Runkle 1985). Large disturbances often create environments with extreme fluctuations in resource levels and in temperature and wind that regulate resource use (McConnaughay and Bazzaz 1987). Thus, the size and severity of a disturbance can have profound influences on plant community dynamics.

Designed disturbance includes activities that create or eliminate site availability. Invasive plant management strategies have included designed disturbance such as cultivation, burning, and herbicides. However, in successional management, designed disturbance is used to alter successional trajectories and to minimize the need for continuous high-energy inputs.

Predicting the influence of herbicide disturbance on plant community dynamics is central to developing successful control strategies, where a desired understory exists. In this simple example, management objectives are aimed at grass production, but the theory and procedures could be useful for any management goal. Kedzi-Webb et al. (2001) proposed using biomass optimization models to predict plant dynamics after using picloram in order to optimize disturbance frequency in a bluebunch wheatgrass (*Agropyron spicatum* Pursh)/Idaho fescue (*Festuca idahoensis* Elmer) habitat dominated by spotted knapweed (*Centaurea maculosa* Lam.). They used easily collected pretreatment data (i.e., spotted knapweed cover) to predict posttreatment desirable biomass (Figure 2). They compared the differences between predicted pretreatment and posttreatment biomass and suggested that cumulative predictive biomass gains (after treatment) could be quantified by developing a biomass optimization model for each year of herbicide control. Once the change in biomass is predicted and the predictions verified, economic analysis based on the value of the cumulative biomass change could be conducted. This example could identify a principle for managing herbicide disturbance frequencies that optimize benefits, such as an increase in desirable plant biomass, based on pretreatment plant community measurements and the predicted posttreatment response.

Controlled Colonization

Colonization, the availability and establishment of various species, is another important cause of succession. Processes directing colonization are dispersal, propagation, and species-specific establishment characteristics. These processes can be modified by factors like propagule dispersal mechanisms, landscape features, species' life histories, and vegetative reproduction. Understanding the movement and fate of seeds is a critical aspect in preventing new introductions and restoring disturbed ecosystems.

Chambers and MacMahon (1994) proposed a conceptual model that outlines the pathways that seeds follow after leaving the parent plant, the dormancy status in which they reside, and some of the biotic and abiotic factors that influence seeds and interact with each species' life history (Figure 3). The movement of germinable seeds from the plant to a surface is Phase I dispersal. Many seeds simply fall beneath the parent plant. Many invasive plants have specialized appendages for wind dispersal, such as sumaras or plumes, or ballistic mechanisms for seed propulsion. Biotic factors that can be modified to influence Phase I dispersal include animal dissemination (Howe 1986; Stiles 1992), frugivory (Fleming 1991), adhesion (Sorenson 1986), and dispersal as

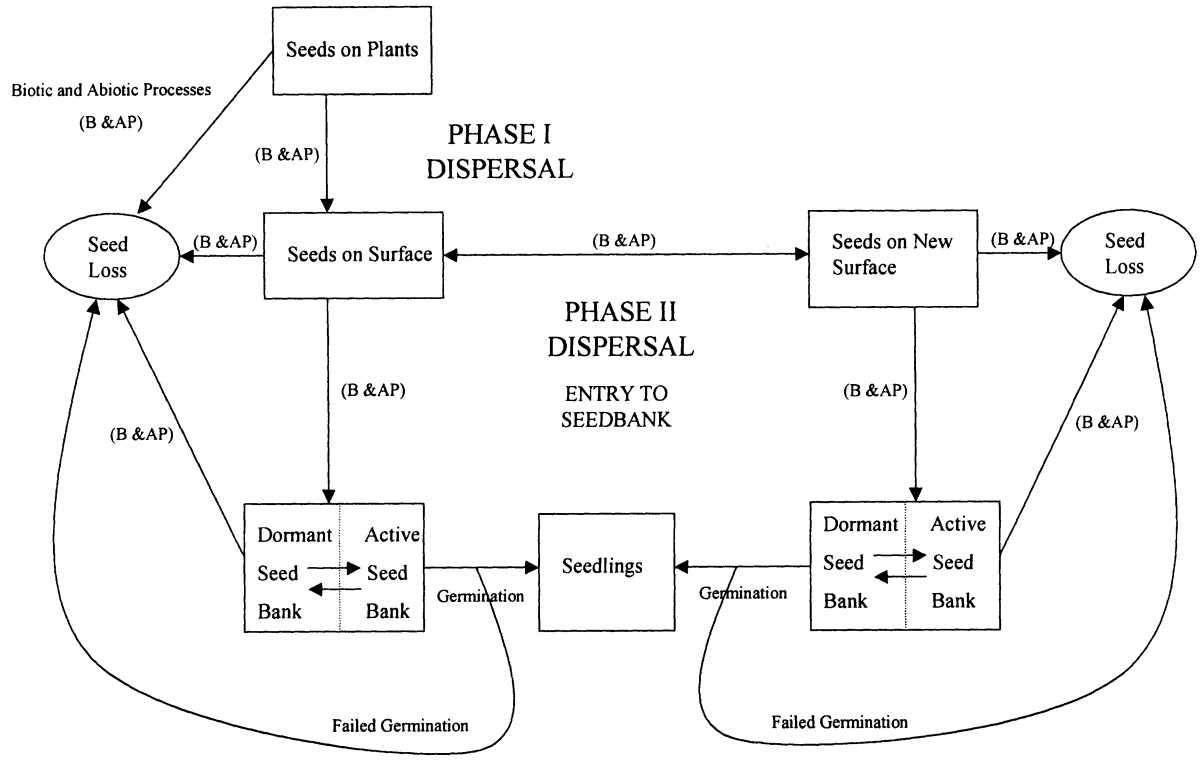

FIGURE 3. Pathways seeds follow, status in which they reside, and biotic and abiotic factors influencing seeds and interacting with species' life history (modified from Chambers and MacMahon 1994).

a result of food hoarding (Vander Wall 1992). Landscape features can aid or hinder seed dispersal. For example, a river may prevent seeds from moving from one side to the other, or it may disperse seeds downstream.

Phase II dispersal includes both horizontal and vertical movement of seeds and vegetative reproductive parts. Physiologically active, nondormant seeds may germinate immediately, remain in the seed bank until proper environmental conditions occur, or acquire enforced dormancy (Baskin and Baskin 1989). Abiotic factors influencing seed dispersal within the soil include the relationship between the seeds' dimensions and the soil surface characteristics or other landscape features. Vertical movement is associated with the surface or size and the quantity of litter, the soil pore size, and the physical characteristics of the seeds (Chambers et al. 1991). The type and intensity of the abiotic forces acting on seeds are largely determined by landscape features, vegetation, wind, precipitation, and temperature within the ecosystem. Consequently, vegetation interspaces serve as avenues of seed transport, occurring primarily in the soil cracks and crevices or under litter-covered canopies (Kaufman et al. 1991). For example, seeds of cheatgrass (*Bromus secalinus* L.) are more likely to remain on littered rather than on bare microsites (Kelrick 1991). Seeds on bare-ground may be subjected to wind and water movement, as well as to herbivory.

Animals play a major role in Phase II dispersal (Vander Wall 1992). Animal digging, burrowing, and tunneling can bury or exhume seeds (Garwood 1989). The primary factors that influence Phase II dispersal include animal foraging behavior, seed attributes and life histories, and seed location in the soil. Assemblies of dispersers differ among locations; therefore, the likelihood of seed harvest and the fates of the harvested seeds depend on the local animal composition (Bullock 1989).

Factors that affect seed mortality include burial depth, abrasion, burning, water logging, and others. It is becoming increasingly clear that seed predation can determine the plant population dynamics, the plant community composition, and the process of succession (Davidson 1993; Hulse et al. 1993). Seed burial by animals may make safe sites for particular plant species. In addition, animals may cache seeds, decreasing the probability of dispersal. It is also possible that seeds are deposited in nutrient-rich environments (Beattie 1985).

Understanding Phase I colonization can lead to the development of spread vector analysis that provides information central to effective prevention programs. Spread vector analysis attempts to correlate known weed infestations with various geographic information systems data. Colonization information can then be used to predict future weed distributions for invasion risk assessment. Successful correlation modeling requires predictor variables with strong relationships to the response. For the prediction of invasive plant distributions, predictor variables should be based on the ecology of the weeds. Research has found that proximity of conspecific (same species) invasive plants is closely related to their distribution (Roberts 2001). The influence of spatial relationships between individuals within a species indicates that plant proximity can be used as a variable in correlation modeling and may function as an indicator of dispersal mechanisms driving patterns of invasive plant spread (Roberts 2001). In addition, resource gradients, geographical information about invasion corridors associated with spread agents (e.g., wildlife trails, rivers, roads), and habitat type

can be used in models to identify spread vectors and to make risk assessments.

Controlled Species Performance

Species performance, i.e., the relative growth and reproduction of species, plays a critical role in determining plant community dynamics. Processes associated with the relative performance of species within the plant community include resource availability, ecophysiological processes, life history, stress, and interference. Factors that modify these processes are site, climate, microbes, litter retention, germination requirements, growth rates, genetic differentiation, reproductive allocation, herbivory, competition, allelopathy, and natural enemies and predators.

Ecologically based weed management attempts to understand the conditions, mechanisms, and processes and their modifying factors well enough to predict transitions. In any system, many processes and interactions may affect plant community composition. However, weed scientists and managers must identify those mechanisms and processes that dictate the direction of succession. The objective is to understand and manipulate the factors that modify processes to favor desired species. Ultimately, the goal is to direct existing plant communities containing undesirable species toward more desirable plant communities (Luken 1990; Rosenberg and Freedman 1984). This is the ecological basis for integrated weed management.

Investigation of processes and mechanisms directing community dynamics is critical in developing ecologically based weed management strategies. R* theory is one of several theories that has been proposed as a mechanism for plant community dynamics (successional change), but the theory needs more testing and has not yet been developed into a principle for management (Tilman 1986). This theory states that the outcome of succession is based on the ability of a plant to sequester a limiting resource. R* is the resource level a species requires to persist in an environment. As succession progresses and available resources become increasingly limited, those species with the lowest R* (i.e., resource requirement) dominate. Knowledge of R*s for species within a plant community could lead to effective weed management with mechanistic predictive capabilities.

R* may provide a mechanistic understanding of plant community dynamics needed for managing land threatened or dominated by nonindigenous plants (Herron et al. 2001). If the theory can be developed into a principle, R* may be used to (1) predict the outcome of succession, (2) provide a mechanism for determining the competitive species required to restore land dominated by invasive weeds, (3) vary resource availability to manage plant community dynamics based on the species' R*, and (4) predict areas susceptible to invasion by nonindigenous species based on patterns and magnitude of resource availability.

In future, invasive plant management must be based on ecological principles and concepts about successional dynamics. These principles must be based on the mechanisms and processes directing succession and must provide guidelines for applied ecologists. Successional management is just one proposed framework based on the general causes of succession, the processes directing it, and factors that can modify those processes. We have provided three examples of how successional management can lead to improved management strategies with predictable outcomes. The need for ecologically based principles and concepts is substantial and largely unmet. Our ability to manage invasive plants effectively depends on our ability to develop these principles and to educate land managers on their use.

Literature Cited

Allen, M. F. 1988. Facilitation of succession by the nonmycotrophic colonizer *Salsola kali* (Chenopodiaceae) on harsh sites effects of mycorrhizal fungi. Am. J. Bot. 75:257–266.

Baker, D. N. 1974. The evolution of weeds. Annu. Rev. Ecol. Syst. 5:1–24.

Baskin, J. M. and C. C. Baskin. 1989. Physiology of dormancy in relation to seed bank ecology. Pages 53–66 *in* M. A. Leck, V. T. Parker, and R. L. Simpson, eds. Ecology of Soil Seed Banks. New York: Academic Press.

Bazzaz, F. A. 1983. Characteristics of populations in relation to disturbance in natural and man modified ecosystems. Pages 259–275 *in* H. A. Mooney and M. Godron, eds. Disturbance and Ecosystems. Components of Response. New York: Springer-Verlag.

Bazzaz, F. A. 1984. Dynamics of wet tropical forests and their species strategies. Pages 233–243 *in* E. Medina, H. A. Mooney, and C. Vazquez-Yanes, eds. Physiological Ecology of Plants in Wet Tropics. Boston, MA: Dr. W. Junk.

Beattie, A. J. 1985. The Evolutionary Ecology of Ant-Plant Mutualisms. London: Cambridge University Press. pp. 77–87.

Bullock, S. H. 1989. Life history and seed dispersal of the short-lived chaparral shrub *Dendromecon rigida* (Papaveraceae). Am. J. Bot. 76:1506–1517.

Carpinelli, M. F. 2000. Designing Weed-Resistant Plant Communities by Maximizing Community Structure and Resource Capture. Ph.D. dissertation. Montana State University, Bozeman, MT. 131 p.

Cavers, P. B. and J. L. Harper. 1967. Studies of plant populations, I. The fate of seed and transplants introduced into various habitats. J. Ecol. 55:59–71.

Chambers, J. C. and J. A. MacMahon. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annu. Rev. Ecol. Syst. 25:263–292.

Chambers, J. C., J. A. MacMahon, and J. H. Haefner. 1991. Seed entrapment in alpine ecosystems: effects of soil particle size and diaspore morphology. Ecology 72:1668–1677.

Clements, F. E. 1916. Plant Succession: An Analysis of the Development of Vegetation. Washington, D.C.: Carnegie Institute Publication 242. pp. 3–7, 75–78.

Clinton, W. J. 1999. Invasive Species Executive Order 13112: Invasive Species. Washington, D.C.: White House, Office of the Press Secretary.

Collins, B. S., K. P. Dunne, and S.T.A. Pickett. 1985. Responses of forest herbs to canopy gaps. Pages 218–234 *in* S.T.A. Pickett and P. S. White, eds. The Ecology of Natural Disturbance and Patch Dynamics. Orlando, FL: Academic Press.

Connell, S. L. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 11:1119–1144.

Davidson, W. D. 1993. The effects of herbivory and granivory on terrestrial plant succession. Oikos 68:25–35.

Fleming, T. H. 1991. Fruiting plant-frugivore mutualisms: The evolutionary theater and the ecological play. Pages 119–144 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernanades, and W. W. Benson, eds. Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions. New York: J. Wiley.

Garwood, N. C. 1989. Tropical soil seed banks: A review. Pages 149–210 *in* M. A. Leck, V. T. Parker, and R. L. Simpson, eds. Ecology of Soil Seed Banks. New York: Academic Press.

Grime, J. P. 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. Chichester, Great Britain: J. Wiley. pp. 238–256, 303–348.

Herron, G.J.R., L. Sheley, B. D. Maxwell, and J. S. Jacobs. 2001. Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. Ecol. Restor. 9:326–331.

Howe, H. F. 1986. Seed dispersal by fruit-eating birds and mammals. Pages 123–190 *in* D. R. Murray, ed. Seed Dispersal. New York: Academic Press.

Hulse, E. J., J. H. Brown, and Q. Guo. 1993. Effects of kangaroo rat

exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. Oecologia 95:520–524.
Kaufman, S., D. B. McKey, M. Hossaert-McKey, and C. C. Horowitz. 1991. Adaptations for a two-phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). Am. J. Bot. 78:970–977.
Kedzie-Webb, S. A. 1999. Relationship Between Spotted Knapweed and Indigenous Plant Assemblages and Prediction of Plant Community Response to Picloram. M.S. thesis. Montana State University, Bozeman, MT. 83 p.
Kedzie-Webb, S. A., R. L. Sheley, J. J. Borkowski, and J. S. Jacobs. 2001. Relationships between *Centaurea maculosa* and indigenous plant assemblages. West. N. Am. Nat. 61:43–49.
Kelrick, M. I. 1991. Factors Affecting Seeds in a Sagebrush-Steppe Ecosystem and Implications for the Dispersion of an Annual Plant Species, Cheatgrass (*Bromus tectorum*). Ph.D. thesis. Utah State University, Logan, UT. 206 p.
Louda, S. M., K. H. Keeler, and R. D. Holt. 1990. Herbivore influences on plant performance and competitive interactions. Pages 413–444 *in* J. B. Grace and D. Tilman, eds. Perspectives on Plant Competition. San Diego: Academic Press.
Luken, J. O. 1990. Directing Ecological Succession. London: Chapman and Hill. pp. 1–18.
MacArthur, R. H. 1962. Generalized theorems of natural selection. Proc. Natl. Acad. Sci. U.S.A. 48:1893–1897.
McConnaughay, K.D.M. and F. A. Bazzaz. 1987. The relationship between gap size and performance of several colonizing annuals. Ecology 68: 411–416.
[NISC] National Invasive Species Council. 2001. Meeting the Invasive Species Challenge: National Invasive Species Management Plan. 80 p.
Pickett, S.T.A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. Bot. Rev. 53:335–371.
Pickett, S.T.A. and P. S. White. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Orlando, FL: Academic Press. pp. 371–384.
Pokorny, M. L. 2002. Plant Functional Group Diversity as a Mechanism for Invasion Resistance. M.S. thesis. Montana State University, Bozeman, MT. 130 p.
Pokorny, R. 1941. Some chlorophenoxyacetic acids. J. Am. Chem. Soc. 63: 1768.
Radosevich, S. R., J. Holt, and C. Ghersa. 1997. Weed Ecology: Implications for Management. New York: J. Wiley. pp. 347–353.
Roberts, E. 2001. Sampling and Modeling Plant Infestations: Techniques for Identifying Invasive Plant Distribution in Rangeland Environments. M.S. thesis. Montana State University, Bozeman, MT.
Rosenberg, D. B. and S. M. Freedman. 1984. Application of a model of ecological succession to conservation and land-use management. Environ. Conserv. 11:323–329.
Runkle, J. R. 1985. Disturbance regimes in temperate forests. Pages 17–34 *in* S.T.A. Pickett and P. S. White, eds. The Ecology of Natural Disturbance and Patch Dynamics. Orlando, FL: Academic Press.
Sagar, G. R. and A. M. Mortimer. 1976. An approach to the study of the population dynamics of plants with special reference to weeds. Ann. Appl. Biol. 1:1–47.
Sheley, R. L. and L. L. Larson. 1996. Emergence date effects on the resource partitioning among diffuse knapweed seedlings. J. Range Manage. 49: 241–244.
Sheley, R. L., T. J. Svejcar, B. D. Maxwell, and J. S. Jacobs. 1996. Successional rangeland weed management. Rangelands 18:155–159.
Sorenson, A. E. 1986. Seed dispersal by adhesion. Annu. Rev. Ecol. Syst. 17:443–463.
Stiles, E. W. 1992. Fruits, seeds and dispersal agents. Pages 87–104 *in* M. Fenner, ed. Seeds. The Ecology of Regeneration in Plant Communities. Wallingford, Great Britain: CAB International.
Tilman, D. 1986. Resources, competition and the dynamics of plant communities. Pages 51–75 *in* Michael Crawley, ed. Plant Ecology. Boston: Blackwell Scientific.
Vander Wall, S. B. 1992. The role of animals in dispersing a "wind-dispersed" pine. Ecology 73:614–621.
Westbrooks, R. 1998. Invasive Plants, Changing the Landscape of America: Fact Book. Washington, D.C.: Federal Interagency Committee for the Management of Noxious and Exotic Weeds (FICMNEW). 109 p.

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