A Theoretical Framework for Developing Successional Weed Management Strategies on Rangeland[1]

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Abstract. Sustainable rangeland management will require successional strategies to deal with the expanding weed problem. These strategies must be consistent with the view that plant communities are dynamic and technology is used to enhance the natural processes and mechanisms that direct vegetation change. The goal is to shift the dynamics toward a desired plant community. A unified conceptual model is necessary to direct the development and application of successional weed management systems. We propose using a resource management model as a conceptual basis for successional weed management. This model is based on the primary causes of succession: site availability, differential species availability, and differential species performance. This model provides the mechanistic framework necessary for developing successional weed management systems and it is meant to enhance communication among rangeland weed managers and scientists.

Additional index words: Community dynamics, disturbance, ecological models.

INTRODUCTION

World agriculture is striving toward a future that provides nourishing food, protects those who work the land, helps stabilize the earth's climate, and safeguards our soil and water. Many rangeland managers and owners have focused weed management efforts on simply controlling weeds, with limited regard to the existing or resulting plant community. Because of environmental, ecological, and economical concerns, the appropriateness and effectiveness of rangeland weed management practices are being questioned. It has become clear that weed management decisions must consider these concerns. The development of future weed management practices must be based on our understanding of the biology and ecology of rangeland ecosystems (2, 8, 23, 24, 26). We believe weed management education should focus on providing land managers the principles and concepts on which to base their decisions, rather than just providing prescriptions for weed control.

Land use objectives must be developed before rangeland weed management plans can be designed. This implies that strictly killing weeds is an inadequate objective, especially for large-scale infestations. However, a generalized objective could be to develop a healthy plant community that is relatively weed-resistant, while meeting other land-use objectives, such as forage production, wildlife habitat development, or recreational land maintenance.

A healthy, weed-resistant plant community consists of a diverse group of species which occupy most of the niches. Diverse communities capture a large proportion of the resources in the system which preempts their use by weeds (34, 41, 42; Figure 1). Weed-resistant plant communities effectively use resources over time and space. These communities may include an early emerging species, such as the shallow-rooted Sandberg's bluegrass (*Poa sandbergii* Vasey), which uses the resources that are available in the upper soil profile early in the growing season and during periods of light precipitation (10). As the season progresses, species which initiate growth later, but continue growth later into the season are needed to use available soil resources from moderate soil depths. Finally, the diverse plant community may include a deep taprooted, very late maturing species, such as alfalfa (*Medicago sativa* L.) or big sagebrush (*Artemisia tridentata* Nutt.). These species are capable of extracting resources from deep in the soil profile and throughout much of the growing season.

Although little is known about the role of many species within the plant community, it has been proposed that maximum diversity provides for stability and resource capture over a wide range of unpredictable conditions (5). This is not to imply that diversity guarantees weed-resistance, or that some virtual monocultures would not resist weed invasions. Once the desired plant community has

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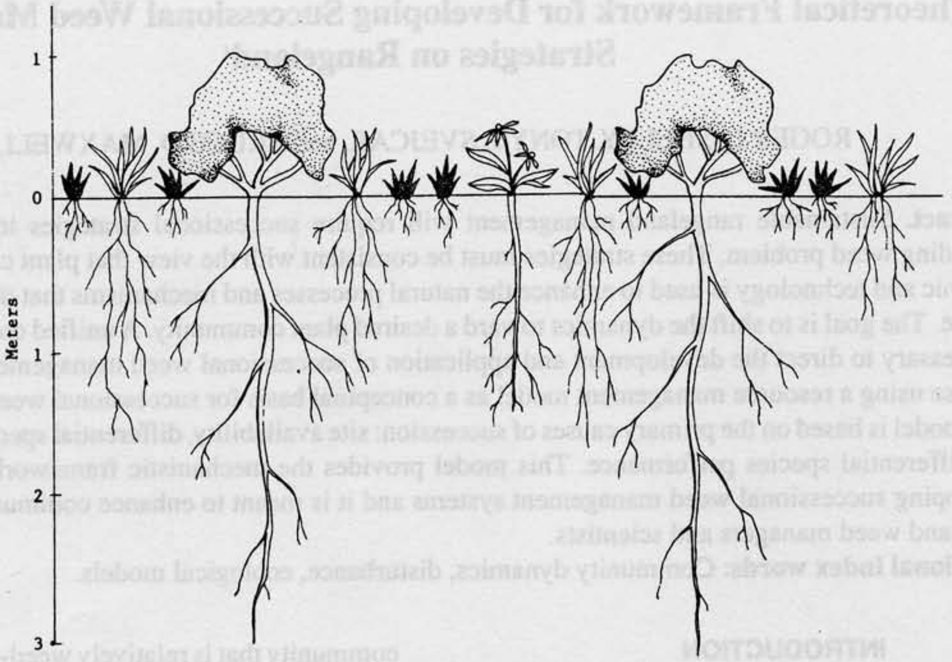

Figure 1. A healthy, relatively weed-resistant plant community composed of early-season, shallow rooted species (black), mid-season species with moderately deep roots (white), and late-season, deep rooted species (grey) (drawn by Susan Kedzie-Webb).

been determined, an ecologically-based weed management system may be developed.

Ecologically-based weed management requires that scientists and managers develop strategies that are based on our current understanding of succession (24). Successional weed management recognizes that plant communities are dynamic and uses technology to enhance natural processes and mechanisms that regulate vegetation change. Ultimately, the goal is to direct weed infested communities on a trajectory toward more desirable plant communities (24, 35, 39, 40, 46).

Development of sustainable rangeland weed management strategies is dependent on our understanding of the ecological principles that determine plant community structure and successional dynamics. The purpose of this publication is to present a conceptual, ecologically-based framework to aid in developing and implementing sustainable rangeland weed management.

CURRENT SUCCESSIONAL THEORY

Clementian ecology has dominated successional theory for most of the 20th century (6). Current successional theory may have begun with the work of MacArthur (25) who proposed a model for species change based upon their individual strategies. He suggested that r-strategists are rapid growing, short-lived, high seed producing species limited to disturbed sites (early secondary succession), whereas K-strategists were generally perennial, highly competitive, and low seed producing species. MacArthur (25) proposed that succession progresses from r- to K-strategists. Later, Grime (14) expanded this model to include an intermediate step. He proposed ruderal species (r-strategists) gave way to competitive species, and finally to stress tolerant (K-strategists) species.

One successional model was developed by Nobel and Slatyer (28) and focused on individual species. They predicted succession based on a list of "vital attributes." Pickett et al. (31) developed this concept into a hierarchial model of succession including the general causes, controlling processes, and their modifying factors (Table 1). The three general causes of succession are site availability, differential species availability, and differential species performance.

Successional weed management must have an ecologically sound conceptual basis from which strategies can be developed and tested. These conceptual models are used for directing data collection, assembling and processing

Table 1. Causes of succession, contributing processes, and modifying factors.[a]

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, prior occupants, herbivory, natural enemies
	Interference	Competition, herbivory, allelopathy, resource availability, predators, other level interactions

[a]Modified from Pickett et al. (31).

Table 2. Components of successional weed management corresponding to the general causes of succession.[a]

Components of successional management	General causes of succession
Designed disturbance	Site availability
Controlled colonization	Differential species availability
Controlled species performance	Differential species performance

[a]Modified from Picket et al. (31).

information, and predicting the outcome of management decisions (52). A successional range management model, developed around the turn of the century (6, 36, 37), assumes succession is unidirectional and has a single persistent climax in the absence of grazing. Grazing pressure is thought to reverse the successional tendency and can be adjusted to create an equilibrium in vegetation (12). Weed invasions may trigger long-term changes in soil conditions by accelerating erosion or changing nutrient availability which results in complex multi-directional successional patterns (19, 22, 52). Furthermore, weeds may invade ungrazed rangelands (45, 50). Thus, a shift in paradigm is necessary for rangeland weed management.

Adoption of a model based upon the current ecological theory of succession is central to the development of successional rangeland weed management strategies. We propose using the resource management model developed by Rosenberg and Freedman (35) and Pickett et al. (31) to provide a theoretical framework for developing successional rangeland weed management strategies. Luken (24) has proposed this approach to natural resource management.

A SUCCESSIONAL RANGELAND WEED MANAGEMENT MODEL

Managing succession requires knowledge of three components corresponding to the three general causes of succession: disturbance, colonization, and species performance (24, 31, 35; Table 2). Within the limits of our knowledge about the conditions, mechanisms, and processes controlling plant community dynamics, these three components can be modified to allow predictable 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 component to the next or repeating a single component through time (Figure 2). This model is driven by both naturally occurring and human-induced processes, and thus is robust enough to allow incorporation of virtually any management decision.

Designed disturbance. Disturbance plays a central role in initiating and altering successional pathways, although a unified disturbance theory has not been developed (32). Natural disturbances, such as landslides, fire, and severe climatic conditions initiate, retard, or accelerate succession, or alter successional pathways. Theories are emerging that suggest large-scale disturbance and patch dynamics contribute to the invasion of intact (pristine) plant communities by rangeland weeds. For example, Tyser and Key (50) found that spotted knapweed (*Centaurea maculosa* Lam.) was capable of expanding into grassland communities in Glacier National Park. Small patch disturbances created by wildlife and roadside activity allowed individual spotted knapweed plants to establish. We believe the aggressive characteristics of many rangeland weeds allow maintenance of small populations. Subsequent large-scale disturbances, such as fire or drought, cause safe site openings, and reduces the competitive ability of the perennial species which favors large-scale invasion by weeds. Succession may be permanently altered (45). In the case of spotted knapweed, large-scale disturbance may not be necessary for invasions. Patch disturbances, such as roadsides, may be sufficient to initiate invasions.

Designed disturbances include activities that are initi-

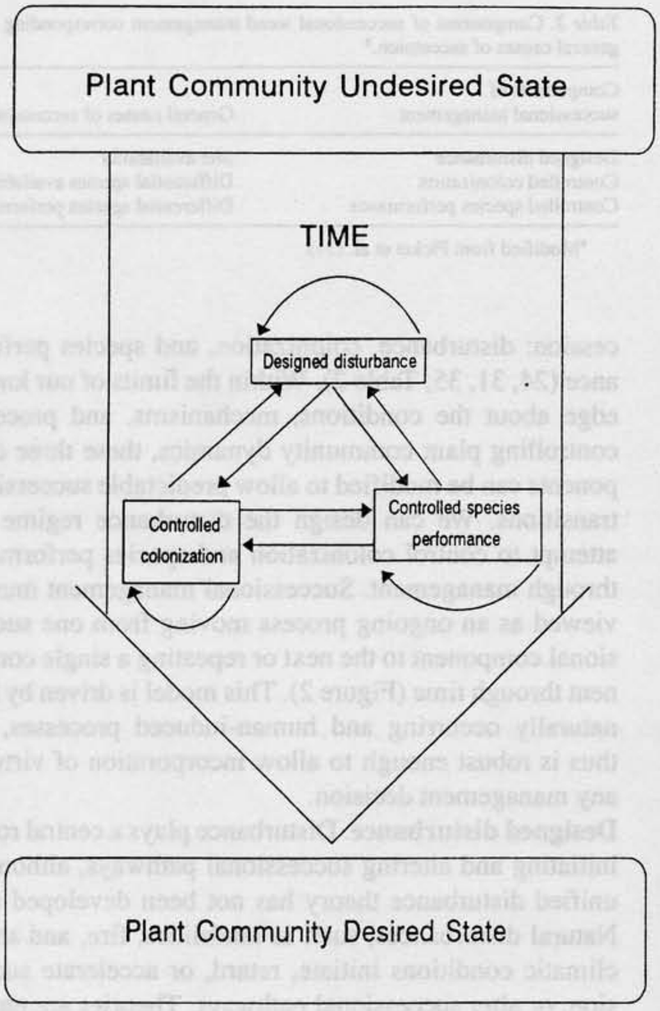

Figure 2. Components of a successional weed management model. Straight lines indicate sequential steps; curved lines indicate repeated steps. Modified from Rosenberg and Freedman (35).

ated to create or eliminate site availability and are aimed at initiating and controlling succession (Figure 3). Weed management strategies have included designed disturbance, such as cultivation, burning, and herbicide applications for decades. However, in successional management, designed disturbance is used to alter successional trajectories and to minimize the need for continuous high energy inputs. The utility of any specific designed disturbance in successional weed management will depend on the range site, plant community type, invading weed species, site history, season, climate (macro and micro), and the management goals.

In the case of spotted knapweed invasion into Glacier National Park, successional planning will require identification of disturbance thresholds and modification of the disturbance. In this example, if roadside disturbance provides a staging area for weed invasion, emphasis could be placed on roadside revegetation with competitive native perennial species. Establishment of a competitive native community should reduce site availability for the weed species.

Controlled colonization. Controlled colonization is the intentional alteration of availability and establishment of various plant species. Colonization may be influenced in a positive or negative manner depending on the species and successional goals (Figure 3). Controlled colonization efforts are directed toward influencing seed banks, propagule pools, and regulation of safe sites for germination and establishment of desirable species. Weed seed banks can be depleted through attrition if seed production is prevented or significantly reduced. Olson et al. (29) found that the number of spotted knapweed seeds in the soil was reduced after three years of intensive sheep grazing, resulting in decreased weed density.

In another example, two seed-feeding flies [*Urophora affinis* Frfld. and *U. quadrifasciata* (Meig.)] have been shown to reduce spotted knapweed seed output by up to 80% (15). Weed seed dispersal can also be limited by not driving vehicles through weed infested areas when seeds are present, not grazing livestock in weed infested areas during flowering and seeding or holding animals for 14 d before moving to uninfested areas, and using hay free of weed seeds (43).

It is possible that introducing seeds of desirable species in small amounts each fall or winter to mimic natural seeding may allow colonization by increasing the probability that seeds are available during favorable environmental conditions. Since weed seeds can be dispersed by livestock (51) and hay (53), using livestock to introduce seeds of desirable species in favorable patches may be feasible, and offer a low input method for controlling colonization. Conceivably, managers could add seeds of desirable species into hay during fall and winter feeding periods to be spread throughout a pasture. In addition, hoof action by livestock may create safe sites, enhancing seedling establishment.

Controlled colonization may include introduction of certain less desirable, but ephemeral species to facilitate establishment of desirable species by creating safe sites for germination and seedling survival. Introduction of early successional species may cause changes in soil properties

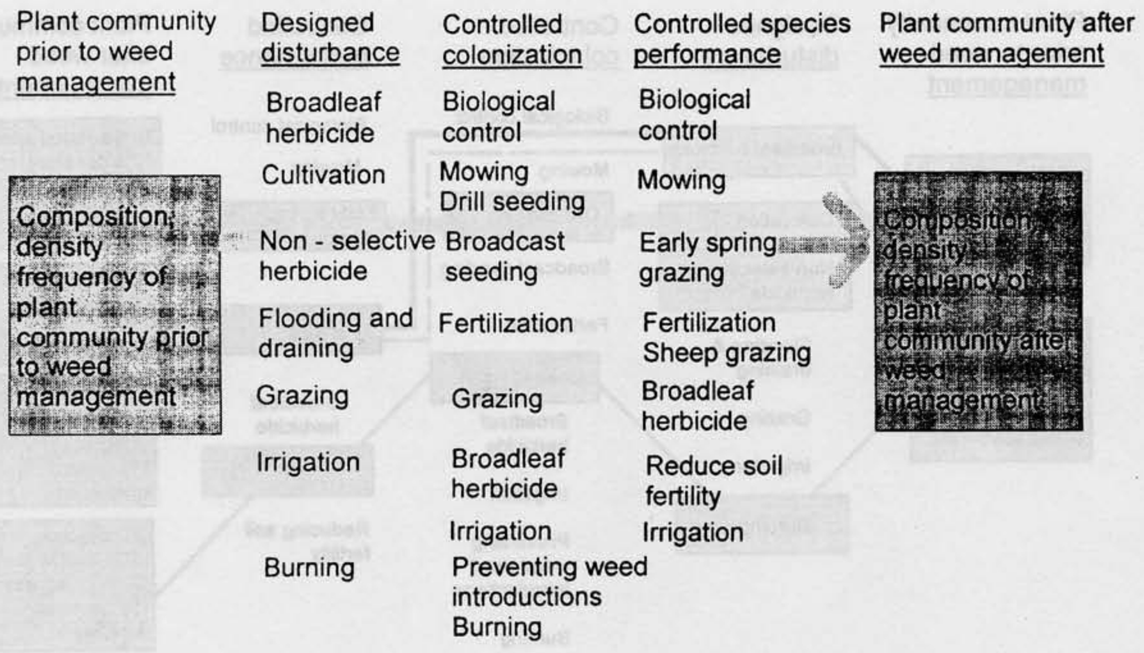

Figure 3. Examples of treatments used to design disturbance, control colonization, and control species performance in successional weed management.

that would facilitate later successional or more desirable species (1).

A specific example of controlled colonization to direct succession is presented by De Pietri (11). The alien species mosqueta rose (*Rosa rubiginosa* L.) can speed the recovery of degraded native forests in Argentina by serving as a nurse plant for native species. The decision not to control mosqueta rose or to place propagules on a site would constitute a controlled colonization decision drawing on the facilitation principle as a mechanism driving succession (7).

Controlled species performance. Controlled species performance involves manipulating the relative growth and reproduction of plant species in an attempt to shift community dynamics in a desirable direction (Figure 3). Biological and chemical weed control, grazing, plant and plant-part removal, altering resource availability, and competitive plantings are techniques to create differential species performance.

A classic example of biological control is provided by Huffaker (16). In many areas of the United States, St. Johnswort (*Hypericum perforatum* L.) has been effectively controlled by two species of beetles [*Chrysolina quadrigemina* (Suffr.) and *C. hyperici* (Foster)]. Many herbicides selectively control weeds (13). In both cases, plant communities can be shifted toward desirable species providing propagules are present and establishment occurs.

Most animals have preferences for certain forages. Selective grazing by herbivores can shift the competitive balance of plant communities (9, 23). For example, in some situations leafy spurge (*Euphorbia esula* L.) can be controlled by sheep or goat grazing (4, 17, 20). Appropriate grazing by animals preferring weeds can shift the plant community toward more desired grasses (18). On the other hand, cattle grazing can selectively reduce grass competitiveness, shifting the community in favor of weeds (44).

Resource availability to plants may be used to influence succession. In some cases, changes in plant communities are related to resource availability and the relative ability of species in the community to extract those resources. To quote Tilman (47), "Because each plant species is constrained to being a superior competitor for particular resource levels, the forces that determine resource levels are critically important in determining vegetation patterns." Thus, another potential successional management strategy would be to influence species performance via soil nutrient manipulation. McLendon and Redente (27) demonstrated that additions of nitrogen inhibited succession from annual to perennial species in a sagebrush steppe site in northwestern Colorado. They concluded that dominance by annuals during the early stages of secondary succession was related

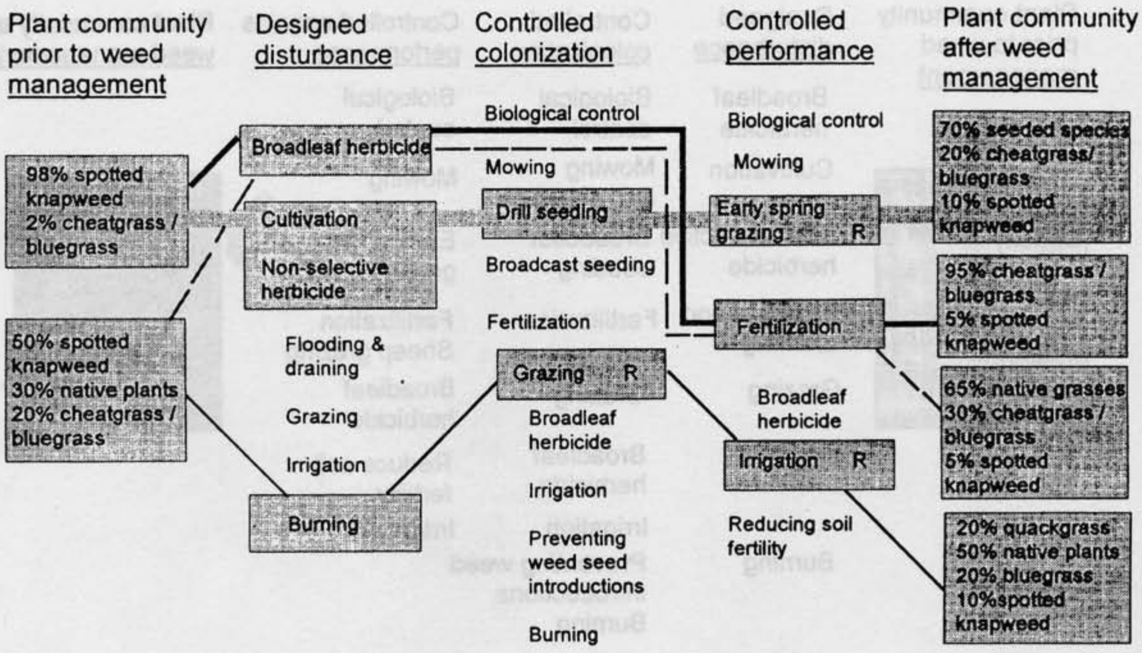

Figure 4. Four spotted knapweed management schematics illustrating successional weed management and its use in weed management planning. R indicates the technique is repeated.

to high nutrient availability. A successional management strategy might be to reduce nutrient availability.

The potential of reducing nutrient availability to foster succession has not been adequately explored. Most of the emphasis in nutrient management has been on increasing availability. However, annual cropping systems have been used to reduce nitrate leaching from agricultural fields. It may be possible to use species with demonstrated abilities to sequester nitrogen, such as rye (*Secale cereale* L.) or mid seral species to reduce resource availability.

Species composition can directly influence nutrient dynamics. Tilman and Wedin (48) studied a range of species with different successional niches, and found that late seral species were very competitive for nitrogen. Late seral species had high below-ground biomass. This creates soils with high carbon/nitrogen ratios, and consequently low nitrogen mineralization. The early seral species were poor competitors for nitrogen, but persist by maintaining rapid growth rates and high seed production. When grown in pairwise competition experiments the late seral species displaced early to mid seral species (49). The ability of a species to lower soil quantities of extractable ammonium and nitrate accounted for the results of the competition trials.

A specific example of successional management via reduced nutrient availability was presented by Oomes (30). He described the restoration of species-rich grasslands from fertilized agricultural grasslands that contained relatively few species. The applied treatment involved mowing twice a year and removing the harvested material. Depending on the site, three to eight years were required to reduce biomass and nitrogen yield to the point where species richness could increase.

Examples. Several schematics using successional weed management are shown for spotted knapweed infested rangeland in Figure 4 (21, 39). In these examples, the plant community prior to weed management is composed of 1) 98% spotted knapweed with a very suppressed understory of cheatgrass (*Bromus tectorum* L.) or Kentucky bluegrass (*Poa pratensis* L.); or 2) 50% spotted knapweed, 30% suppressed native species, and 20% cheatgrass and/or bluegrass. Two successional weed management systems are shown for each situation. In these examples, the resulting plant community is influenced by both the weed management system and the initial plant community. Weed management actions should be selectively integrated to ensure that the three components of the successional management model are addressed in a complementary manner, based on the composition of the existing plant community.

Climatic variation introduces a random element that can influence the short-term outcome.

The successional weed management model presented in this paper allows for integration of currently available tools. Unfortunately, with conceptual models of this type, there are seldom large comprehensive research projects that have tested all possible options for a particular plant community. Development of successional weed management plans will require use of existing research information, management experience, and monitoring of successes and failures to adjust future plans.

DISCUSSION

Rangeland managers are searching for useful models on which to base their decisions (3, 22, 38). A shift in paradigm from that of linear succession to state-and-transition models is occurring in much of the range management profession (52). However, as currently applied, most state-and-transition models are empirical and do not have predictive capability. Our proposed framework would provide a mechanistic explanation of weedy plant responses, and a means of developing testable hypotheses associated with weed management efforts. Observational information which lacks a mechanistic explanation is difficult to extrapolate beyond the observational conditions. On rangeland, this point is particularly important because succession often requires long time frames (decades in some cases). Lack of short-term response may tempt managers and scientists alike to abandon sound management systems.

Adopting the successional weed management model may help bridge the gap between the "art" and "science" of rangeland weed management. To a great extent, weed management is a planning process, whereas weed science is the body of theory on which weed managers base their planning (33). The relationship between these complementary endeavors seems clear, but bridging the gap can be difficult. Often, reductionist research seems to lose sight of management, and land managers seem to lose sight of the relevance of theory. The proposed model may begin to provide the theoretical framework necessary for both weed managers and scientists to develop ecologically-based rangeland weed management. We feel that a unified conceptual framework will improve communication among scientists and managers. The framework may also prove useful in conflict resolution efforts associated with weed management.

Given the rapid spread of rangeland weeds during the past several decades, there seems to be a need for better integration and coordination of individuals and organizations involved in rangeland weed management. The framework we propose is based on currently accepted ecological principles, can accommodate information from a wide variety of sources, and can serve as a communication tool. We suggest that the concepts presented in this paper serve as a starting-point in the larger discussion of how to focus efforts on managing the expanding rangeland weed problem.

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