



Investigating the potential of using R^* theory to manage nonindigenous plant invasions
by Jane Marie Mangold

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of
Philosophy in Land Resources and Environmental Sciences
Montana State University
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Abstract:

R^* theory has been proposed as a mechanism for plant community dynamics, but the theory is poorly tested and has not been developed into a principle for management. This theory states that the outcome of succession is based on the ability of a plant to sequester a limiting resource when it is below the uptake level of neighboring species. R^* is the resource level a species requires to persist in an environment, and the species with the lowest R^* dominates over time. Knowledge of the R^* s for species within a plant community could lead to effective weed management with predictive capabilities.

The overall objective of this research was to explore R^* theory's potential for managing nonindigenous plant invasions on western rangeland. Specific objectives included: 1) determining the most influential limiting resource for a western rangeland plant community, 2) determining R^* s for two native species and a nonindigenous invader, 3) predicting the outcome of succession based upon species' R^* , and 4) altering resource availability to favor desirable species based upon their R^* .

Three studies were conducted beginning in 2000. For Study 1, availability of essential plant resources were altered and the plant community was sampled for a biomass increase. Results of Study 1 suggested nitrogen was the major limiting resource for the dominant functional group. Study 2 was a greenhouse study that attempted to quantify the R^* for nitrogen for three species. The R^* for annual sunflower was 0.6 ppm $\text{NO}_3\text{-N}$; the R^* for bluebunch wheatgrass was less than 0.6 ppm $\text{NO}_3\text{-N}$; and spotted knapweed's R^* was between 0.4 and 0.6 ppm $\text{NO}_3\text{-N}$. Two- and three-species mixtures suggested estimated R^* s accurately predicted the outcome of competition between natives, but not with natives and spotted knapweed. Study 3 tested succession dynamics under natural and nitrogen-manipulated conditions. Soil nitrogen was altered by nitrogen and sucrose additions. Annual sunflower did not persist. Spotted knapweed biomass increased with nitrogen addition but did not decrease with carbon addition, even though soil $\text{NO}_3\text{-N}$ was below its R^* . Bluebunch wheatgrass appeared unaffected by nitrogen manipulation, but soil $\text{NO}_3\text{-N}$ concentration was not decreased below its R^* .

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Doctor of Philosophy

in

Land Resources and Environmental Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2004

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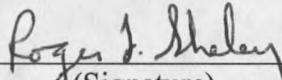
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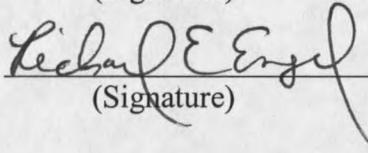


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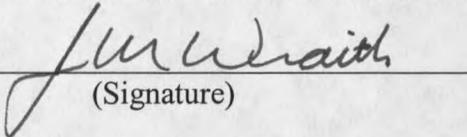
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ACKNOWLEDGEMENTS

I wish to thank Dr. Roger Sheley for the opportunity to pursue this degree and for his guidance, generosity, and patience. Drs. Richard Engel, Jeff Jacobsen, Tony Svejcar, and Cathy Zabinski are greatly appreciated for serving as committee members and mentors. I also wish to thank Dr. Jim Jacobs for his advice and guidance. Several fellow graduate students and field assistants provided support, advice, and humor throughout my program, and I wish to acknowledge them for their friendship and assistance.

Special thanks to my husband, parents, brothers, sisters, and running partner who provided moral support and encouragement throughout my graduate program. I thank them all from the bottom of my heart.

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ABSTRACT

R* theory has been proposed as a mechanism for plant community dynamics, but the theory is poorly tested and has not been developed into a principle for management. This theory states that the outcome of succession is based on the ability of a plant to sequester a limiting resource when it is below the uptake level of neighboring species. R* is the resource level a species requires to persist in an environment, and the species with the lowest R* dominates over time. Knowledge of the R*s for species within a plant community could lead to effective weed management with predictive capabilities.

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Three studies were conducted beginning in 2000. For Study 1, availability of essential plant resources were altered and the plant community was sampled for a biomass increase. Results of Study 1 suggested nitrogen was the major limiting resource for the dominant functional group. Study 2 was a greenhouse study that attempted to quantify the R* for nitrogen for three species. The R* for annual sunflower was 0.6 ppm NO₃-N; the R* for bluebunch wheatgrass was less than 0.6 ppm NO₃-N; and spotted knapweed's R* was between 0.4 and 0.6 ppm NO₃-N. Two- and three-species mixtures suggested estimated R*s accurately predicted the outcome of competition between natives, but not with natives and spotted knapweed. Study 3 tested succession dynamics under natural and nitrogen-manipulated conditions. Soil nitrogen was altered by nitrogen and sucrose additions. Annual sunflower did not persist. Spotted knapweed biomass increased with nitrogen addition but did not decrease with carbon addition, even though soil NO₃-N was below its R*. Bluebunch wheatgrass appeared unaffected by nitrogen manipulation, but soil NO₃-N concentration was not decreased below its R*.

LITERATURE REVIEW AND SYNTHESIS:
TOWARD SUCCESSIONAL MANAGEMENT OF NONINDIGENOUS, INVASIVE
PLANTS IN WESTERN RANGE AND WILD LANDS

Introduction

Plant ecologists have been interested in temporal changes in plant community composition for centuries. Such change, often referred to as succession, was described as early as 300 B.C. by early scientists like Theophrastus (300 B.C.). Although the term succession was coined early by Thoreau (1860), Clements' (1916, 1920, 1928, 1936) exhaustive studies appear to be responsible for its general acceptance. Clementsian succession postulated that species succeeded one another through time as the previous species aided the establishment of the next until a deterministic, stable climatic endpoint was reached (Clements 1916). Today, the term succession does not necessarily mean Clementsian succession, as many models have emerged over the last 150 years that attempt to describe or explain changes in plant community composition over time.

During the last century in the western U.S., succession has included a new participant: nonindigenous, invasive species. Nonindigenous plant invasions can dramatically change the rate and direction of succession (Anable et al. 1992, Billings 1990); the structure, organization, and function of ecosystems (Lacey et al. 1989, Whisenant 1990, D'Antonio and Vitousek 1992, Gerlach and Rice 1996, Olson 1999a, LeJeune and Seastedt 2001); and the aesthetic and economic value of range and wild lands (Weiser 1995, Hirsch and Leitch 1996, ATTRA 1997).

In spite of over 50 years of aggressive weed control, invasive plants remain a significant ecological and economic crisis. Invasive plants infest over 40 million ha in

the United States (NISC 2001) and spread at nearly 14 percent per year (Westbrooks 1998). Currently, when successional trajectories are changed by the presence of invasive plants, the symptoms (weeds) of invasion are treated, with minimal regard to the underlying processes that contributed to and supported the invasion. We apply control methods such as herbicides, natural enemies, and grazing animals, without having designed a strategy to influence the cause of the problem. For sustainable management, scientists and land managers should address fundamental ecological processes and how they have been altered to allow the establishment and persistence of invasive plants (Sheley and Krueger-Mangold 2003).

Enduring invasive plant management should be based on ecological principles. Principles and concepts in ecology, the basic science behind nonindigenous plant management, has allowed the design and implementation of sustainable management with predictable outcomes that focuses on development and maintenance of healthy, desirable plant communities (Sheley et al. 1996, Sheley and Rinella 2001). Because invasion is fundamentally a result of plant community compositional change, we should strive to understand the ecological processes directing succession, investigate how nonindigenous species alter such processes, and use this knowledge to modify processes that favor desired species. A mechanistic, process-based framework of succession applicable to management was proposed by Pickett et al. (1987), applied to natural resource management by Luken (1990), and extensively developed for invasive plant management by Sheley et al. (1996), Sheley and Rinella (2001), Anderson (2003), Bard et al. (2003), and Sheley and Krueger-Mangold (2003).

Pickett et al. (1987) proposed a successional management framework that is mechanistic and hierarchical, and lends itself to understanding and manipulating 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 1.1). For succession to proceed, safe sites need to be present. Second, species propagules need to reach those sites. Third, the plant community composition along the successional trajectory depends on the relative performance of those species that are present. These general causes apply to all cases of plant community change, regardless of spatial and temporal scales, and can guide our search for more specific causes (Pickett et al. 1987).

Specific processes or conditions that contribute to the three general causes of succession form the second level of the hierarchy (Table 1.1). These include broad categories such as disturbance, resource supply, and interference. Processes emphasized by other successional models can be incorporated into the successional management framework to develop an improved mechanistic, robust model of succession.

The final level of the hierarchy is most detailed and includes site specific modifying factors that influence the outcome of succession. Examples for the process of disturbance include size, severity, and patchiness of the disturbance, time interval between disturbances, and the predisturbance history (Table 1.1). Through management, we can better understand and even affect the process of disturbance by manipulating the size, severity, and patchiness of disturbance. Essentially, modifying factors are tools in our toolbox that can be used to shift successional trajectories towards management goals. The third level of the hierarchy could be expanded through inclusion of other

successional models because they may increase management options for invasive species by addressing additional ecological processes. Management strategies are expanded when viewed within the context of a new and improved successional management framework.

Table 1.1. 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
	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, Allocation, reproduction timing and degree
	Life history	Climate, site-history, prior occupants, herbivory, natural enemies
	Stress	Climate, site-history, prior occupants, herbivory, natural enemies
	Interference	Competition, herbivory, allelopathy, resource availability, predators, other level interactions

^aModified from Pickett et al. 1987

Luken (1990) further developed successional management for the use of natural resource management. He formulated three components of successional management corresponding to the three general causes of succession (Pickett et al. 1987): site availability could be created by designed disturbance, species availability could be

regulated by controlled colonization, and species performance could be controlled by a variety of strategies that affect the fitness of a population.

Successional management was developed specifically for nonindigenous plant invasions by Sheley et al. (1996). They proposed that plant communities currently dominated by invasive plants could be restored to weed-free, healthy plant communities by using the three general causes of succession (Pickett et al. 1987) and Luken's (1990) three components of successional management. For example, disturbance could be created with an herbicide application; colonization could be controlled by drill or broadcast seeding; and species performance could be controlled with grazing. The three causes of succession and their associated processes and modifying factors should be addressed in management to move a plant community from an undesired state to a desired state (Sheley et al. 1996).

Later, successional management for invasive plants was expanded to evaluate the potential efficacy of biocontrol agents by understanding how biocontrol agents affect dispersal, stress, and interference of target and non-target plants (Sheley and Rinella 2001). Anderson (2003) tested the successional management framework on rangeland infested by nonindigenous species. She found that by increasingly addressing the three general causes of succession, the successional trajectory towards a desired plant community was accelerated. Finally, Bard et al. (2003) proposed augmentative restoration in which the three general causes of succession were assessed within a specific site. Landscape heterogeneity provided varying degrees to which the causes of succession and their associated processes were intact to allow recovery. When

deficiencies were found, management (modifying factors) augmented the causes and processes to create desired plant communities.

Adoption of this mechanistic, process-based framework has been hindered because it has been associated with a particular successional paradigm, especially that of Clements (1916). Adoption has also been slowed because ecologists desire more contemporary successional models that usually emphasize a particular aspect of plant community dynamics, for example competition (Grime 1979, Tilman 1982). The successional management framework could be enhanced by integrating various components of the prevailing successional models into a single, robust, unified model that maintains practical usefulness.

This paper attempts to contribute to our understanding of mechanistic successional models and how they might be used to guide the implementation of invasive plant management on range and wild lands. I present a brief historical review of some dominant successional models and evaluate the successional processes on which they are based. Each successional model emphasizes particular processes or groups of processes, and in many cases there is substantial overlap. I discuss how each model and its associated processes might be incorporated into successional management to create a unified, mechanistic, process-based model as a framework for ecologically-based invasive plant management. To illustrate the potential usefulness of a unified, process-based successional framework, I propose to expand our understanding of a competition-based model, attempt to define its role in plant community dynamics based on the successional management framework, and apply the competition-based model to management of nonindigenous plants and restoration of invasive plant dominated land.

Successional Models and Associated Ecological Processes

Facilitation

Connell and Slatyer (1977) provided a mechanism to explain Clementsian succession (Clements 1916) by suggesting succession was directed by the process of facilitation. They proposed early successional species alter the environment in favor of mid- and, ultimately, late successional species. The majority of evidence supporting facilitation comes from sites where primary succession has occurred (Crocker and Major 1955, Lawrence et al. 1967, Olson 1958, Rousset and Lepart 2000, Gagne and Houle 2001).

Facilitation is a self-perpetuating process that influences how well a suite of species establishes and persists at a particular period during succession. For example, on glacial moraines in Alaska, nitrogen-fixing alder (*Alnus crispa* Pursh) is dominant early in succession and aids in soil nitrogen (N) accumulation that is necessary for subsequent establishment of other species (Crocker and Major 1955). The successional management framework currently includes facilitation as affecting species performance through the processes of resource availability and capture and interference.

Facilitation contributes to the successional management framework by promoting nurse crops and hydraulic lift as modifying factors that managers can manipulate to alter resource availability and capture and interference. Evidence of nurse plant relationships, or plant-plant relationships where a mature plant protects a young plant beneath it by ameliorating harsh microclimatic conditions like soil dessication and low soil nutrient concentrations, occurs with a wide variety of species (Callaway 1995). For example,

researchers have found that cactus seedling survival is highest in the shade of a nurse plant (Withgott 2000). In some cases, the beneficiary may outlive its nurse plant. For example, creosote bushes (*Larrea tridentata* Cov.) were disproportionately associated with dead white bursage (*Ambrosia dumosa* Payne), a species critical to the initial establishment of creosote (McAuliffe 1988). On the other hand, many species of understory plants appear to depend on facilitative relationships with overstory plants throughout their life span (Callaway 1995). Either way, plant community composition is ultimately changed through species replacement or increased species richness. Nurse crops have been used primarily in cropping systems (Hartwig and Ammon 2002), but restoration of invasive plant-infested range and wild land may experience similar benefits of nurse plants to those in cropping systems. In cropping systems, nurse crops decrease water runoff and soil erosion (Hartwig 1988), add organic material to the soil (Hartwig and Ammon 2002), increase N availability if the nurse crop is a legume (Fox and Piekielek 1988), sequester excess N (Corak et al. 1991), and control weeds (Else and Ilnicki 1989). Nurse plants may facilitate restoration by ameliorating harsh environmental conditions and utilizing excess soil water and nutrients otherwise available for exploitation by invasive species (Herron et al. 2001).

Hydraulic lift is another facilitative mechanism that could increase the number of modifying factors currently included in the successional management framework. During hydraulic lift one species draws up water from deep in the soil profile and releases it into shallow soil layers where it is then used by nearby understory plants (Lambers et al. 1998). Big sagebrush (*Artemisia tridentata* Nutt.), which has a deep root system, has been found to increase water availability for shallower-rooted understory

plants (Richards and Caldwell 1987). Dawson (1993) documented that sugar maple (*Acer saccharum* Marsh.) provided understory plants with 3% to 60% of their total water use. On semi-arid range and wild lands, hydraulic lift may aid in the establishment of desirable species during restoration of lands infested by nonindigenous species.

Preservation of species with the potential for hydraulic lift, such as big sagebrush, may aid in establishment of desirable species during restoration. On the other hand, bare soil around these species may be susceptible to invasion because of increased water availability. Invasion may be more likely when resource availability increases (Burke and Grime 1996, Davis and Pelsor 2001, Kolb et al. 2002).

Humans are facilitating the large increase in nonindigenous invasions over the last century by altering nutrient cycles. More specifically, large scale application of N fertilizer, increased atmospheric N deposition, altered fire regimes, and indirect fertilization through cattle grazing may have decreased the historical N limitation under which many indigenous species have evolved (Hooper and Johnson 1999). Indigenous species, which often are slow growing and have low N requirements, may no longer have a competitive edge over short-lived, nonindigenous species that have high N requirements (Bobbink et al. 1998, Herron et al. 2001).

Inhibition

A second mechanistic model of succession proposed by Connell and Slatyer (1977) is inhibition. While facilitation implies that only certain species have the ability to establish and persist to adulthood under early successional conditions, with inhibition that any species that can establish and survive to adulthood will persist because it secures

available resources and inhibits the invasion of subsequent species. Late successional species cannot grow to maturity in the presence of early successional species, unlike facilitation where late successional species rely on early successional species for establishment. Because of this, the inhibition model implies that succession may not progress in a linear manner if earlier species prevent any further invasion (Connell and Slatyer 1977).

In most cases, a single successional theory may involve multiple causes and processes. Inhibition can be modified by many factors affecting species availability and species performance. Like the facilitation model, many of these factors are already included in the successional management framework, and the inhibition model contributes additional modifying factors useful for management of invasive plant-infested land. The primary, influential processes responsible for inhibition include seed dispersal, species' ecophysiological traits, and interference.

Based on this model, a species must initially disperse its propagules to the site immediately following a disturbance in order to establish, similar to that described in successional management (Connell and Slatyer 1977). Dispersal affects plant community composition more strongly than environmental factors or competitive interactions (del Moral 1999). The dispersal vector (eg. wind or wildlife) is a factor that can be modified to control the rate of establishment, and thus, succession. Dispersal vectors can, in part, determine the development of spatial structure in plant communities (Foster and Gross 1999).

Additional modifying factors in the dispersal process include sequence, rate, and frequency of dispersal events, which can have large effects on community composition

(Booth and Swanton 2002). The arrival of propagules to new sites has been targeted as a primary factor in weed prevention programs (Sheley et al. 1999). The arrival of nonindigenous species to a new site is primarily through human-aided movement and natural, rare events (storms and floods) that span long distances (Smith 1999, Mack and Lonsdale 2001, Novak and Mack 2001). By controlling sequence, rate, and frequency of dispersal, managers may be able to modify invasion or improve current restoration techniques.

Species' ecophysiological traits, or their "vital attributes," affect which species initially establish, persist, and then prevent the establishment of other species (Nobel and Slatyer 1980). Knowledge of "vital attributes," which are crucial for a species' role in the sequence of vegetation replacement, forecast potentially dominant species in a plant community (Pickett 1982). Vital attributes include germination requirements, nutrient assimilation rates, growth rates, and genetic differentiation. Identification of vital attributes of invasive species could be very beneficial to successful management because managers can capitalize on differences among natives and invasive species. Modification in ecophysiological traits of an invasive species from its native range to its new range may provide novel management options. Comparisons between native range and introduced range can be made in an attempt to understand biotic and abiotic conditions that may be responsible for the differences (Callaway and Aschehoug 2000, Hierro and Callaway 2003). The discrepancies can then be targeted for manipulation through management.

Inhibition can also include interference which refers to the reduction of fitness of neighboring plants due to behavioral mechanisms, which do not directly involve

limited, shared resources (Crawley 1997b). Production of allelopathic chemicals is an example of interference. In the context of the inhibition model of succession, plant-plant interactions where only one species benefits are most appropriate. Evidence exists suggesting some nonindigenous invasive species are allelopathic (Kelsey and Locken 1987, Callaway and Aschehoug 2000), but other evidence suggests otherwise (Dietz et al. 1996, Keay et al. 2000, Conway et al. 2002). Although allelopathy is included as a modifying factor of interference in the successional model, I believe its role in establishment and persistence of nonindigenous species requires a firmer understanding before it can be effectively applied to management.

An additional modifying factor for consideration in successional management of nonindigenous species is mycorrhizal associations. Some evidence suggests competitive relationships between native and nonindigenous, invasive species may be mediated through mycorrhizae. In one study, spotted knapweed biomass was 66% greater when grown with Idaho fescue (*Festuca idahoensis* Elmer) in the presence of arbuscular mycorrhizal (AM) fungi than when AM fungi were absent (Marler et al. 1999). The authors concluded AM fungi may have provided linkage between the two species that allowed transfer of nutrients and photosynthate between plants.

Arbuscular mycorrhizal fungi primarily benefit the host plant by increasing nutrient uptake, especially phosphorus (P), and water uptake under drought stress (Lambers et al. 1998). Invasive species may be better host plants for AM fungi and develop more extensive hyphal networks than native rangeland species, thereby increasing their access to phosphorus (Zabinski et al. 2000). Changes in N supply rates

may have shifted some western rangelands from a system that was limited by one common resource to a system in which P and/or water limit species (LeJeune and Seastedt 2001). If so, AM fungi may increasingly impact plant community composition and ecosystem functioning (Johnson et al. 2003). As this area of research continues to expand and techniques for identifying AM fungi improve, our knowledge of mechanisms by which AM fungi influence plant community dynamics will increase and methods of applying this information to management will follow.

Tolerance

In some scenarios succession occurs because species tolerant of more stressful environmental conditions (shade, moisture, nutrients, allelochemicals, grazing) replace species less tolerant of those conditions (MacArthur 1962, Grime 1979). Initial floristic composition was first described by Egler (1954) and was later expanded upon by Connell and Slatyer (1977). In this model, all species are present initially by chance migration of propagules to the disturbance site. Early successional species modify the environment so it becomes less suitable for recruitment of early successional species (inhibition), but this modification has little to no effect on the establishment and persistence of later successional species (Connell and Slatyer 1977). Instead, the location of a species on the successional trajectory is influenced by its life history. Late successional species appear later because they grow more slowly, are longer lived, and allocate resources to belowground growth rather than seeds (K-strategists; MacArthur 1962). Through time, earlier species that grow quickly and produce copious amounts of seeds are eliminated because they allocate resources to reproduction and dispersal rather than to a competitive

plant structure (r-strategists) (MacArthur 1962). If the occurrence or frequency of disturbance remains low, those species that tolerate stressful conditions like low nutrient availability, shading, and herbivory, will continue to dominate (Grime 1979).

Successional management currently incorporates the tolerance model through the processes of disturbance, propagule pool, life history, and stress. According to the tolerance model, disturbance drives changes in plant community composition. An intermediate level of disturbance favors the highest degree of diversity in a plant community (Huston 1979). The tolerance model (Connell and Slatyer 1977) and the intermediate disturbance hypothesis (Huston 1979) do not suggest additional factors that modify disturbance, but they prompt us to carefully consider the timing and severity of disturbance and how timing and severity may affect our management objectives. For example, if high species diversity increases invasion resistance (Symstad 2000, Dukes 2001), intermediate levels of timing and severity may be most appropriate.

The propagule pool is important because only those species present after a disturbance are included in the successional trajectory. Immediately following either an unexpected or planned disturbance, management should focus on components of the propagule pool. As an example, consider a landowner who has range, forest, or other cover types to manage. Burning or mechanical removal of unwanted trees and shrubs results in resprouting of many of the same species from the remaining root systems. Where root systems are killed, the plant community is fundamentally altered (Egler 1954). Modification to the existing propagule pool through destruction of roots and reseedling with desirable species is a simple concept that could be included as a modifying factor in the successional management framework.

The successional management framework may be expanded to include propagule removal through shallow tilling to destroy roots and reseeding with seed mixes appropriate for land use objectives as an additional modifying factor for propagule pool. Shallow tilling may be appropriate for some nonindigenous, invasive species where few other options are available. Intensive, consistent tilling has been used to manage leafy spurge (Dersheid et al. 1960, 1963) and Dalmatian toadflax (Parker and Peabody 1983). Lym and Messersmith (1993) found tilling several times in the fall before a hard frost for three years was as effective as an herbicide treatment for reducing the root system of leafy spurge. Tilling should be combined with reseeding with desirable species for development of a healthy plant community that meets specific management objectives (Sheley et al. 1996).

Life history may prove useful for managing invasion because many nonindigenous, invasive plants possess characteristics of r-strategists (Bazzaz 1986) while many desirable, late successional species on western range and wild land, such as bluebunch wheatgrass (*Agropyron spicatum* Pursh), are stress-tolerant K-strategists (Redente et al. 1992, Aerts 1999). Even though many invasive plants display life history traits characteristic of early successional species, some species invade and persist in relatively undisturbed, perennial native plant communities (DiTomaso 2000, Blicher et al. 2002). This suggests some species may be tolerant of low-nutrient conditions in addition to exploiting readily available resources following a disturbance (Blicher et al. 2002). Tolerance model used in conjunction with other successional models that are process-based, may provide a framework for understanding this flexibility in life history traits in response to varying degrees of resource availability.

Tolerance for stressful climates, site-history, prior occupants, herbivory, and natural enemies is comprehensively included in the successional management framework. As with the process of life history, some invasive species appear to possess a wide tolerance range for stressful environmental conditions and this may explain a large part of their success (Mack 1996, Blicher et al. 2002).

Community Assembly Theory

Community assembly theory was introduced by Diamond (1975) to explain patterns of bird assemblages on New Guinea islands. The basic premise is that biological communities are assembled through time due to various processes acting on the species pool (Booth and Swanton 2002). This model considers plants to be assembled entities and investigates the processes that formed these assemblages (Booth and Swanton 2002). Depending on historical successional processes, succession may have alternative endpoints (Lockwood 1997). This theory echoes that of Gleason (1917) who postulated there could be several endpoints along a successional trajectory depending on the individual traits of species and details of the processes that shaped the plant community along the successional trajectory. This is in contrast to the first three successional models presented that proposed linear successional trajectories with specific and determined outcomes.

Several ecological processes outlined in the successional management framework shape community assemblages and appear legitimate for applications to management, especially for nonindigenous, invasive plants (Belyea and Lancaster 1999). First, the relevance of dispersal to successional outcomes is unquestionable (del Moral 1999,

Foster and Gross 1999, Booth and Swanton 2002). The processes of disturbance, propagule pool, resource supply, and stress (Mack 1996, Weaver et al. 2001) largely affect whether or not a population becomes established after arrival and shape successional outcomes. Finally, interference mechanisms such as competition (Grace and Tilman 1990), mutualism (Withgott 2000), and herbivory (Crawley 1997a) are integral to the success or demise of a plant population within a community.

Some of the successional models outlined in this paper contain similar processes responsible for changes in plant community composition. For community assembly theory, I will focus on propagule pool, resources, and plant-animal interactions because they offer additional modifying factors for the successional management framework that have not been mentioned previously. Disturbance will be discussed later in greater detail under a different successional model.

Knowledge of which propagules are available and their germination requirements can increase our availability of modifying factors. For example, dyer's woad is an invasive mustard whose fruits contain a water-soluble germination inhibitor (McConnell et al. 1999). Control efforts for dyer's woad should be focused on periods following heavy precipitation when germination is likely. Similar information on other invasive species could be used to manage seedling populations, limit recruitment, and decrease seed production.

Propagule pool and its modifying factors should also be considered when attempting to restore plant communities that have been invaded by nonindigenous species. A potential method for modifying propagule pool is seed coating, which has been used primarily in crop and horticultural settings (Robani 1994, Hirano et al. 2000,

Volin et al. 2000). Seed coating technology may have value in range and wild land restoration to treat desirable species with coatings that would alter germination, decrease susceptibility to pests and pathogens, or alleviate abiotic stress. For example, alfalfa seeds treated with peat and lime produced significantly greater plant emergence and plant survival than non-coated seeds in field trials in the midwestern and western U.S. (Walsh and Turk 1988), and are especially helpful for alfalfa establishment under conditions of limited moisture (Turk 1983). Seed coatings may increase establishment during restoration of semi-arid rangeland that is infested with invasive plants. To decrease competition between seeded, desired species and invasive species, I foresee coatings that delay germination until an appropriate time, preferably after invasive species have been adequately controlled through other techniques such as use of herbicides or grazing practices.

Landscape heterogeneity is an additional modifying factor that can affect resource supply. Heterogeneity found throughout the landscape should be used to enhance management and restoration, rather than viewed as an obstacle (Bard et al. 2003). Heterogeneous environments may facilitate high functional guild richness (Fargione et al. 2003). High richness in functional guilds may increase resistance to invasion because invading species perform better when their traits and patterns of resource use differ from resident species (Pokorny 2002);

Plant-animal interactions, a modifying factor of interference, may affect community composition. Grazing with multiple classes of livestock can alter plant community composition. Certain classes of livestock, such as sheep and cattle, preferentially graze different plant growth forms. Sheep prefer forbs whereas cattle

prefer grasses. Some wild ungulates, such as mule deer, prefer shrubs (Olson 1999b). These inherent diet preferences can cause a shift in species composition of native plant communities (Bowns and Bagley 1986). Because cattle, the dominant class of livestock on semi-arid, western rangeland since the mid-1800s (Olson 1999b), selectively graze native grasses, native grasses are at a competitive disadvantage for limited soil water and nutrients, and improperly grazed grasslands are prone to invasion. The nonindigenous, invasive forbs spotted knapweed (*Centaurea maculosa* Lam.) and leafy spurge have been effectively controlled with sheep grazing (Landgraf et al. 1984, Olson et al. 1997). Grazing with multiple classes of livestock and considering wildlife carrying capacities may equalize grazing pressure across plant growth forms and even help control nonindigenous, invasive plants.

Community assembly theory continues to emerge in ecology and provides a foundation for understanding mechanisms of invasion and extinction, community response to disturbance, and success or failure of community restoration (Booth and Swanton 2002). Although more narrow in scope, community assembly theory emphasizes processes contained in the successional management framework. Given these qualifications, community assembly theory holds promise for nonindigenous, invasive plant management. Management programs should focus on external and internal processes that govern plant community dynamics, and not simply on killing the weed, i.e. treating the symptom of invasion (Sheley and Krueger-Mangold 2003). Under this theory, many options exist for modification of successional processes to limit the spread of invasive plants.

Fluctuating Resource Availability

The theory of fluctuating resource availability as a mechanism for invasion by nonindigenous species was developed by Davis et al. (2000) and Davis and Pelsor (2000). This theory states that a plant community becomes more susceptible to invasion by new species whenever there is an increase in unused resources.

Fluctuating resource availability theory emphasizes the processes of disturbance and its affect on resource availability. Disturbance may cause a decline in resource use by plants or an increase in resource supply rates, thus leading to increasing resource availability (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, Jacobs and Sheley 2003).

Human impacts on environmental processes and climatic variability over the past century may be new modifying factors in successional management. Increases in atmospheric CO₂ is predicted to increase water use efficiency of resident species and a subsequent increase in soil water availability (Dukes and Mooney 1999). Global eutrophication resulting from anthropogenic activities like large scale N fertilizer application, increased atmospheric N deposition, altered fire regimes, and indirect fertilization through cattle grazing may have decreased the historical N limitation under which many indigenous species have evolved (Hooper and Johnson 1999). Both these modifying factors are predicted to increase invasion in the future (Dukes and Mooney 1999). Therefore, invasion prevention measures may be necessary, such as establishing

additional species or functional guilds into existing plant communities as an effort to increase resource capture and decrease the chance of invasion (Pokorny 2002).

This theory essentially condenses invasion into one factor, resource fluctuation. However, there can be many causes of resource fluctuation, and this theory proposes many possibilities to manipulate resource availability through the process of disturbance. Because nonindigenous plant invasion has been strongly linked to disturbance (Parker et al. 1993, Burke and Grime 1996, Symstad 2000, Thompson et al. 2001), this model of succession may be very applicable to management.

State-and-Transition Model

Clementsian (Clements 1916) succession prevailed as the successional model shaping range management in the mid-1900s. As an alternative, Westoby et al. (1989) proposed the state-and-transition model for succession on rangelands, especially for semi-arid to arid rangelands. Discrete states of vegetation are possible through space and time as a result of natural events (weather, fire) or management actions (grazing strategies, burning, fertilization). This heterogeneity presents managers with opportunities and hazards. Opportunities consist of climatic circumstances under which management action such as fire, heavy grazing, or removal of grazing, can produce a favorable transition. Hazards are climatic circumstances under which failure to burn, heavily graze, or remove grazing can produce an unfavorable transition. By considering succession as a series of opportunities and hazards, managers are encouraged to seize the opportunities and evade the hazards (Westoby et al. 1989).

While indirectly addressing the influence of disturbance on succession, the state-and-transition model does not emphasize the process of disturbance or other ecological processes that allow the existence of multiple vegetative states. Instead, state-and-transition focuses primarily on climatic conditions like drought, excessive precipitation, and timing of precipitation, which are largely beyond the control of the land manager (Westoby et al. 1989). Other variables may lead to multiple vegetative states such as spatial scale of a disturbance, historic natural and anthropogenic events, and the effect of climatic variability on disturbance patterns (Sprugel 1991). This model will be strengthened by incorporation into the successional management framework because it will expand its transitions to include other ecological processes responsible for plant community compositional change, thereby increasing the number of opportunities in which to improve the current condition of a plant community.

The state-and-transition model proves useful to the successional management framework in its recognition that there are multiple non-equilibrium states in which a plant community may exist (Westoby 1989, Sprugel 1991). Multiple steady states are affected by the three general causes of succession (Pickett et al. 1987) (Figure 1.1).

In turn, the causes of succession affect steady states. This is useful to ecologists and managers because it recognizes plant communities are dynamic and encourages opportunistic, progressive action to seek a positive transition in the state of the vegetation, depending on land use objectives (Sheley et al. 1996). This is especially applicable for management of nonindigenous plant invasions on rangelands and I have included non-equilibrium states as a modifying factor of the disturbance process.

Evidence suggests nonindigenous, invasive plants may participate in succession with a

variety of roles and with various degrees of persistence (Luken 1997). Vankat and Snyder (1991) found various growth forms of nonindigenous species participated in succession much like native species. Dominance by an invasive species can be a non-equilibrium successional state and, with proper management actions, capable of being restored to a more desirable state (Pickett et al. 2001). The challenge for managers lies in determining correct management actions.

Resource Ratio Hypothesis

Like the fluctuating resource availability model (Davis et al. 2000), the resource ratio model of plant succession (Tilman 1977, 1982, 1984, 1988) incorporates resource supply rate and use in the plant community. However, this model primarily focuses on the processes of resource supply and interference instead of disturbance. This model states that succession is a result of species' unique requirements for essential plant resources, specifically soil nutrients and light. Species performance as affected through the process of interference, more specifically competition for resources in limited supply, is the cornerstone of this theory.

A trade-off between allocation to aboveground and belowground biomass exists for plants (Lambers et al. 1998). To compete for light, plants allocate resources to aboveground tissue; to compete for soil nutrients, plants allocate resources to belowground tissue (Lambers et al. 1998). According to the resource ratio hypothesis, early successional species are better competitors for soil nutrients, and late successional species are better competitors for light. As succession progresses, species attain dominance when the soil nutrient:light ratio results in maximum population growth rate

relative to competing species. Heterogeneity throughout a landscape in abiotic and biotic factors provides varying soil nutrient:light concentrations and allows co-existence even in late successional communities where only the most competitive species should dominate (Tilman 1982, 1988).

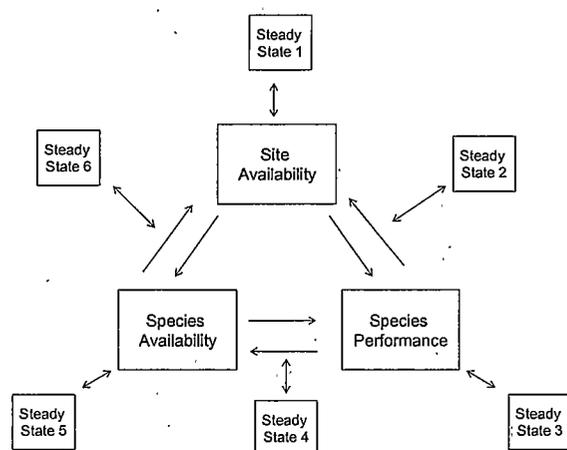


Figure 1.1. Incorporation of state-and-transition model (Westoby et al. 1989) into the successional management framework (Pickett et al. 1987). Steady states are affected by the three general causes of succession. The three general causes of succession may affect transitions from one steady state to another. The various steady states can be viewed as opportunities to affect the three general causes of succession, and the three general causes of succession can be modified through management to shift successional trajectories towards more desirable steady states.

As a central component of the resource ratio model of succession, Tilman (1982) postulated that the outcome of competition could be predicted by a species' R^* , the amount of a resource necessary for a species to maintain a stable population within a habitat. 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 of competition predicts that a species with a lower R^* will competitively displace a species with a higher R^* under equilibrium conditions (Tilman 1982, 1984, 1988).

Resource ratios and species' R^* may be added to the successional management framework as modifying factors under the processes of resources and interference.

The resource ratio hypothesis may provide insight into understanding competitive interactions between native and nonindigenous, invasive species. More specifically, knowledge of species' R^* for various limiting resources may be used to predict the outcome of plant community dynamics, identify areas susceptible to invasion by nonindigenous species based on patterns of resource availability and resource ratios, choose species for revegetation that have lower R^* s than nonindigenous species, and will be more resistant to re-invasion, and alter resource availability to direct succession toward a desirable plant community.

Unified Successional Management Model

The successional models presented above are different perspectives on a similar phenomenon, the change in plant community composition through time. Dissimilarities and similarities in the models, and in other mechanistic successional models not presented here (Cowles 1911, Odum 1969, Whittaker 1970, Drury and Nisbet 1973, Grime 1979, Peet 1992, Gitay and Wilson 1995), can be rectified through agreement that ecological processes are responsible for changes in plant community composition through time. I present the unification of successional models through a mechanistic, process-based successional management framework that takes into account many ecological processes and environmental variables (Table 1.2).

Table 1.2. Causes of succession, contributing processes, and additional modifying factors from various successional models discussed above. Modifying factors shown in bold have been incorporated from other successional models discussed in the text. Successional models and relevant citations are listed in italics under processes.^a

Causes of Succession	Processes	Modifying Factors
Site Availability	<u>Disturbance</u> <i>Fluctuating Resource Availability</i> (Davis et al. 2000) <i>State-and-Transition</i> (Westoby et al. 1989)	Size, severity, time intervals, patchiness, predisturbance history, increased atmospheric CO₂, eutrophication, many non-equilibrium states
Species Availability	<u>Dispersal</u> <i>Inhibition</i> (Connell and Slatyer 1977) <i>Community Assembly</i> (Gleason 1917, Diamond 1975) <u>Propagule pool</u> <i>Tolerance, Initial Floristic Composition</i> (Egler 1954, Connell and Slatyer 1977) <i>Community Assembly</i>	Dispersal mechanisms and landscape features, vector, sequence, rate, frequency Land use, disturbance interval, species life history, tilling, reseeding, precipitation patterns, seed coatings
Species Performance	<u>Resource supply</u> <i>Facilitation</i> (Clements 1916, Connell and Slatyer 1977) <i>Community Assembly</i> <i>Resource Ratio Hypothesis</i> (Tilman 1977, 1982, 1984, 1988) <u>Ecophysiology</u> <i>Inhibition</i> (Connell and Slatyer 1977) <u>Life history</u> <i>Tolerance</i> (MacArthur 1962, Connell and Slatyer 1977, Grime 1979)	Soil, topography, climate, site history, microbes, litter retention, hydraulic lift, landscape heterogeneity, resource ratios Germination requirements, assimilation rates, growth rates, genetic differentiation, changes between native and introduced ranges Allocation, reproduction timing and degree, plasticity
	<u>Stress</u> <i>Tolerance</i>	Climate, site-history, prior occupants, herbivory, natural enemies, plasticity
	<u>Interference</u> <i>Facilitation</i> <i>Inhibition</i> <i>Community Assembly</i> <i>Resource Ratio Hypothesis/R* theory</i> (Tilman 1977, 1982, 1984, 1988)	Competition, herbivory, allelopathy, resource availability, predators, other level interactions, nurse crops, mycorrhizae, multiple classes of grazing, R*, soil impoverishment

^aModified from Pickett et al. 1987

This model can be used to explain successional dynamics at any site if adequate information is available on the disturbance regime, species availability, and knowledge of species life history, ecophysiology, response to herbivory, and other ecological traits (Pickett et al. 1987). Furthermore, succession can be explained in a process-based framework that includes many successional models that have been proposed in the past. The successional model supports the development of testable hypotheses about plant community change, including the invasion of nonindigenous species (Sheley et al. 1996).

The successional management framework (Pickett et al. 1987) has already been used to manage nonindigenous, invasive species (Sheley et al. 1996). My proposed model is improved in that it incorporates several mechanistic models of succession and offers additional suggestions for techniques to manage invasive plants. This model warrants further testing and application to range and wild lands invaded by nonindigenous plants.

Incorporation of R* Theory into Successional Management for Nonindigenous Plant Invasions

In the following chapters I explore how a successional model, in this case resource ratio hypothesis and species' R^* (Tilman 1982, 1984, 1988), can be incorporated into the unified, process-based successional management framework to manage nonindigenous plant invasions. This example applies directly to controlling species performance in infested range and wild lands through the process of interference in the form of competition for limited soil resources.

Recall that a species' R^* is the minimum resource level required by the population to persist in the plant community (Tilman 1982, 1988). Accordingly, late successional species should have lower R^* s than early successional species because they dominate as succession progresses and resource availability decreases. Life history traits of late successional species, such as high root allocation, efficient nutrient conservation mechanisms, low maximal growth rates, and low susceptibility to herbivory allow them to outperform early successional species under low soil nutrient conditions (Tilman and Wedin 1991).

While there are exceptions, most nonindigenous, invasive species display life history traits similar to early successional species (Baker 1974, Bazzaz 1986, Roy 1990). This supposition is supported by research that indicates enhanced performance of nonindigenous species when N availability is increased. For example, additions of nitrogen inhibited succession from the invasive, annual cheatgrass (*Bromus tectorum* L.) to indigenous perennial species in a sagebrush steppe site in northwestern Colorado (McLendon and Redente 1991). Studies abound that indicate high N availability encourages the establishment and dominance of nonindigenous, invasive plant species (Story et al. 1989, Huenneke et al. 1990, Milchunas and Lauenroth 1995, Burke and Grime 1996, Maron and Connors 1996, Wedin and Tilman 1996, Alpert and Maron 2000). Results from these studies suggest nonindigenous, invasive plants have high R^* s.

R^* may serve as a quantitative summary variable for species traits and biotic and abiotic processes that influence plant community dynamics (Tilman 1990). For example, Tilman and Wedin (1991) found that the outcome of succession was predicted by the relative ability of species to persist under low concentrations of plant-available N.

Monocultures of the late successional grasses little bluestem (*Schizachyrium scoparium* Nash) and big bluestem (*Andropogon gerardi* Vitman) had lower soil concentrations of N (lower R*s) than the early successional grasses rough bentgrass (*Agrostis scabra* Willd.) and quackgrass (*Agropyron repens* L.) and displaced them in pairwise competition experiments.

Past studies suggest that successional dynamics can be altered by changes in resource availability, especially N availability. In old-field succession, fertilization with N increased the abundance of annual forbs and grasses relative to perennials (Paschke et al. 2000). Other evidence indicates late successional species increase in dominance when soil N concentration is low (McLendon and Redente 1991, Tilman and Wedin 1991, Wedin and Tilman 1993, Pashke et al. 2000). "Soil impoverishment" has been proposed as a tool to promote the growth of desirable species over undesirables in restoration projects (Morgan 1994). "Soil impoverishment" is carried out by the addition of large amounts of carbon. Carbon is quickly decomposed by a flourishing soil microbial community, which in turn immobilizes available N for a period of time (McLendon and Redente 1992, Morgan 1994). Impoverishment treatments reduced nonindigenous plant growth, with no decrease in growth of indigenous prairie species (Morgan 1994). In another study, nutrient impoverishment via removal of organic matter has been found to promote the establishment of late successional grasses in pasture restoration (Ewing 2002). Bluebunch wheatgrass was found to be more competitive with spotted knapweed when grown with an annual rye nurse crop, which appeared to decrease soil N concentrations (Herron et al. 2001). I propose investigating "soil impoverishment" as a modifying factor for affecting species performance through the process of interference.

While evidence is plentiful suggesting N availability is a key process in plant community dynamics, including invasion by nonindigenous species, some research results are less clear. In one study, N increased aboveground biomass, but had no effect on displacement or persistence of certain species or on diversity in old-field succession in Michigan (Huberty et al. 1998). The effect of resource availability on successional dynamics remains an unanswered question.

Application of R^* theory in the context of successional management is a novel approach to understanding and managing nonindigenous plant invasions. R^* theory was developed in a model system using freshwater algae (Tilman 1977). The application of R^* theory to terrestrial vascular plants has been most aggressively tested in old-field succession on an N poor sand plain in Minnesota (Tilman 1984, Gleeson and Tilman 1990, Tilman and Wedin 1991, Wilson and Tilman 1991). Vigor of R^* theory in semi-arid rangeland and its incorporation into successional management is untested. Further investigation, especially in regards to successional management of nonindigenous species, is necessary.

Concluding Remarks

For ecologists and land managers, understanding the processes that determine structure and composition of plant communities is vital because when these processes are modified, either naturally or by management, change in community composition ensues. I have provided a mechanistic, process-based framework that incorporates several successional models to further understand and better manage successional dynamics, including invasions by nonindigenous species. As natural and agronomic lands become

increasingly impacted by a growing human population and its associated activities, management towards desirable, properly functioning plant communities will become ever more critical.

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