



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  
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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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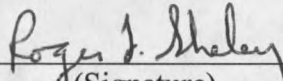
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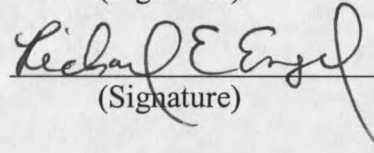
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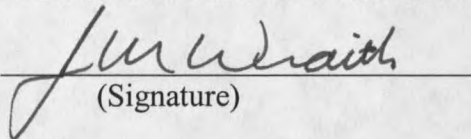
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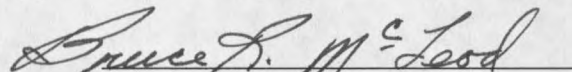
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## TABLE OF CONTENTS

1. LITERATURE REVIEW AND SYNTHESIS: TOWARDS SUCCESSIONAL MANAGEMENT OF NONINDIGENOUS, INVASIVE PLANTS IN WESTERN RANGE AND WILD LANDS .....	1
Introduction.....	1
Successional Models and Associated Ecological Processes.....	7
Facilitation .....	7
Inhibition.....	9
Tolerance.....	13
Community Assembly Theory.....	16
Fluctuating Resource Availability .....	20
State-and-Transition.....	21
Resource Ratio Hypothesis .....	23
Unified Successional Management Model .....	25
Incorporation of R* Theory into Successional Management for Nonindigenous Plant Invasions.....	27
Concluding Remarks.....	30
References Cited.....	32
2. IDENTIFICATION OF THE LIMITING RESOURCE WITHIN A SEMI-ARID PLANT ASSOCIATION .....	43
Introduction.....	43
Methods.....	45
Study Sites .....	45
Experimental Design.....	46
Sampling .....	47
Weather Data .....	47
Statistical Analysis.....	48
Results.....	48
Climate (Average Temperature and Precipitation).....	48
Total Aboveground Biomass .....	49
Total Aboveground Grass Biomass .....	49
Total Aboveground Idaho fescue Biomass .....	49
Total Forb Biomass.....	51
Total Belowground Biomass.....	52
Discussion.....	52
References Cited .....	59

## TABLE OF CONTENTS - CONTINUED

3. COMPARING THE R*S OF A NATIVE, EARLY SUCCESSIONAL FORB, A NATIVE LATE SUCCESSIONAL GRASS, AND A NONINDIGENOUS INVADER .....	63
Introduction.....	63
R* Theory of Plant Competition.....	63
Nitrogen as a Limiting Resource .....	65
Nonindigenous Plant Invasions.....	66
Methods.....	69
Model System .....	69
Procedures.....	69
Sampling .....	71
Plant and Soil Nitrogen Analysis.....	72
Statistical Analysis.....	72
Results.....	73
Plant Biomass.....	73
Results from T-tests for Monocultures .....	73
Analysis of Variance.....	74
Plant Tissue N.....	75
Soil NO <sub>3</sub> <sup>-</sup> , NH <sub>4</sub> <sup>+</sup> , and Total Plant Available N Concentration .....	77
Discussion .....	78
Response of Species in Monoculture.....	78
Response of Species in Mixtures .....	82
Plant Tissue N.....	87
Soil N Concentrations .....	88
Conclusion .....	89
References Cited .....	90
4. CONTROLLING SPECIES PERFORMANCE USING NITROGEN AND SUCROSE AMENDMENTS .....	96
Introduction.....	96
Managing Nonindigenous Plant Invasions Using Successional Management .....	97
Species Performance as Affected by Nutrient Availability .....	99
Methods.....	101
Study Sites .....	101
Experimental Design.....	102
Sampling .....	103
Statistical Analysis.....	104
Model Selection .....	104

## TABLE OF CONTENTS - CONTINUED

Regression Analysis.....	106
Soil N Concentration and Species Biomass.....	108
Results.....	109
Regression Analysis.....	109
Absolute Biomass .....	113
Soil NO <sub>3</sub> <sup>-</sup> , NH <sub>4</sub> <sup>+</sup> , and Total Plant Available N Concentration.....	114
Discussion .....	116
Competitive Dynamics.....	116
Absolute Plant Biomass and Soil N Availability.....	118
Effectiveness of Sucrose Amendments as a Method for Lowering N Availability.....	120
Conclusion and Management Implications.....	121
References Cited .....	124
5. SUMMARY AND IMPLICATIONS OF RESEARCH.....	132



## LIST OF TABLES

Table	Page
1.1. Causes of succession, contributing processes, and modifying factors.....	4
1.2. Causes of succession, contributing processes, and additional modifying factors from various successional models discussed above .....	26
2.1. Surface depth of water (cm) added per month at each site .....	46
2.2. P-values from ANOVA for main effects and interactions .....	51
3.1. Treatment codes and descriptions of species combinations .....	70
3.2. Reagents and molarities used in N-free 0.1 Hoagland's solution.....	71
3.3. P-values from ANOVA for main effects and interaction on species biomass.....	74
3.4. Effect of growth period on annual sunflower biomass .....	75
3.5. Effect of treatment on annual sunflower and spotted knapweed biomass per plants.....	76
3.6. Effect of treatment by growth period interaction on bluebunch wheatgrass biomass and percent tissue N.....	76
3.7. P-values from ANOVA for main effects and interaction on species tissue N.....	76
3.8. Effect of growth period on spotted knapweed tissue N .....	77
3.9. P-values from ANOVA for main effects and interaction on soil $\text{NO}_3^-$ , $\text{NH}_4^+$ , and total plant available N concentration .....	78
3.10. Effect of treatment by growth period interaction on soil $\text{NO}_3^-$ , $\text{NH}_4^+$ , and total plant available N concentration.....	79

## LIST OF TABLES - CONTINUED

Table	Page
4.1. Causes of succession, contributing processes, and modifying factors.....	98
4.2. Treatment application dates in 2003 .....	103
4.3. Competition models used for predicting species biomass .....	105
4.4. Adjusted coefficients of determination ( $r^2$ ) from three models for predicting bluebunch wheatgrass and spotted knapweed biomass at Red Bluff and Story Hills .....	106
4.5. Model P-values for regressions predicting bluebunch wheatgrass/spotted knapweed biomass per tiller or plant from bluebunch wheatgrass and spotted knapweed densities.....	109
4.6. Regression coefficients and adjusted coefficients of determination ( $r^2$ ) for predicting bluebunch wheatgrass biomass ( $\text{mg tiller}^{-1}$ ) at Story Hills .....	110
4.7. Calculated variance ratios and critical F-values for accepting null hypothesis .....	110
4.8. Regression coefficients and adjusted coefficients of determination ( $r^2$ ) for predicting spotted knapweed biomass ( $\text{mg plant}^{-1}$ ) at Red Bluff.....	111
4.9. Regression coefficients and adjusted coefficients of determination ( $r^2$ ) for predicting spotted knapweed biomass ( $\text{mg plant}^{-1}$ ) at Story Hills .....	112
4.10. P-values from ANOVA for spotted knapweed and bluebunch wheatgrass absolute biomass at Red Bluff and Story Hills .....	114
4.11. Treatment effect on spotted knapweed absolute biomass.....	114
4.12. P-values from ANOVA for soil $\text{NO}_3^-$ , $\text{NH}_4^+$ , and total plant available N concentration at Red Bluff and Story Hills.....	115
4.13. Effect of treatment on Red Bluff soil $\text{NO}_3^-$ , $\text{NH}_4^+$ , and total plant available N concentrations.....	115

LIST OF TABLES - CONTINUED

Table	Page
4.14. Effect of treatment on Story Hills soil $\text{NO}_3^-$ , $\text{NH}_4^+$ , and total plant available N concentrations.....	115

## LIST OF FIGURES

Figure	Page
1.1. Incorporation of state-and-transition model into the successional management framework.....	24
2.1. Monthly temperatures and precipitation at study sites .....	50
2.2. Total aboveground biomass as affected by resource treatment across sites .....	51
2.3. Total biomass of all grasses and Idaho fescue as affected by resource treatment .....	52
2.4. Limiting resource in various plant associations of western Montana along moisture and temperature gradient.....	58
3.1. Graphical representation of $R^*$ for any given species for any given essential resource .....	64
3.2. Effect of growth period on mean biomass per plant of annual sunflower, bluebunch wheatgrass, and spotted knapweed when grown in monoculture .....	74
3.3. Possible relationship between spotted knapweed, bluebunch wheatgrass, nitrogen availability, and phosphorus availability, as explained by the resource ratio hypothesis.....	86
4.1. Response surface of bluebunch wheatgrass biomass per tiller versus bluebunch wheatgrass and spotted knapweed densities at Story Hills in non-amended plots .....	110
4.2. Response surface of spotted knapweed biomass per plant versus spotted knapweed and bluebunch wheatgrass densities at Story Hills in N amended plots .....	113

## 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 NO<sub>3</sub>-N; the R\* for bluebunch wheatgrass was less than 0.6 ppm NO<sub>3</sub>-N; and spotted knapweed's R\* was between 0.4 and 0.6 ppm NO<sub>3</sub>-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 NO<sub>3</sub>-N was below its R\*. Bluebunch wheatgrass appeared unaffected by nitrogen manipulation, but soil NO<sub>3</sub>-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.<sup>a</sup>

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

<sup>a</sup>Modified 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 CO<sub>2</sub> 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).

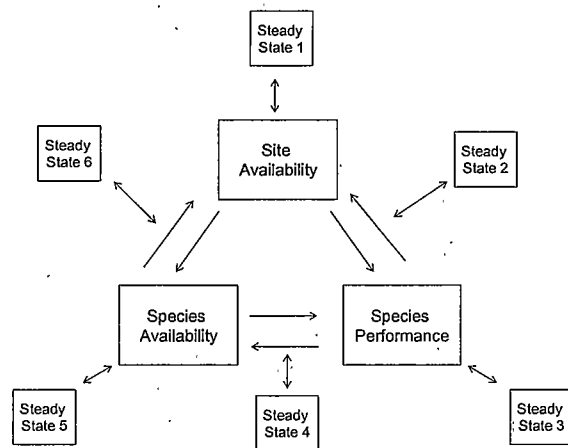


Figure 1.1. Incorporation of state-and-transition model (Westoby et al. 1989) into the successional management framework (Pickett et al. 1987). Steady states are affected by the three general causes of succession. The three general causes of succession may affect transitions from one steady state to 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.<sup>a</sup>

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, <b>increased atmospheric CO<sub>2</sub>, eutrophication, many non-equilibrium states</b>
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, <b>vector, sequence, rate, frequency</b>  Land use, disturbance interval, species life history, <b>tilling, reseeding, precipitation patterns, seed coatings</b>
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, <b>hydraulic lift, landscape heterogeneity, resource ratios</b>  Germination requirements, assimilation rates, growth rates, genetic differentiation, <b>changes between native and introduced ranges</b> Allocation, reproduction timing and degree, <b>plasticity</b>
	<u>Stress</u> <i>Tolerance</i>	Climate, site-history, prior occupants, herbivory, natural enemies, <b>plasticity</b>
	<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, <b>nurse crops, mycorrhizae, multiple classes of grazing, R*, soil impoverishment</b>

<sup>a</sup>Modified 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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## IDENTIFICATION OF THE LIMITING RESOURCE WITHIN A SEMI-ARID PLANT ASSOCIATION

### Introduction

Succession is affected by abiotic factors, such as soil and climate, as well as biotic factors such as interactions with competitors, mutualists, herbivores, and pathogens (Crawley 1997). Understanding processes responsible for succession provides insight into specific interactions, like competition, among species or groups of species. These interactions may affect species presence/absence in a community, spatial pattern of species (clumped versus random), water and nutrient status of soils and plants, and niche differentiation (Fowler 1986).

Competition for the essential resources of water, nutrients, and light is an important process structuring plant communities (Schoener 1983, Tilman 1990, Wilson and Tilman 1991). Competition for limited resources has been used to explain successional dynamics (MacArthur 1972, Tilman 1984, Huston and Smith 1987, McLendon and Redente 1991, Tilman and Wedin 1991a, 1991b, Huston and DeAngelis 1994, Davis et al. 2000). Competition for resources was identified as a factor affecting plant performance in the successional management framework (Pickett et al. 1987). The resource base at the outset of succession and its change over time, can influence the outcome and rate of succession (Pickett et al. 1987). Knowledge of resource base, including possible resource limitation, may be useful for predicting successional outcomes and forecasting the impact of management on those outcomes (Sheley and Krueger-Mangold 2003).



Nitrogen (N) is the limiting plant resource in most terrestrial systems (Vitousek and Howarth 1991, Hopkins 1995). Studies have found N to increase plant community biomass more than any other resource addition (Owensby et al. 1972, Bobbink 1991, McLendon and Redente 1991, Tilman and Wedin 1991a, 1991b, Paschke et al. 2000). The Idaho fescue (*Festuca idahoensis* Elmer)/bluebunch wheatgrass (*Agropyron spicatum* Pursh) plant association is widespread throughout the Pacific Northwest and typical of rangeland in western Montana (Mueggler and Stewart 1980). In other plant associations typical of western grasslands, research has indicated that water, N, or phosphorus (P) limits plant growth (Lauenroth et al. 1978, LeJeune and Seastedt 2001, Svejcar and Sheley 2001).

The propensity of studies within the Idaho fescue/bluebunch wheatgrass plant association that involve nonindigenous, invasive species suggests it is at high risk of invasion (Olson et al. 1997, Jacobs and Sheley 1999, Jacobs et al. 2000, Kedzie-Webb et al. 2002). Therefore, it is important to identify the major limiting resource within the Idaho fescue/bluebunch wheatgrass plant association. The occurrence of a specific resource limitation can be incorporated into the successional management framework (Pickett et al. 1987). Identification of the primary limiting resource may be useful for understanding the underlying patterns of invasion and for managing nonindigenous plant invasions (Sheley et al. 1996).

My objective was to determine the resource most limiting to plant growth within an Idaho fescue/bluebunch wheatgrass plant association. I hypothesized that the addition of N would increase plant biomass more than additions of water, P, potassium (K), or

sulfur (S). I also hypothesized that a 50% decrease in the amount of ambient sunlight would have no effect on plant growth. Based on prior research and research from others who have worked in more mesic grasslands (Tilman and Wedin 1991a, 1991b), I believed the Idaho fescue/bluebunch wheatgrass plant association occurs where water is adequate for survival of semi-arid, native species and N alone limits plant growth.

## Methods

### Study Sites

The study was conducted on two sites in western Montana. Site 1 was located at Redbluff Research Ranch about 2 km east of Norris, Montana (45° 35' N, 111° 39' W) (hereafter referred to as Redbluff). Elevation is 1505 meters, with 305 mm of annual precipitation. Soils are a fine-loamy, mixed, frigid Calcic Argiustoll. Frequently encountered species at Redbluff included Idaho fescue, bluebunch wheatgrass, needle-and-thread grass (*Stipa comata* Trin. and Rupr.), red threeawn (*Aristida longiseta* Steud.), hairy goldenaster (*Chrysopsis villosa* (Pursh) Nutt.), dotted gayfeather (*Liatrus punctata* Hook), salsify (*Tragopogon dubius* Scop.), and vetch (*Vicia americana* Muhl.).

Site 2 was located in the Story Hills about 5 km northeast of Bozeman, Montana (45° 36' N, 111° 34' W) (hereafter referred to as Story Hills). Elevation at Story Hills is 1478 meters, with 432 mm annual precipitation. Soils are a clayey-skeletal, mixed Typic Argiboroll. Common plant species at Story Hills included Idaho fescue, bluebunch wheatgrass, western wheatgrass (*Agropyron smithii* Rydb.), prairie junegrass (*Koelaria pyramidata* (Lam.) Beauv.), yarrow (*Achillea millefolium* L.), false dandelion (*Agoseris*

*glauca* Pursh), yellow alyssum (*Alyssum alyssoides* L.), cudweed sagewort (*Artemisia ludoviciana* Nutt.), biscuitroot (*Lomatium ambiguum* Nutt.), lupine (*Lupinus* spp.), Hood's phlox (*Phlox hoodii* Richardson), longleaf phlox (*Phlox longifolia* Nutt.), and salsify. Both sites were considered late-seral plant communities (Mueggler and Stewart 1980).

### Experimental Design

In spring (Redbluff) and fall (Story Hills) 2000, I applied six essential plant resources to 2.5 x 5.0 m plots. Treatments included the addition or reduction of essential plant resources: 1) water added at a rate of about 12% of the 50 year average for May, June, and July (plus ambient precipitation) (Table 2.1), 2) light reduction of 50%, 3) 112 kg N ha<sup>-1</sup>, 4) 60 kg P ha<sup>-1</sup>, 5) 112 kg K ha<sup>-1</sup>, and 6) 112 kg S ha<sup>-1</sup>. I also included an untreated control. In addition to these main treatments, I addressed potential interactions of water with other essential resources by applying water in combination with all resources except for the untreated control (double water addition, light reduction plus water, N plus water, P plus water, K plus water, and S plus water).

Table 2.1. Surface depth of water (mm) added per month at each site.

Site	May	June	July	Total
Red Bluff	7	8	2	17
Story Hills	9	9	2	20

Water was applied every other week during May, June, and July using backpack sprayers. Light reduction was accomplished during May, June, and July using shade

tents with mesh that excluded 50% ambient sunlight. Nutrients were broadcast as granular forms of ammonium nitrate ( $\text{NH}_4\text{NO}_3$ ), potassium chloride (KCl), magnesium sulfate ( $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ ), and triple superphosphate ( $\text{Ca}(\text{H}_2\text{PO}_4) \cdot \text{H}_2\text{O}$ ) in a single spring (Redbluff) or fall (Story Hills) application. The complete factorial was arranged in a randomized block design and replicated four times at each site.

### Sampling

Aboveground biomass by species was sampled during peak standing crop 2000 (Redbluff) and 2001 (Story Hills). Aboveground biomass was determined by clipping plants in three 20 x 50 cm plot frames placed randomly on the ground within each plot. Clipped samples were oven-dried at 60° C for 48 hours. Below ground biomass was sampled at Story Hills in 2001 after aboveground biomass was harvested. Redbluff soils were too rocky for sampling belowground biomass. Belowground biomass was sampled by collecting a composite of three soil cores (164.5 cm<sup>3</sup>) per plot to a 70 mm depth. Roots were carefully washed to remove soil, oven-dried for 48 hours at 60° C, and weighed.

### Weather Data

Monthly average maximum and minimum temperatures and precipitation data from 1892-2001 (Redbluff) and 1907-2001 (Story Hills) were compiled from the Western Regional Climate Center (NCDC 2002). Observations were taken from stations located at Norris, Montana, (Redbluff) and Montana State University, Bozeman, Montana, (Story Hills).

### Statistical Analysis

Data were analyzed for main effects and interactions using generalized linear model analysis of variance (SPSS, Inc. 1999). Transformations of aboveground biomass were performed to normalize the data and homogenize variances. Data from both sites were pooled because the two sites did not differ in their response to treatments (data not shown). Mean separations were accomplished using Tukey's multiple comparison procedure at  $\alpha=0.05$  significance level (Neter et al. 1996). Independent sample T-tests at  $\alpha=0.05$  significance level were used to compare means where two factors were present (i.e. site and water addition) (SPSS, Inc. 1999). P-values are reported for transformed data (Table 2.2). For ease of interpretation, means of non-transformed data are presented, with means separated by Tukey's poc hoc tests performed on transformed data (Neter et al. 1996).

### Results

#### Climate (Average Temperature and Precipitation)

Average monthly temperatures for Redbluff and Story Hills were within the long-term average (Figure 2.1a and 2.1b). Average monthly precipitation for 2000 and 2001 was typically similar to or less than the long-term average. Exceptions to this included June 2000 and October 2001 at Redbluff and October 2000 and June 2001 at Story Hills, when average monthly precipitation exceeded the historical average (Figure 2.1c and 2.1d).

### Total Aboveground Biomass

Total aboveground biomass was affected by the main effects of site, water, and resource treatments (Table 2.2). Biomass was greater at Story Hills than Redbluff ( $186.4 \text{ g m}^{-2}$  vs.  $85.7 \text{ g m}^{-2}$ ;  $P < 0.01$ ). Water addition decreased total aboveground biomass from  $142 \text{ g m}^{-2}$  (no water) to  $130 \text{ g m}^{-2}$  (water addition) (Figure 2.2). Of all resource treatments, addition of N yielded the highest total aboveground biomass ( $184.5 \text{ g m}^{-2}$ ). This was higher than any other resource treatment, but not the control ( $138.8 \text{ g m}^{-2}$ ) (Figure 2.2).

### Total Aboveground Grass Biomass

The main effects of water and resource treatments affected total aboveground grass biomass (Table 2.2). Grass biomass was higher in plots that did not receive water ( $75.4 \text{ g m}^{-2}$ ) than in plots where water was added ( $59.5 \text{ g m}^{-2}$ ) ( $P < 0.01$ ). Nitrogen produced the highest aboveground grass biomass, which was about 1.8 times greater than that of the control (Figure 2.2). No other treatment was significantly different from the control.

### Total Aboveground Idaho fescue Biomass

Idaho fescue was analyzed alone because of its widespread occurrence at both sites. The results were similar to total aboveground grass biomass results (Table 2.2). The main effect of water decreased Idaho fescue biomass by 20% compared to the control ( $56.3 \text{ g m}^{-2}$  versus  $45.0 \text{ g m}^{-2}$ , respectively). Addition of N increased Idaho fescue biomass over that of the control and higher than that of any other treatment (Figure 2.3).

Idaho fescue biomass was 2.2 times greater in plots with N addition when compared to the control.

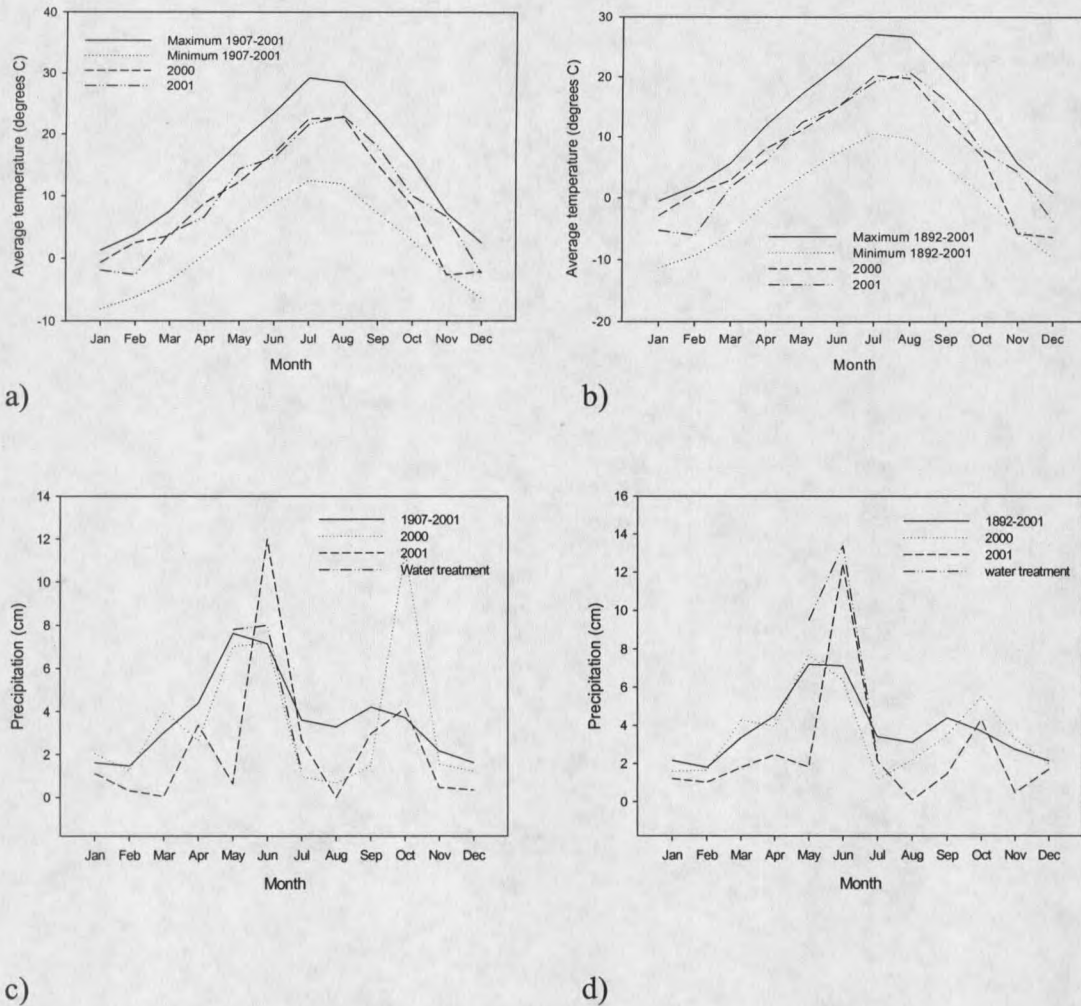


Figure 2.1. Monthly temperatures and precipitation at study sites. Long-term monthly average maximum/minimum temperatures and average monthly temperature for 2000 and 2001 at a) Redbluff and b) Story Hills. Long-term average monthly precipitation, average monthly precipitation for 2000 and 2001, and precipitation plus water treatment for c) Redbluff and d) Story Hills.

### Total Forb Biomass

Total forb biomass was only affected by site (Table 2.2). Redbluff forb biomass was substantially lower than Story Hills forb biomass ( $12.4 \text{ g m}^{-2}$  versus  $81.2 \text{ g m}^{-2}$ ).

Table 2.2. P-values from ANOVA for main effects and interactions (where applicable).

Source	Df	Total	Grass	Fescue	Forb	Belowground
Rep	3	0.08	0.10	0.59	0.08	0.55
Site (s)	1	<0.01	0.83	0.69	<0.01	n.a.
Water (w)	1	0.04	<0.01	0.02	0.80	0.93
Resource (r)	5	<0.01	<0.01	<.01	0.62	0.91
w * r	5	0.64	0.62	0.34	n.a.	0.22
s * w * r	5	0.41	n.a.	n.a.	n.a.	n.a.

Total = total aboveground biomass, Grass = total aboveground grass biomass, Fescue = total Idaho fescue biomass, Forb = total aboveground forb biomass, Belowground = total belowground biomass, n.a. = not applicable.

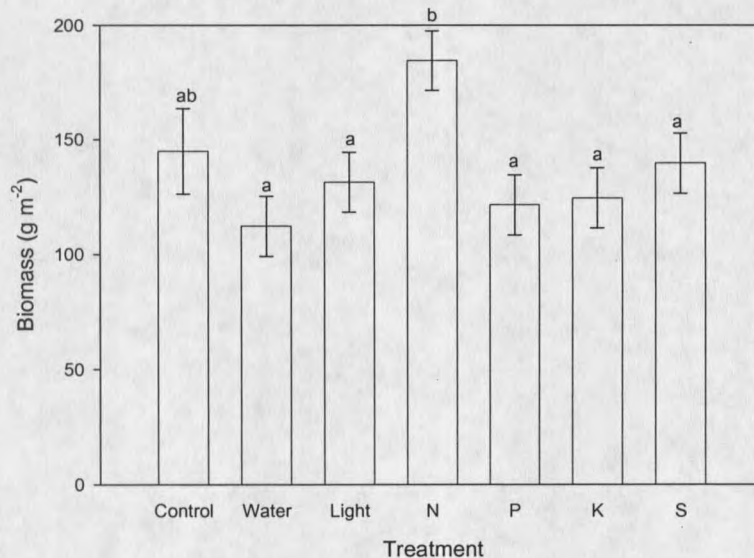


Figure 2.2. Total aboveground biomass as affected by resource treatment across sites (log<sub>10</sub> transformation). Actual means are presented. Letters separate means that are significantly different. Error bars show mean  $\pm$  1.0 SE.



### Total Belowground Biomass

Belowground biomass (at Story Hills only) was not affected by any treatment (Table 2.2). Values ranged from 0.005 to 0.061 g biomass cm<sup>-3</sup> soil (mean = 0.021 g biomass cm<sup>-3</sup> soil).

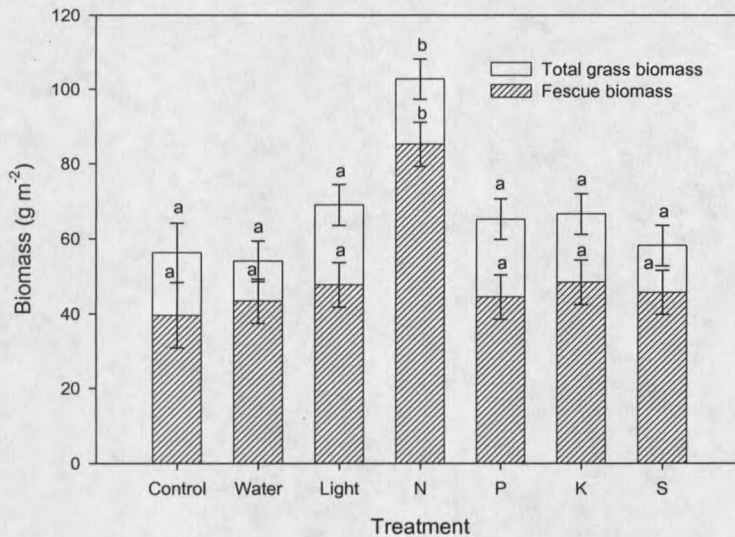


Figure 2.3. Total biomass of all grasses and Idaho fescue as affected by resource treatment (square root transformation). Actual means are presented. Letters separate means within plant groups that are significantly different. Error bars show mean  $\pm$  1.0 SE.

### Discussion

Results indicated that N is the most limiting resource for the dominant functional group in the Idaho fescue/bluebunch wheatgrass plant association at the two study sites. This result is consistent with the hypothesis that N would increase plant biomass more than additions of P, K, or S. It is also consistent with other researchers who found N to be the primary limiting factor controlling plant growth (Owensby et al. 1972, Bobbink

1991, McLendon and Redente 1991, Tilman and Wedin 1991a, 1991b, Paschke et al. 2000).

Nitrogen is often a limiting factor of plant growth because plants demand relatively large amounts for incorporation into amino acids, proteins, and other nitrogenous organic molecules, such as chlorophyll and hormones (Hopkins 1995). Other major nutrients (P, K, S, Ca, Mg, Mn) originate from soil minerals and can accumulate to a greater extent on soil exchange sites. Nitrogen, on the other hand, originates from the atmosphere and rarely accumulates on soil exchange sites (Fenn et al. 1998). Nitrogen's high mobility in the soil contributes to its scarcity for plant uptake (Vitousek and Howarth 1991). Nitrogen limitation can be exacerbated by soil microbes that compete with plants for inorganic soil nitrogen, especially ammonium ( $\text{NH}_4^+$ ) (Jackson et al. 1989).

Although N increased total aboveground biomass more than any other resource addition, the increase was not significantly greater than the control. Typically, soils of late successional plant communities, such as those of the sites used in this study, have low nutrient concentrations (McLendon and Redente 1991, Dukes and Mooney 1999, Paschke et al. 2000). Late successional native species with low nutrient supply often show a limited response to increase in soil nutrients as a consequence of adaptations which promote conservative nutrient use, loss, and uptake (Chapin 1991, Chapin et al. 1993).

Effects of N addition on biomass were most pronounced in native grasses, especially Idaho fescue. In contrast, native forbs did not respond to any resource

addition. Results are consistent with studies where N amendments increased grass biomass without increasing the biomass of forbs or shrubs (Shaver and Chapin 1980, Heil and Diemont 1983, Maron and Jefferies 1999). Growth forms may differ in their nutrient requirement for maximum growth. For example, the tissue calcium concentration at which 90% of the maximum yield is achieved is about twice as high for dicots as for monocots (Loneragan 1968, Loneragan and Snowball 1969, as cited in Marschner and Romheld 1983). Response to increased nutrients in plants from low nutrient habitats may be more strongly related to nutrient uptake rates, root distribution patterns, or seasonality of nutrient demands in relation to availability (Shaver and Chapin 1980). The precise physiological mechanisms for such discrepancies are unknown (Lambers et al. 1998).

Although the sites were characterized as Idaho fescue/bluebunch wheatgrass plant associations (Mueggler and Stewart 1980), the majority of biomass in this study was that of Idaho fescue. When analyzed separately, Idaho fescue responded strongly to N additions. When Idaho fescue was excluded from the analysis, resource treatment effects on grass biomass were non-significant. A study in the tall-grass prairies of Kansas showed that net photosynthesis and stomatal conductance of co-dominant big bluestem (*Andropogon gerardii* Vitman) and Indiangrass (*Sorghastrum nutans* (L.) Nash) differed in response to water and N additions (Silletti and Knapp 2001). Combined, these studies suggest that using competition for limiting resources as a modifying factor of succession may be most effective when constructed specifically on the response of the dominant species. The greater the degree to which a species contributes to overall plant community

biomass, the higher the likelihood of meeting management goals through incorporating competition into successional management.

The water treatment did not act independently nor did it interact with N to increase plant community biomass. Water did not increase plant community biomass, even though yearly precipitation for 2000 and 2001 were 77% and 74% of average, respectively (NCDC 2002). I suspected that during drought water availability would be more important than N availability for structuring community dynamics. However, similar outcomes occurred in Colorado where N was most influential in plant community dynamics even in dry years (74% and 77% of average precipitation) (McLendon and Redente 1991).

Owensby et al. (1972) reported similar results when they added water and N separately and in combination to upland bluestem range in Kansas. Even in a drought year, water and water plus N additions failed to increase above ground biomass. They theorized that aboveground biomass production may not be directly associated with water availability for a given growing season. Erratic aboveground biomass production as a response to variable precipitation may result in variable accumulation of N at different stages of the N cycle. For example, several years of high precipitation may cause an increase in biomass and high sequestration of N in nonavailable organic forms. In contrast, a series of years with below normal precipitation could result in an accumulation of available N in the soil. Thus, production may be influenced by previous years' precipitation (Owensby et al. 1972), and not increased by water addition in a given growing season.

Surprisingly, the main effect of water addition decreased total aboveground biomass, native grass biomass, and Idaho fescue biomass. I admit that a reduction in biomass with water addition is rather difficult to explain. The Idaho fescue/bluebunch wheatgrass plant association is ecologically adapted for survival under a given precipitation regime (35-50 cm year<sup>-1</sup>) (Mueggler and Stewart 1980). Both sites were towards the upper end of the precipitation regime characteristic of the Idaho fescue/bluebunch wheatgrass plant association (about 45 cm yr<sup>-1</sup>); therefore, I speculate that adding water may have elevated water availability beyond the ecological amplitude of the species present at the site and detrimentally affected aboveground biomass. Even though 2000 and 2001 yearly precipitation totals were 77% and 74% of average, respectively, the water treatment increased total precipitation for May, June, and July above the long-term average by about 70% at Red Bluff and 80% at Story Hills. Water not used by the plant community for biomass accumulation may have leached available N beyond the rooting zone of plants, thus limiting N supply and decreasing biomass (Pierzynski et al. 2000). This explanation is further supported by the trend of increased plant biomass when N was added but not when N and water were applied together.

Some evidence suggests P may limit plant growth in grasslands (LeJeune and Seastedt 2001). Low concentration (100-3,000 mg P kg<sup>-1</sup>) and water solubility (<0.01 mg P L<sup>-1</sup>) of P in soil make it a potential nutrient limiting factor for plant growth in many systems (Sharpley 2000). I did not find P, or any other resource treatment, to increase total plant biomass over that of the control. This suggests that perhaps in low-resource environments, competition may not play as large a role in plant dynamics within this

plant association. Instead, those species that are tolerant of stressful conditions may persist and dominate (Grime 1979).

Based on my findings and the results of other research, I have conceptualized a gradient of plant associations typical of western Montana, progressing from warm and dry to cool and moist climatic conditions (Figure 2.4). On the warmer, drier portion of the gradient, water, N, and possibly P appear to limit plant growth (Lauenroth et al. 1978, LeJeune and Seastedt 2001, Svejcar and Sheley 2001). Along the cool, moist section of the gradient, water is not limited and N appears to be the major limiting resource (Sollins et al. 1980, Franklin and Halpern 2000, Garrison et al. 2000). The Idaho fescue/bluebunch wheatgrass plant association occurs within the mesic portion of the gradient, but where plant associations are still dominated by grasses. Above this point, water becomes more plentiful and trees and shrubs become ubiquitous in plant communities. I believe this plant association occurs along the gradient where water availability is ample and N alone is limiting plant growth.

Competition for N influences plant community dynamics in grasslands more mesic than those of western Montana (Tilman and Wedin 1991b). It is often assumed that water, not N, is the limiting resource in semi-arid systems. My results suggest that competition for N, especially among grasses, may be a critical factor even in semi-arid grasslands. The information obtained from this research is a crucial initial step for developing successional management strategies to control species performance within an Idaho fescue/bluebunch wheatgrass plant association.

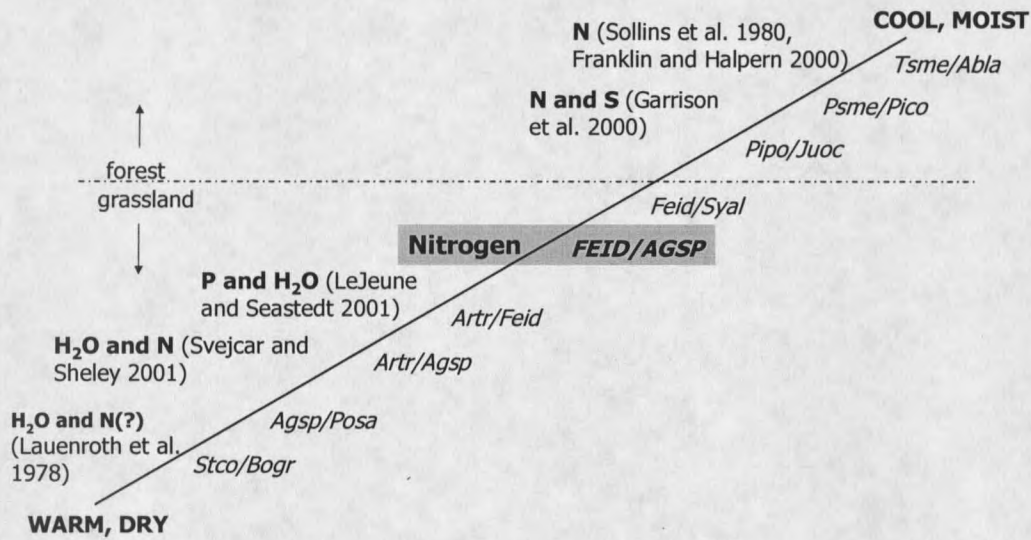


Figure 2.4. Limiting resource in various plant associations of western Montana along a moisture and temperature gradient. Plant associations are listed to the right of the diagonal line. Research results identifying limiting resources are listed to the left of the diagonal line.

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## COMPARING THE R\*S OF A NATIVE, EARLY SUCCESSIONAL FORB, A NATIVE, LATE SUCCESSIONAL GRASS, AND A NONINDIGENOUS INVADER

### Introduction

Competition for essential resources, such as nutrients and light, is an important force structuring plant communities. Competition has been used to create models for explaining plant community dynamics (Grime 1979, Vance 1984, Huston and DeAngelis 1994). To develop principles for management and accurately forecast the outcomes of plant community dynamics where competition is a primary, influential factor, models must be mechanistic rather than phenomenological in nature (Silander and Pacala 1990, Tilman 1990).

### R\* Theory of Plant Competition

A mechanistic model of resource competition was developed by Tilman (1981, 1982, 1984, 1988), who postulated that the outcome of competition could be predicted by a species'  $R^*$ . The  $R^*$  is the amount of a resource that a species requires to maintain a birth rate equal to its mortality rate, hence a population growth rate of zero. Any resource level higher than  $R^*$  leads to an increase in population size; any value lower than  $R^*$  leads to a decrease in population size (Figure 3.1).  $R^*$  theory of competition predicts that a population with a lower  $R^*$  will competitively displace a population with a higher  $R^*$  under equilibrium conditions (Tilman 1982, Tilman 1988).

$R^*$  for a resource in limited supply is determined by a model based on the Monod (1950) equation, which is a good approximation of the growth function of many

populations. Under equilibrium conditions,  $R^* = km / (r - m)$ , where  $k$  equals the half saturation constant, or the resource availability at which growth reaches half of the maximal growth rate;  $m$  equals the mortality rate; and  $r$  equals the maximum growth rate (Tilman 1982).  $R^*$ s for selected species have been determined by growing them in monoculture (Tilman and Wedin 1991a and 1991b). When the population reaches equilibrium, soil is analyzed for the limiting resource, usually soil nitrogen (N) content. The resulting soil resource concentration is considered the species'  $R^*$  for the plant resource of interest.

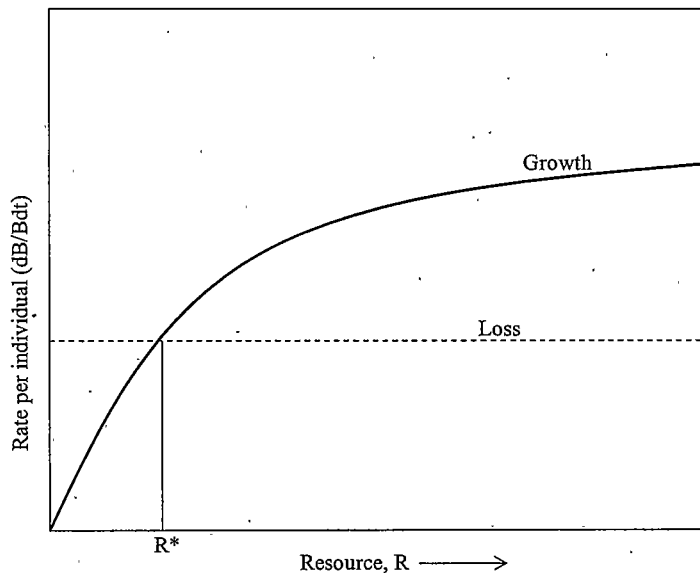


Figure 3.1. Graphical representation of  $R^*$  for any given species for any given essential resource. Adapted from Tilman (1982).

According to  $R^*$  theory, late successional species have lower  $R^*$ s than early successional species because they dominate as secondary succession progresses and resource availability decreases (Tilman 1986, Tilman and Wedin 1991b). Morphological and physiological characteristics of late successional species, such as high allocation to

root mass, 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 1991a).  $R^*$  may serve as a summary variable for species' traits and abiotic conditions that influence plant community dynamics. For example, Tilman and Wedin (1991b) 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 nitrate ( $\text{NO}_3^-$ ) (i.e. lower  $R^*$ s) than the early successional grasses bentgrass (*Agrostis scabra* Willd.) and quackgrass (*Agropyron repens* L.) and displaced them in pairwise competition experiments (Tilman and Wedin 1991b).

#### Nitrogen as a Limiting Resource

Nitrogen is the most limiting resource in many plant communities (Tilman 1984, McLendon and Redente 1991, Fenn et al. 1998, Franklin and Halpern 2000). In a companion study, N increased aboveground plant biomass of the dominant functional group more than any other resource addition in an Idaho fescue (*Festuca idahoensis* Elmer)/bluebunch wheatgrass (*Agropyron spicatum* Pursh) plant association (Krueger-Mangold et al. 2004). Nitrogen often limits plant growth because plants demand relatively large amounts for incorporation into amino acids, proteins, and other nitrogenous organic molecules, such as chlorophyll and hormones (Hopkins 1995). Other major nutrients (P, K, S, Ca, Mg, Mn) originate from soil minerals and organics

and can accumulate to a greater extent on soil exchange sites; N, on the other hand, primarily originates from the atmosphere, is linked to organic matter, and rarely accumulates on soil exchange sites (Fenn et al. 1998). Nitrogen's high mobility in the soil contributes to its scarcity for plant uptake (Vitousek and Howarth 1991). Nitrogen limitation can be exacerbated by soil microbes that significantly compete with plants for inorganic soil N, especially ammonium ( $\text{NH}_4^+$ ) (Jackson et al. 1989).

Manipulation of N availability may affect plant community dynamics. For example, additions of N inhibited succession from the invasive, annual cheatgrass (*Bromus tectorum* L.) to indigenous native perennial species in a sagebrush steppe site in northwestern Colorado (McLendon and Redente 1991). Conversely, applications of sucrose, which enhanced microbial activity and lowered N availability, accelerated succession toward native, late successional species. In another study, the addition of N increased annual forbs and grasses relative to perennial species, while reduction of N increased the relative abundance of perennials (Paschke et al. 2000). During prairie restoration in Minnesota, carbon (C) additions decreased weed biomass by 54% and resulted in a sevenfold increase in prairie species biomass (Blumenthal et al. 2003).

### Nonindigenous Plant Invasions

Nonindigenous plant invasions continue to pose a significant threat to the integrity of semi-arid rangelands. In the United States, invasive plants currently infest over 40 million hectares (NISC 2001) and continue to spread at nearly 14% per year (Westbrooks 1998). The organization, structure, and function of plant communities are fundamentally changed when invasive species become established (Lacey et al. 1989,

Whisenant 1990, D'Antonio and Vitousek 1992, Gerlach and Rice 1996, Olson 1999, LeJeune and Seastedt 2001).

The effects of N availability on invasion by nonindigenous species are likely to become more important as N inputs by humans increase (Vitousek et al. 1997, Dukes and Mooney 1999, Hooper and Johnson 1999). Plant ecologists have found that plant communities remain in early successional status when N availability is high (McLendon and Redente 1991, Tilman and Wedin 1991b, Redente et al. 1992, Paschke et al. 2000). Increasing N availability may favor early successional, fast-growing, high N-demanding species like *Centaurea* species (LeJeune and Seastedt 2001). Therefore, the rate of invasion by nonindigenous species may increase as global N availability increases from human inputs (Vitousek et al. 1997, Alpert and Maron 2000). Once established, nonnative species may perpetuate high N availability through positive feedback mechanisms such as less C allocation to belowground structure, reduced C storage in soil, reduced root and litter ratios of C to N, and increased N mineralization and leaching (LeJeune and Seastedt 2001). Management of nonindigenous, invasive plants through manipulations of N availability may become necessary as human activities increasingly impact the environment.

A firm understanding of the mechanisms that direct changes in plant community composition is required for successful management of plant invasions (Allen 1988, Louda et al. 1990, Sheley and Krueger-Mangold 2003). Mechanistic models have allowed the development and implementation of strategies with predictable outcomes (Anderson 2003, Rinella 2003).  $R^*$  theory may provide insight into mechanisms of



competition and resource availability responsible for successional changes.  $R^*$  theory was developed in a model system using freshwater algae (Tilman 1981). 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 1991a and 199b, Wilson and Tilman 1991). Applicability and usefulness of  $R^*$  theory in semi-arid rangeland is untested. Furthermore, application of  $R^*$  theory is a novel approach to managing nonnative plant invasions and predicting outcomes of invasive plant management.

The objective of this research was to attempt to quantify the  $R^*$  for N for the nonindigenous invader spotted knapweed (*Centaurea maculosa* Lam.) and two native species, annual sunflower (*Helianthus annuus* L.) and bluebunch wheatgrass. I hypothesized that the early successional species, annual sunflower, would have the highest  $R^*$  for N; the late successional species, bluebunch wheatgrass, would have the lowest  $R^*$ ; and the nonindigenous invader, spotted knapweed, would have an  $R^*$  lower than that of annual sunflower, but greater than bluebunch wheatgrass. I hypothesized  $R^*$ s from monocultures could successfully predict the outcome of competition in two- and three-species mixtures. Therefore, as N availability decreased, the biomass of a species with a higher  $R^*$  would decrease below that of the monoculture when grown in polyculture with a species that had a lower  $R^*$ .

## Methods

### Model System

Spotted knapweed was chosen as a representative nonindigenous, invasive species. Spotted knapweed is a deep-rooted, perennial forb native to Eurasia. Historically, it has spread rapidly throughout the northwestern United States. In the 1960s, it was documented in 20 counties in the Pacific Northwest and by 1980 it had spread to 48 counties. By 1999 it was found in 326 counties in the Northwest, including every county in Washington, Idaho, Montana, and Wyoming (Sheley et al. 1999). Annual sunflower and bluebunch wheatgrass were chosen as representative early and late successional native species, respectively. All species occur in the Idaho fescue/bluebunch wheatgrass plant association widespread throughout western Montana (Mueggler and Stewart 1980).

### Procedures

Field soil from the surface (15 cm) was collected from Montana State University (MSU) Redbluff Research Ranch about 2 km east of Norris, Montana (45° 35' N, 111° 39' W). Soil was characterized as a fine-loamy, mixed, frigid Calcic Argiustoll. Field soil was mixed 3:1 with sterilized sand from the MSU Plant Growth Center to dilute N concentration and aid in infiltration and permeability during watering. The amended soil was placed into 15 cm x 15 cm x 38 cm pots. Annual sunflower, bluebunch wheatgrass, and spotted knapweed were seeded into pots in the greenhouse in monoculture, two- and three-species treatments (Table 3.1) beginning April 2002. The monoculture contained

six plants of one species; the two-species treatments contained three plants of each species; and the three-species treatments contained two plants of each species. Seeds were covered with 2 mm of soil and misted daily until emergence. Upon emergence, plants were randomly thinned to six plants per pot and watered lightly every other day. Thirty-six days after thinning, pots were watered to capacity weekly with 1240 ml water followed by 300 ml of N-free 0.1 modified Hoagland's solution (Table 3.2). In addition to monocultures and mixtures, one pot in each replication was plant-free and received N-free Hoagland's solution; one pot in each replication contained all three species and was watered with 0.1 modified Hoagland's solution containing N to provide controls. Growth periods (GP) averaged about ten weeks and ran from 06/07/02 through 08/14/02 (GP1), 11/13/02 through 02/14/03 (GP2), and 05/29/03 through 07/30/03 (GP3). Each monoculture and species mixture was replicated six times. Pots were placed in a greenhouse in a randomized block design. Photoperiod in the greenhouse was extended to 16-hours per day using 1000 watt metal halide lamps. Temperatures were kept at 22°C day and 18°C night.

Table 3.1. Treatment codes and descriptions of species combinations.

Treatment Code	Description
A	Annual sunflower monoculture
B	Bluebunch wheatgrass monoculture
S	Spotted knapweed monoculture
AB	Annual sunflower/bluebunch wheatgrass mixture
AS	Annual sunflower/spotted knapweed mixture
BS	Bluebunch wheatgrass/spotted knapweed mixture
All	Annual sunflower/bluebunch wheatgrass/spotted knapweed mixture
All +N	Annual sunflower/bluebunch wheatgrass/spotted knapweed mixture watered with N-rich Hoagland's solution
No plants	Pot with soil only and no plants

Table 3.2. Reagents and molarities used in N-free 0.1 Hoagland's solution.

Salt	Molarity
CaCl <sub>2</sub> *	1.0 M
K <sub>2</sub> SO <sub>4</sub> *	0.5 M
KH <sub>2</sub> PO <sub>4</sub>	0.5 M
MgSO <sub>4</sub>	0.5M
Fe-HEDTA	100 mM
MnSO <sub>4</sub>	60 mM
ZnSO <sub>4</sub>	20 mM
H <sub>3</sub> BO <sub>3</sub>	20 mM
CuSO <sub>4</sub>	20 mM
NaMoO <sub>4</sub>	0.6 mM

\*N-rich solution substituted Ca(NO<sub>3</sub>)<sub>2</sub> in place of CaCl<sub>2</sub> (same molarity), KNO<sub>3</sub> in place of K<sub>2</sub>SO<sub>4</sub> (same molarity) and added FeNO<sub>3</sub> (50 mM).

Between growth periods, the pots were placed in a vernalization chamber.

Annual sunflower was germinated during the period the pots were in the vernalization chamber and replanted at the beginning of each growth period. Thus, I was comparing progressively more mature bluebunch wheatgrass and spotted knapweed plants to annual sunflower that was the same age over each growth period.

### Sampling

Aboveground biomass was harvested by species from each pot at the end of each growth period. Biomass was placed in paper bags, dried (48 hr, 60 degrees C), and weighed. Soil was sampled by compositing three 1.2 x 18 cm cores from each pot, also at the end of each growth period. Sampling belowground biomass was not possible because it would destroy any root mass between successive growth periods.

I did not sample seed production. Because I used an annual and an invasive forb, both of which can only reproduce through seeds, and a perennial bunchgrass that also

reproduces vegetatively, seed production would not be an accurate measure of the ability of the species to persist.

#### Plant and Soil Nitrogen Analysis

To determine whether plant tissue N changes through time, plant tissue was ground to pass a 1 mm sieve and chemically analyzed for total N using a Leco CNS-2000 dry combustion Analyzer (Leco Corporation, St. Joseph, Michigan). Soil samples collected from the pots were air-dried and crushed to pass a 2 mm sieve prior to chemical analyses. Inorganic soil N ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) was determined from 1 M KCl extracts of soils (5 g soil:50 ml extractant). Aliquots of filtered extracts were analyzed for nitrate-N ( $\text{NO}_3\text{-N}$ ) and ammonium-N ( $\text{NH}_4\text{-N}$ ) using Cd reduction and salicylate colorimetric methods, respectively (Mulvaney 1996).

#### Statistical Analysis

Analysis of variance (ANOVA) (SAS Institute Inc. 1990) was used to determine the effects of replication, treatment (monoculture, 2- and 3-species mixtures, Table 3.1) and GP on individual biomass per plant, plant tissue N, and soil  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$  and total plant available N concentrations. The model used for analysis was a split-plot in time with replication and treatment as the whole plots and GP as the split-plot. Whole plot effects were tested using replication x treatment as the error term and split-plot effects were tested using the residual as the error term. When a significant model P-value ( $P \leq 0.05$ ) was calculated, mean separations for significant main effects and interactions were achieved using Fisher's protected least significant difference ( $\text{LSD}_{\alpha=0.05}$ )

comparisons (Peterson 1985). In addition to ANOVA, each species mean biomass per plant in the monoculture treatment was compared between growth periods using independent samples t-tests (SAS Institute Inc. 1990). In cases where data failed to meet the assumptions of normality and equality of variances based on diagnostic plots, data were square-root or log10 transformed as indicated in the Tables and Figures presented.

## Results

### Plant Biomass

Results from T-tests for Monocultures. Annual sunflower biomass decreased by about 80% from GP1 to GP2 and GP3, and remained the same between GP2 and GP3 (Figure 3.2). Bluebunch wheatgrass monoculture mean biomass did not change from GP1 to GP2, but decreased by about 50% from GP2 to GP3 (Figure 3.2). Spotted knapweed monoculture mean biomass decreased by about 30% from GP1 to GP2 and was intermediate between the two growth periods during GP3 (Figure 3.2).

Analysis of Variance. Growth period affected biomass of annual sunflower, while having no effect on spotted knapweed biomass (Table 3.3). The main effect of treatment only impacted annual sunflower and spotted knapweed biomass (Table 3.3). Growth period and treatment interacted with bluebunch wheatgrass biomass.

Mean biomass of annual sunflower decreased by about 90% from GP1 to GP2, but then increased by about 80% from GP2 to GP3 (Table 3.4). The A treatment resulted in the highest mean annual sunflower biomass, although it did not differ from the AB and All treatments (Table 3.5). The lowest mean annual sunflower biomass was found in the

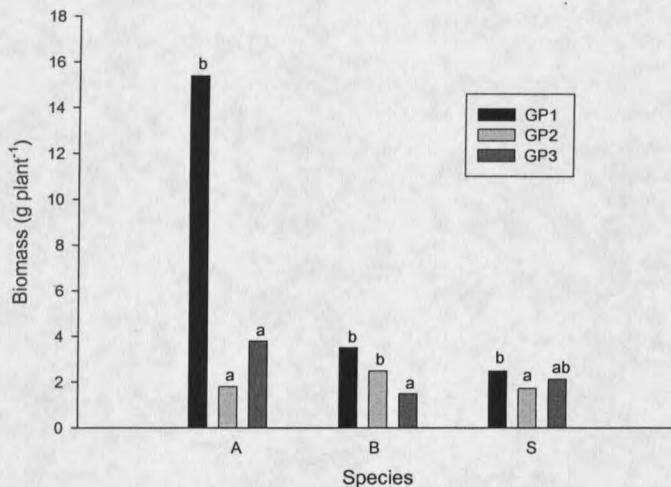


Figure 3.2. Effect of growth period on mean biomass per plant of annual sunflower (A), bluebunch wheatgrass (B), and spotted knapweed (S) when grown in monoculture (log<sub>10</sub> transformation). Actual means are presented. Different letters separate means that are significantly different within a species based on P-values ( $P \leq 0.05$ ) and confidence intervals of transformed means. GP1, GP2, and GP3 represent growth periods one, two, and three, respectively.

AS, All, and All+N treatments. Mean spotted knapweed biomass was lowest when grown in monoculture (Table 3.5). All other planting treatments were similar and resulted in higher mean spotted knapweed biomass than the monoculture.

Table 3.3. P-values from ANOVA for main effects and interaction on species biomass (square root transformation).

Source	Df	Annual sunflower	Bluebunch wheatgrass	Spotted knapweed
Rep	5	0.14	0.45	0.18
Treatment	8	0.01	<0.01	0.01
GP	2	<0.01	<0.01	0.13
Treatment x GP	16	0.10	0.02	0.17

Mean bluebunch wheatgrass biomass was highest in monoculture during GP1 (Table 3.6). Biomass decreased from GP1 to GP3 in monoculture, but that trend was not consistent in the other treatments. When grown with annual sunflower, bluebunch wheatgrass biomass did not change compared to the monoculture during GP2 and GP3. In general, mean bluebunch wheatgrass biomass decreased when grown with spotted knapweed (BS, All, and All+N treatments), but this effect was somewhat ameliorated in the All+N treatment during GP1 (Table 3.6).

Table 3.4. Effect of growth period on annual sunflower biomass (square root transformation). Actual lsmeans are presented. Different letters separate lsmeans that are significantly different.

Growth Period	Biomass (g plant <sup>-1</sup> )
1	9.52 c
2	0.70 a
3	4.12 b

Table 3.5. Effect of treatment on annual sunflower and spotted knapweed biomass per plant (square root transformation). Actual lsmeans are presented. Different letters separate lsmeans that are significantly different within the column.

Treatment	Annual sunflower (g plant <sup>-1</sup> )	Spotted knapweed (g plant <sup>-1</sup> )
A	7.00 c	--
S	--	2.11 a
AB	6.54 bc	--
AS	3.72 ab	4.02 b
BS	--	3.74 b
All	3.94 abc	4.02 b
All+N	2.16 a	4.99 b

#### Plant Tissue N

Growth period affected tissue N percentage of spotted knapweed and interacted with treatment to affect bluebunch wheatgrass tissue N (Table 3.7). Annual sunflower tissue N was unaffected by any main effects or interactions.



Table 3.6. Effect of treatment by growth period interaction on bluebunch wheatgrass biomass and percent tissue N (square root transformation). Actual lsmeans are presented. Different letters separate lsmeans that are significantly different within a column.

Treatment	GP	Biomass (g plant <sup>-1</sup> )	Tissue N (%)
B	1	3.50 g	1.42 d
	2	2.49 f	0.80 bc
	3	1.49 d	0.97 c
AB	1	2.58 ef	1.40 d
	2	2.85 f	0.65 ab
	3	1.89 d	0.56 a
BS	1	0.88 c	1.37 d
	2	0.23 a	0.77 c
	3	0.34 ab	1.00 c
All	1	0.51 bc	1.37 d
	2	0.37 ab	0.73 ab
	3	0.61 bc	0.58 ab
All+N	1	1.51 d	1.31 d
	2	0.91 c	0.66 ab
	3	0.55 bc	0.74 ab

Spotted knapweed tissue N percentage decreased from about 1.6% to 1.3% from GP1 to GP2 and did not decrease any further during GP3 (Table 3.8). The highest tissue N percentage for bluebunch wheatgrass, about 1.4%, occurred during GP1 regardless of treatment (Table 3.6). During GP2 and GP3, the AB, All, and All+N treatments experienced the lowest percentage of tissue N of about 0.7%. The B and BS treatments resulted in similar tissue N percentages (about 0.9 to 1.0%) for GP2 and GP3.

Table 3.7. P-values from ANOVA for main effects and interaction on species tissue N (square root transformation).

Source	Df	Bluebunch wheatgrass	Spotted knapweed
Rep	5	0.11	0.11
Treatment	8	0.03	0.12
GP	2	<0.01	<0.01
Treatment x GP	16	0.01	0.07

### Soil NO<sub>3</sub>-N, NH<sub>4</sub>-N, and Total Plant Available N Concentration

Growth period and treatment interacted to affect soil NO<sub>3</sub>-N, NH<sub>4</sub>-N, and total plant available N (Table 3.9). The lowest concentrations of soil NO<sub>3</sub><sup>-</sup> were found during GP3 in all treatments except the spotted knapweed monoculture (Table 3.10). The concentration of NO<sub>3</sub><sup>-</sup> in the majority of the treatments during GP3 was below the detection limit (0.05 ppm), therefore the mean was arbitrarily set at 0.03 ppm. The mean for the S treatment after three growth periods was 0.38 ppm NO<sub>3</sub>-N, while that for the A and B treatment was 0.03 ppm. Soil NO<sub>3</sub>-N concentration generally decreased throughout successive growth periods, except for the no plants treatment where NO<sub>3</sub>-N was highest during GP1 and GP2.

Table 3.8. Effect of growth period on spotted knapweed tissue N (square root transformation). Actual lsmeans are presented. Different letters separate lsmeans that are significantly different within a species.

Growth period	Tissue N (%)
1	1.55 b
2	1.27 a
3	1.30 a

Like NO<sub>3</sub>-N, the lowest NH<sub>4</sub>-N concentrations occurred in all treatments during GP3, ranging from about 0.7 to 1 ppm NH<sub>4</sub>-N (Table 3.10). Similar to NO<sub>3</sub>-N concentrations, the highest NH<sub>4</sub>-N concentration (26.3 ppm NH<sub>4</sub><sup>+</sup>) was found in the no plants treatment during GP2. Except for the A, S, BS, and no plants treatments, soil NH<sub>4</sub>-N generally decreased throughout successive growth periods. Total plant available N showed similar trends to NO<sub>3</sub>-N and NH<sub>4</sub>-N.

Table 3.9. P-values from ANOVA for main effects and interaction on soil  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , and total plant available N concentration.

Source	Df	$\text{NO}_3\text{-N}$	$\text{NH}_4\text{-N}$	Total Plant Available N
Rep	5	0.53	<0.01	0.02
Treatment	8	<0.01	<0.01	<0.01
GP	2	<0.01	<0.01	<0.01
Treatment x GP	16	<0.01	<0.01	<0.01

### Discussion

#### Response of Species in Monoculture

The objective of this study was to quantify the  $R^*$  for annual sunflower, bluebunch wheatgrass, and spotted knapweed.  $R^*$ s for N have been quantified by growing species in monoculture until population growth equals zero, then analyzing the soil for N content (Tilman and Wedin 1991a and 1991b, Wedin and Tilman 1993). Although most plants can use both  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$  in soil solution (Barber 1995), previous tests of  $R^*$  theory found the best estimator of  $R^*$  was soil  $\text{NO}_3\text{-N}$  concentration when a species is grown in monoculture;  $R^*$ s based on soil  $\text{NO}_3\text{-N}$  concentration successfully predicted the outcome of competition between two species in six out of six cases (Wedin and Tilman 1993). By growing the plants for three growth periods, I believed soil N would be depleted to a level where growth would decrease, thus arriving upon species'  $R^*$ s. Biomass has been used as a proxy for fitness (Tilman 1984, Tilman and Wedin 1991b, Wedin and Tilman 1993); I interpreted a decrease in biomass as a decrease in fitness and an indication that soil N concentrations were approaching a species  $R^*$ .

Table 3.10. Effect of treatment by growth period interaction on soil NO<sub>3</sub>-N, NH<sub>4</sub>-N, and total plant available N (log<sub>10</sub> transformation). Actual lsmeans are presented. Different letters separate lsmeans that are significantly different.

Treatment	GP	NO <sub>3</sub> -N (ppm)	NH <sub>4</sub> -N (ppm)	Total Plant Available N (ppm)
A	1	1.00 cd	1.61 b	2.62 cd
	2	0.60 cd	3.37 f	3.97 efg
	3	0.03 a	0.72 a	0.74 a
B	1	1.58 h	3.33 ef	4.92 gh
	2	0.55 c	2.68 cdef	3.23 def
	3	0.03 a	1.01 a	1.04 ab
S	1	1.45 cdefgh	2.28 bc	3.73 def
	2	0.60 cd	3.58 def	4.18 efg
	3	0.38 b	0.97 a	1.35 b
AB	1	1.32 gh	2.83 cdef	4.15 efg
	2	0.55 c	2.43 cdef	2.98 de
	3	0.03 a	0.82 a	0.84 a
AS	1	0.90 cedfgh	2.57 cdef	3.47 efg
	2	0.68 cdefg	2.22 bcd	2.90 de
	3	0.03 a	0.73 a	0.76 a
BS	1	1.07 cdefgh	2.78 cdef	3.85 efg
	2	0.65 cdef	3.88 f	4.53 fg
	3	0.03 a	0.88 a	0.90 ab
All	1	1.32 fgh	2.68 cdef	4.00 efg
	2	0.50 c	2.33 bcde	2.83 cde
	3	0.03 a	0.77 a	0.80 a
All+N	1	1.32 efgh	2.98 cdef	4.30 fg
	2	0.57 cde	2.17 bcd	2.74 de
	3	0.03 a	0.81 a	0.83 a
No plants	1	4.38 i	2.33 bcde	6.72 h
	2	5.83 i	26.31 g	32.15 i
	3	1.25 defgh	0.89 a	2.13 c

For the three monocultures, mean biomass per plant decreased with time, but species' did not respond similarly. After two growing periods annual sunflower and spotted knapweed biomass had decreased, while bluebunch wheatgrass biomass remained the same. Simultaneously, soil NO<sub>3</sub>-N decreased where the plants were grown in monoculture. Rapid growth rates of species like annual sunflower and spotted knapweed

are associated with rapid exploitation of readily available resources (Crawley 1997) and may have declined relatively quickly even with only a 0.5 ppm decline in soil  $\text{NO}_3\text{-N}$ .

A trend of increasing biomass, though not statistically significant, occurred for annual sunflower and spotted knapweed during GP3 even though soil  $\text{NO}_3\text{-N}$  continued to decrease. An invasive forb that spreads through prolific seed production (Sheley et al. 1999), and an annual forb employ different life history strategies than a native, perennial bunchgrass (Lambers et al. 1998). Under stressful conditions annual plants, or those perennials that reproduce through seed only, may partially invest in reproduction followed by an all-out commitment to seed production (Cohen 1971, Crawley 1997). I speculate that annual sunflower and spotted knapweed may have employed this strategy and responded to extremely low soil N availability by increasing aboveground biomass that would ultimately support seed production and subsequent generations. From this study I can only speculate about increased seed production as a result of stressful conditions. Further research in a field setting where many biotic and abiotic factors are included, such as pollinating insects, would be necessary to make any further conclusions regarding allocation patterns, including seed production.

In contrast to annual sunflower and spotted knapweed, bluebunch wheatgrass is a perennial bunchgrass adapted to persist under N-limiting conditions (Charley 1977) and can reproduce by seeds and vegetatively (Stubbendieck et al. 1992). Under stressful conditions, perennial species like bluebunch wheatgrass may increase belowground biomass as a mechanism for survival (Crawley 1997). In comparison to annual sunflower and spotted knapweed during GP3, I believe bluebunch wheatgrass may have begun

allocating more resources to root mass rather than aboveground biomass. Sampling roots to determine root to shoot ratios, may have indicated a switch in allocation from aboveground to belowground biomass. The degree of alteration in root to shoot ratios may be different among species based on their life history strategies (Redente et al. 1992, Barbour et al 1999). Basing conclusions on the response of root mass and root to shoot ratios may be prone to inaccuracies; adaptive changes to low nutrient supply are complex as plants may change their root architecture in addition to, or in place of, increasing their root mass (Fitter 1997).

I believe  $R^*$ s for all three species were being approached by the end of three growth periods. All treatments were still maintaining relatively robust populations, in spite of very low soil  $\text{NO}_3\text{-N}$  concentrations. Therefore, I can only make tentative conclusions regarding quantification of  $R^*$ s that are based on declining aboveground biomass of individual plants. Annual sunflower biomass was reduced during GP2 which corresponded to a soil  $\text{NO}_3\text{-N}$  concentration of 0.6 ppm. Bluebunch wheatgrass mean aboveground biomass did not decrease until GP3 when soil  $\text{NO}_3\text{-N}$  was below the detection limit of 0.05 ppm. Spotted knapweed biomass response was not as simple; it decreased during GP2 when soil  $\text{NO}_3\text{-N}$  was 0.6 ppm, but then increased slightly during GP3 when soil  $\text{NO}_3\text{-N}$  concentration decreased further to about 0.4 ppm. I estimate spotted knapweed's  $R^*$  to be between 0.4 and 0.6 ppm. These results support my hypothesis that the  $R^*$ s of annual sunflower and spotted knapweed are greater than that of bluebunch wheatgrass.  $R^*$ s for our species are very similar to those found in other studies that quantified  $R^*$ s for select species (Tilman and Wedin 1991b, Wedin and

Tilman 1993). In those studies,  $R^*$ s of the early successional grasses were between 0.1 and 0.3 ppm  $\text{NO}_3\text{-N}$  and  $R^*$ s for late successional grasses were below 0.05 ppm  $\text{NO}_3\text{-N}$ .

Results from the monocultures are consistent with my hypothesis that annual sunflower's  $R^*$  would be greater than spotted knapweed's  $R^*$  and spotted knapweed's  $R^*$  would be greater than bluebunch wheatgrass'. Perhaps I would have been able to make more accurate assessments of  $R^*$ s for annual sunflower and spotted knapweed, if the study had lasted for one to two more growth periods. As mentioned earlier, there appeared to be a trend of increasing biomass for spotted knapweed and possibly for annual sunflower during GP3. One to two more growth periods may have allowed us to determine whether this trend continued. The  $R^*$  for bluebunch wheatgrass appeared to have been lower than could be detected, therefore subsequent growth periods would not have helped to quantify a precise  $R^*$ .

#### Response of Species in Mixtures

I hypothesized estimated  $R^*$ s from monocultures could successfully predict the outcome of competition in two- and three-species mixtures. Species biomass results in combination with our predicted species'  $R^*$ s, however, produced varying responses in regard to  $R^*$  theory.

Estimated  $R^*$ s for annual sunflower and spotted knapweed successfully predicted the response of the two species grown in polyculture. Annual sunflower, with an estimated  $R^*$  of 0.6 ppm  $\text{NO}_3\text{-N}$ , produced less biomass when grown with spotted knapweed, whose estimated  $R^*$  is lower, approximately 0.4-0.6 ppm  $\text{NO}_3\text{-N}$ .  $R^*$  theory predicts that a population with a lower  $R^*$  will competitively displace a population with a

higher  $R^*$  (Tilman 1982, 1988). I had predicted that annual sunflower would have a higher  $R^*$  than spotted knapweed and its biomass would decrease when grown with spotted knapweed. This is similar to results from other tests of  $R^*$  theory (Tilman and Wedin 1991a, 1991b). In those studies, the biomass of quackgrass when grown with Kentucky bluegrass (*Poa pratensis* L.) decreased below that of quackgrass grown alone, and quackgrass had a higher  $R^*$  for N than Kentucky bluegrass.

I could not successfully predict the outcome of mixtures of spotted knapweed and bluebunch wheatgrass based on estimated  $R^*$ s. Because I concluded that spotted knapweed's  $R^*$  for N is higher than that of bluebunch wheatgrass, I would have predicted spotted knapweed's biomass to decrease below that of the monoculture when grown with bluebunch wheatgrass. Conversely, spotted knapweed biomass was higher when grown with the bluebunch wheatgrass and annual sunflower. Bluebunch wheatgrass biomass decreased when grown with spotted knapweed compared to when grown in monoculture. Similar to my results, Blicker et al. (2002) found spotted knapweed biomass was greater when grown with bluebunch wheatgrass than with itself or with western wheatgrass, another species native to semi-arid rangeland. These results suggest spotted knapweed may be a superior competitor for a resource other than N (LeJuenne and Seastedt 2001) or complex plant-plant interactions may be occurring that permit spotted knapweed to outcompete bluebunch wheatgrass under low N conditions even though its  $R^*$  for  $\text{NO}_3\text{-N}$  is higher. This was a pot study, and additional growth periods may have been required for some competitive relationships to become more evident.



$R^*$  is a component of the resource ratio hypothesis (Tilman 1982, 1984, 1988, 1997). It is possible for two species to be limited by different resources within the same environment. Species X may be the better competitor for resource X (lower  $R^*$  for resource X) and an inferior competitor for resource Y, while species Y may be the better competitor for resource Y (lower  $R^*$  for resource Y) and an inferior competitor for resource X. In environments with low resource X to resource Y ratios, species X will dominate; likewise, in environments with high resource X to resource Y ratios, species Y will dominate. Species X and Y may coexist in intermediate environments where each species is limited by a different resource.

It may be possible that spotted knapweed and bluebunch wheatgrass are limited by different nutrients and that spotted knapweed is not the better competitor for N, but is a better competitor for another nutrient. In a greenhouse study, spotted knapweed was not found to be a better competitor for N than bluebunch wheatgrass or Idaho fescue (Lindquist et al. 1996). In a mixed-grass prairie, diffuse knapweed (*Centaurea diffusa* Lam.) biomass did not respond to N additions, but responded strongly to phosphorus (P) additions (LeJeune and Seastedt 2001). Callaway and Aschehoug (2000) found spotted knapweed to be a better competitor for P than three native grass species of western Montana, including bluebunch wheatgrass.

I speculate that bluebunch wheatgrass may be a superior competitor for N, but spotted knapweed may be a superior competitor for P. Within the pots, the N to P ratio may have allowed the coexistence of spotted knapweed and bluebunch wheatgrass, even though spotted knapweed appears to have a lower  $R^*$  for N (Figure 3.3). This

discrepancy in species abilities to compete for different resources has been proposed as a mechanism for invasion of western, semi-arid grasslands by knapweed species (LeJeune and Seastedt 2001). Historic N-limitation has been altered by human activities such as increased atmospheric N deposition, reduced fire frequency, and possibly, direct and indirect fertilization resulting from cattle grazing (Seastedt et al. 1991, Vitousek et al. 1997, Belsky and Gelbard 2000). As a result, western, semi-arid grasslands may instead be limited by P or co-limited by P and water. The species that is able to sequester the next most limiting resource after N should become dominant. Evidence suggests knapweeds may possess that ability (Callaway and Aschehoug 2000, LeJeune and Seastedt 2001).

Alternatively, my results may be indicative of an allelopathic effect that was more pronounced than a competitive effect under low N conditions. Spotted knapweed roots secrete (-)-catechin, a phytotoxin that is believed to contribute to spotted knapweed's invasive behavior (Bais et al. 2002, 2003). In addition, cnicin, a sesquiterpene lactone present in spotted knapweed, has been suspected of being an allelopathic substance (Kelsey and Locken 1987). *Centaurea* spp. reduced the biomass of several bunchgrasses native to semi-arid, western rangeland when grown together in pots; when activated C, which ameliorates chemical effects, was added to the pots, the effect of knapweed on native bunchgrass biomass was reduced (Callaway and Aschehoug 2000, Ridenour and Callaway 2001). The results of these experiments coupled with my results suggest allelopathy may play an important role in the overall competitive balance between spotted knapweed and bluebunch wheatgrass.

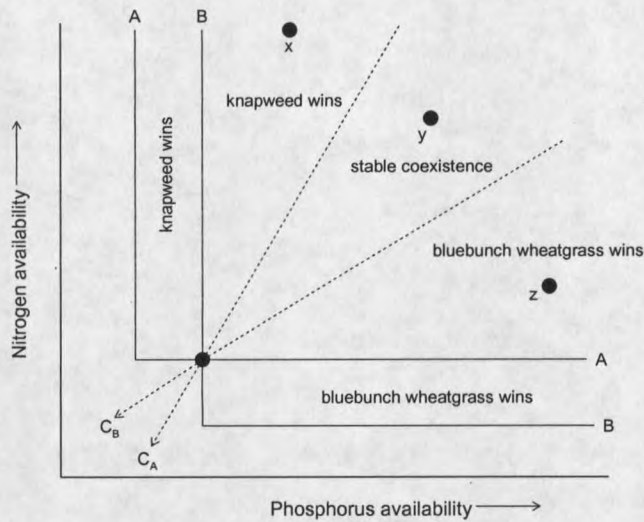


Figure 3.3. Possible relationship between spotted knapweed, bluebunch wheatgrass, nitrogen availability, and phosphorus availability, as explained by the resource ratio hypothesis (Tilman 1982). A and B represent resource-dependent zero net growth isoclines (reproductive rate = mortality rate) for spotted knapweed and bluebunch wheatgrass, respectively.  $C_A$  and  $C_B$  represent spotted knapweed and bluebunch wheatgrass consumption vectors, respectively.  $x$  (low N:P ratio),  $y$  (intermediate N:P ratio), and  $z$  (high N:P ratio) represent resource supply points. The isoclines cross because spotted knapweed is a better competitor for P (lower  $R^*$ ) and bluebunch wheatgrass is a better competitor for N (lower  $R^*$ ). The point where the isoclines cross is an equilibrium N:P ratio where both species can coexist. At supply point  $x$ , spotted knapweed dominates because P is low and spotted knapweed is a better competitor. At supply point  $z$ , bluebunch wheatgrass dominates because N is low and bluebunch is a better competitor. At supply point  $y$ , the two species coexist as each species is relatively more limited by a different resource. For habitats with supply points within the region defined by consumption vectors of the two species, the consumption of N and P by the two species will eventually reduce resource levels to the equilibrium point. Along a resource ratio gradient from  $x$  to  $y$  to  $z$ , there is a smooth transition from dominance by spotted knapweed, to coexistence, to bluebunch wheatgrass.

The competitive relationship between spotted knapweed and bluebunch wheatgrass may also have been mediated through mycorrhizae. In one study spotted knapweed was 66% larger when grown with Idaho fescue in the presence of arbuscular

mycorrhizal (AM) fungi than when AM fungi were absent (Marler et al. 1999). The authors believed AM fungi may have provided a linkage between the two species that allowed transfer of nutrients and photosynthate between plants. Although I did not test the roots within the pots for presence of AM fungi, the field soil I used had not been sterilized and the presence of AM fungi was likely.

Based on my results and the results of other studies (Marler et al. 1999, Callaway and Aschehoug 2000, Ridenour and Callaway 2001, Blicher et al. 2002, Olson and Blicher 2002), I believe spotted knapweed may possess characteristics which allow it to dominate a plant community even though its  $R^*$  for N is higher than that of co-existing species.  $R^*$  theory alone may not be an appropriate mechanism for explaining plant community dynamics when nonindigenous, invasive species such as spotted knapweed are present. Instead, a more comprehensive model including resource ratios and interference mechanisms such as allelopathy and mycorrhizae may have to be incorporated to fully understand plant community dynamics in the presence of a nonindigenous invasive species.

#### Plant Tissue N

My intentions concerning plant tissue N were exploratory, therefore I did not present any specific hypotheses concerning plant tissue N. Tilman and Wedin (1991a) found very few differences in tissue N concentrations among five grassland species. Similarly, in this study plant tissue N provided little insight into determining  $R^*$ s and interpreting competitive relationships. It has been suggested that minimal tissue nutrient content at which a species can grow is a measure of its nutrient use efficiency (Tilman

1990). Low minimal tissue nutrient content increases competitive advantage, but as the magnitude of plant N tissue content becomes smaller, the advantage decreases. Measured tissue N values were on the low end of what is typical for healthy plants (1-4%) (Raven et al. 1986). Because plant tissue N concentrations were relatively low in this study, I speculate that competitive advantages offered by tissue nutrient content were probably not contributing to a large degree.

### Soil N Concentrations

Soil  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$ , and total plant available N concentrations for the monocultures and two- and three-species mixtures at the end of GP3 were all low, comparable to the N-poor grassland soil in Minnesota, USA, where  $R^*$  theory has been researched (Tilman 1984). According to  $R^*$  theory, the species with the lowest  $R^*$  in the plant community, the pots in this study, should reduce N to its  $R^*$  and the other species with higher  $R^*$ s should diminish in dominance (Tilman 1982, 1988). Soil  $\text{NO}_3\text{-N}$  concentrations support  $R^*$  theory in this manner; whenever bluebunch wheatgrass was present, soil  $\text{NO}_3\text{-N}$  was reduced to levels similar to its  $R^*$ . A similar result occurred with  $\text{NH}_4\text{-N}$  and total plant N concentrations, with the addition that the S treatment reduced soil  $\text{NH}_4\text{-N}$  to the same level as the other treatments.

In the pots that had no plants, soil N increased during GP2. I believe this was a result of mineralization of organic matter. At the beginning of the study, soil C to N ratios may have been lower due to greater soil N availability. This may have caused net mineralization (Stevenson and Cole 1999a). No plants were available to utilize the N flux, therefore soil N concentrations increased. During GP3 soil N decreased. This was a

surprising result and can not be easily explained. Weekly watering may have created wetting and drying cycles different than field-moist soils (Stevenson and Cole 1999b). Wetting and drying of soil may kill microorganisms, convert organic N to more soluble compounds which are utilized by microorganisms, or expose new surfaces and substrates for microbial attack (Stevenson and Cole 1999b). I speculate that such complex interactions among plants, soil microbes, and environmental factors were likely involved.

### Conclusion

Knowledge of species'  $R^*$ s may be used to predict the outcome of succession, identify areas susceptible to invasion by nonnative species based on patterns of resource availability, choose species for revegetation that have lower  $R^*$ s than non-indigenous species, and alter resource availability to direct succession toward a desirable plant community. I conclude that predicting the outcome of succession, identifying areas susceptible to invasion, and choosing species for revegetation with lower  $R^*$ s than non-indigenous species may be effective only if resource ratios in the soil and interference mechanisms are determined.

To improve our understanding of  $R^*$  theory in the hopes of applying it to management of nonindigenous plant invasions in the future, we must incorporate belowground biomass as well as aboveground biomass into our sampling procedures so that root to shoot ratios can be investigated. Analyzing soil for P as well as N would allow us to explore resource ratios as a mechanism for coexistence. Finally, extending the duration of the study would provide more accurate estimates of  $R^*$ s.

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## CONTROLLING SPECIES PERFORMANCE USING NITROGEN AND SUCROSE AMENDMENTS

### Introduction

Scientists and land managers have been interested in temporal changes in plant community composition for hundreds of years (Theophrastus 300 B.C.). Many models attempt to mechanistically explain succession in order to predict its outcome (Cowles 1911, Clements 1916, Gleason 1917, Egler 1954, MacArthur 1962, Odum 1969, Whittaker 1970, Connell and Slatyer 1977, Grime 1979, Huston 1979, Tilman 1982, Pickett et al. 1987, Westoby et al. 1989, Davis et al. 2000). Most of these models focus on ecological processes that direct plant community dynamics, such as competition (Tilman 1982) or disturbance (Davis et al. 2000).

One emerging phenomenon has caused reconsideration of the ecology of succession. Range and wild lands are being invaded by nonindigenous plants, resulting in an unprecedented, rapid change in plant community composition across the United States. Invasive plants infest over 40 million hectares in the United States (NISC 2001) and continue to spread at an estimated 14% per year (Westbrooks 1998). The organization, structure, and function of plant communities may be altered when invasive plants dominate (Lacey et al. 1989, Whisenant 1990, D'Antonio and Vitousek 1992, Gerlach and Rice 1996, Olson 1999, LeJeune and Seastedt 2001). Because invasion by nonindigenous plants is fundamentally a successional phenomenon, it may be possible to apply successional models to management of invasive plants and predict the plant

community change prior to implementing particular management strategies (Sheley et al. 1996, Rinella 2003).

#### Managing Nonindigenous Plant Invasions Using Successional Management

A hierarchical successional framework that lends itself to understanding and manipulating plant community dynamics was developed by Pickett et al. (1987). The first hierarchical level identifies three general causes of succession: site availability, species availability, and species performance (Table 4.1). The second level of the hierarchy identifies ecological processes that direct the three general causes of plant community change, including disturbance, colonization, resource supply, ecophysiology, life history, stress, and interference. The final hierarchical level is most detailed and includes site specific modifying factors that influence the outcome of plant dynamics. Modifying factors can be manipulated to direct successional trajectories towards meeting management goals. Successional management can be used to explain and predict successional dynamics at any site if adequate information is available on the disturbance regime, site conditions, species availability and species characteristics (Pickett et al. 1987). Furthermore, succession can be explained in the event that a new species is added to the community, especially with respect to nonindigenous invasion (Luken and Thieret 1997).

Successional management has been theoretically applied to management of natural resources, including invasive plant-dominated rangelands (Luken 1990, Sheley et al. 1996, Sheley and Rinella 2003, Anderson 2003, Bard et al. 2003). Successional management of nonindigenous plant-dominated rangeland focuses on controlled

disturbance, controlled colonization, and controlled species performance, and uses current technology to modify their associated processes to shift undesirable, weed-infested plant communities toward domination by desired species. For example, Anderson (2003) found that as management techniques increasingly addressed the three general causes of succession, establishment of native grasses on invasive plant-dominated rangeland improved.

Table 4.1. Causes of succession, contributing processes, and modifying factors.<sup>a</sup>

Causes of Succession	Processes	Modifying Factors
Site Availability	Disturbance	Size, severity, time intervals, patchiness, predisturbance history, increased atmospheric CO <sub>2</sub> , eutrophication, many non-equilibrium states
Species Availability	Dispersal	Dispersal mechanisms and landscape features, vector, sequence, rate, frequency
	Propagule pool	Land use, disturbance interval, species life history, tilling, reseeding, precipitation patterns, seed coatings
Species Performance	Resource supply	Soil, topography, climate, site history, microbes, litter retention, hydraulic lift, landscape heterogeneity, resource ratios
	Ecophysiology	Germination requirements, assimilation rates, growth rates, genetic differentiation, changes between native and introduced ranges
	Life history	Allocation, reproduction timing and degree, plasticity
	Stress	Climate, site-history, prior occupants, herbivory, natural enemies, plasticity
	Interference	Competition, herbivory, allelopathy, resource availability, predators, other level interactions, nurse crops, mycorrhizae, multiple classes of grazing, R*, soil impoverishment

<sup>a</sup>Modified from Pickett et al. 1987

### Species Performance as Affected by Nutrient Availability

Species performance, one of the causes of succession, may be modified by soil nutrient availability. Evidence suggests nonindigenous, invasive species outperform indigenous species when nutrient availability, especially nitrogen (N), is high (Huenneke et al. 1990, Milchunas and Lauenroth 1995, Burke and Grime 1996, Maron and Connors 1996, Kolb et al. 2002, Herron et al. 2001, Blumenthal et al. 2003). Invasive plants display characteristics of early successional species with fast relative growth rates, high seed output, and high potential to absorb nutrients when nutrient availability is high (Baker 1974, Bazzaz 1986, Roy 1990). Conversely, indigenous species often considered desirable on semi-arid rangeland possess traits of late successional species such as slow relative growth rates, low potential to absorb nutrients when soil content is high, vegetative reproduction, and intense competition in low soil nutrient environments (MacArthur 1962, Tilman and Wedin 1991b).

R\* theory is a component of the resource ratio hypothesis (Tilman 1982, 1988) and one of several theories proposed as a model predicting successional change. It holds promise for explaining nonindigenous, invasive plant and native plant response to varying availabilities of soil N. R\* theory states that the outcome of succession is based on the relative ability of a population to sequester a limiting resource. R\* of a species is the minimum level of a nutrient required for maintenance of the population. The population with the lowest R\* dominates under conditions of limited N availability (Tilman 1982, 1988). R\*s for selected species have been determined by growing them in monoculture (Tilman and Wedin 1991a and 1991b). Upon reaching equilibrium (birth



rate=mortality rate), the soil N concentration is considered the  $R^*$ . The application of  $R^*$  theory on semi-arid rangeland as a principle for altering the process of resource uptake during successional management of invasive plant-dominated land is untested.

Ecologists have proposed applying carbon sources to reduce N availability and alter the performance of invasive species during restoration projects (Morgan 1994, Alpert and Maron 2000, Paschke et al. 2000, Blumenthal 2003, Svejcar 2003). Carbon addition increases soil microbial biomass and N is immobilized by the microbial community, creating a temporary depletion of plant-available N (Redente et al. 1992, Morgan 1994). To date, studies testing the effectiveness of carbon additions as a management tool for nonindigenous species have produced mixed conclusions (Seastedt et al. 1996, Hopkins 1998, Reever Morgan and Seastedt 1999, Alpert and Maron 2000, Lowe et al. 2002, Blumenthal 2003, Brockinton 2003).

The first objective of this study was to determine the potential to predict the outcome of succession within an Idaho fescue (*Festuca idahoensis* Elmer)/bluebunch wheatgrass (*Agropyron spicatum* Pursh) (Mueggler and Stewart 1980) plant association using  $R^*$  theory. Successional dynamics among annual sunflower (*Helianthus annuus* L.) (early successional forb), bluebunch wheatgrass (late successional grass), and spotted knapweed (*Centaurea maculosa* Lam.) (invasive forb) were predicted based upon species  $R^*$ s. In Chapter 3,  $R^*$ s for the three species were estimated as 0.6 ppm  $\text{NO}_3\text{-N}$  for annual sunflower, <0.05 ppm  $\text{NO}_3\text{-N}$  for bluebunch wheatgrass, and 0.4 ppm  $\text{NO}_3\text{-N}$  for spotted knapweed. I hypothesized that if soil N concentration decreased over time, bluebunch

wheatgrass biomass and competition intensity would increase relative to the other two species.

The second objective of this study was to determine the influence of modifying soil N concentration on successional dynamics, to further test the R\* theory, and to test the potential of soil nutrient alteration as a modifying factor to direct plant communities toward desired species. I hypothesized that if N availability decreased by sucrose amendment, bluebunch would increase its biomass and competitive ability relative to the other two species; as soil N availability increased by N amendment, annual sunflower and/or spotted knapweed would increase their (its) biomass and competitive ability relative to the other two species.

## Methods

### Study Sites

The study was conducted on two sites in western Montana characterized as an Idaho fescue (*Festuca idahoensis* Elmer)/bluebunch wheatgrass (*Agropyron spicatum* Pursh) habitat type (Mueggler and Stewart 1980). Site 1 was located at Redbluff Research Ranch about 2 km east of Norris, Montana (45° 35' N, 111° 39' W) (hereafter referred to as Redbluff). The elevation is 1505 meters, with 305 mm of annual precipitation. Soils are a fine-loamy, mixed, frigid Calcic Argiustoll. Frequently encountered species at Redbluff included Idaho fescue, bluebunch wheatgrass, needle-and-thread grass (*Stipa comata* Trin. and Rupr.), red threeawn (*Aristida longiseta* Steud.),

hairy goldenaster (*Chrysopsis villosa* (Pursh) Nutt.), dotted gayfeather (*Liatrus punctata* Hook), salsify (*Tragopogon dubius* Scop.), and vetch (*Vicia americana* Muhl.).

Site 2 was located in Story Hills about 5 km northeast of Bozeman, Montana (45° 36' N, 111° 34' W) (hereafter referred to as Story Hills). Elevation at Story Hills is 1478 meters, with 432 mm annual precipitation. Soils are a clayey-skeletal, mixed Typic Argiboroll. Common plant species at Story Hills included Idaho fescue, bluebunch wheatgrass, western wheatgrass (*Agropyron smithii* Rydb.), prairie junegrass (*Koelaria pyramidata* (Lam.) Beauv.), yarrow (*Achillea millefolium* L.), false dandelion (*Agoseris glauca* Pursh), yellow alyssum (*Alyssum alyssoides* L.), cudweed sagewort (*Artemisia ludoviciana* Nutt.), biscuitroot (*Lomatium ambiguum* Nutt.), lupine (*Lupinus* spp.), Hood's phlox (*Phlox hoodii* Richardson), longleaf phlox (*Phlox longifolia* Nutt.), and salsify. Both sites are considered late successional plant communities (Mueggler and Stewart 1980).

### Experimental Design

Sites were plowed to a 15-cm depth with a moldboard plow and lightly tilled on 15 September (Red Bluff) and 16 September (Story Hills) 2000. Glyphosate [N-(phosphonomethyl)glycine] was applied at 2.3 kg a.i./ha on 24 October 2000 to kill vegetation that germinated or re-sprouted following plowing and tilling. Rocks were removed by hand raking. Dead Plant material was also removed to minimize the potential for N leaching in the soil.

Monocultures and mixtures of annual sunflower, bluebunch wheatgrass, and spotted knapweed were arranged in an addition series matrix (Spitters 1983). Four

densities were factorially arranged in combinations of 0, 1000, 2000, and 4000 seeds  $m^{-2}$ . Seeds of each species were hand-broadcasted on 1.5 x 1.5 m plots in October 2000. Density combinations were established in a randomized-complete-block design and replicated three times at each site. Plants were grown for 3 seasons. During 2001 and 2002, 2% glyphosate solution was wiped onto non-seeded species in an attempt to maintain desired combinations.

In April 2003, each plot in the addition series matrix was divided into three subplots. Nitrogen was applied to a randomly chosen subplot in each whole plot. Sucrose was applied to a second subplot in each plot. The remaining subplot of each plot was not amended and considered a control. The N amendment consisted of 112 kg N  $ha^{-1}$  applied as granular ammonium nitrate ( $NH_4NO_3$ ) in three increments every 30 days (Table 4.2). Sucrose was applied approximately every 14 days at 100 g C  $m^{-2}$  (Table 4.2), based upon data provided by Brockinton (2003). Both chemicals were hand-broadcasted on the soil surface of each subplot.

Table 4.2. Treatment application dates in 2003.

Red Bluff	Story Hills
27 April—sucrose and N	28 April—sucrose and N
12 May—sucrose	14 May—sucrose
27 May—sucrose and N	28 May—sucrose and N
09 June—sucrose	12 June—sucrose
25 June—sucrose and N	26 June—sucrose and N

### Sampling

Plant density and biomass of annual sunflower, bluebunch wheatgrass, and spotted knapweed were sampled mid through late July 2003. Density of plants and grass

tillers were determined by counting the number of plants or grass tillers in a 30 cm x 130 cm frame placed randomly on the ground within each subplot. Biomass was determined by clipping and separating species within the frame used for counting density. Clipped samples were dried at 60° C for 48 hours and weighed.

Three two-cm wide soil cores were collected from within the area where plants were sampled to a depth of 12 to 15 cm from each subplot. Subsamples were composited for inorganic nitrogen analyses. Soil samples were dried at 42° C and sieved through a 2 mm screen prior to chemical analyses. Inorganic soil nitrogen ( $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$ , and total available N) was determined on 1 M KCl extracts from soil (5 g soil:50 ml extractant). Aliquots of filtered extracts were analyzed for  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$  using Cd reduction and salicylate colorimetric methods, respectively (Mulvaney 1996).

At Red Bluff all three replications were sampled. At Story Hills two replications were sampled and the third replication remained undisturbed for future sampling and quantification of long-term community dynamics.

### Statistical Analysis

Model Selection. Annual sunflower had disappeared from the plots at both sites after three years and was not included in any analysis. Three competition models were explored for the best, most consistent fit (Table 4.3). The first model was based on the model developed by Spitters (1983) and used densities of spotted knapweed and bluebunch wheatgrass to predict spotted knapweed or bluebunch wheatgrass biomass. The second model was also based on the model developed by Spitters (1983), but used density of bluebunch wheatgrass and biomass of spotted knapweed to predict bluebunch

wheatgrass biomass, and vice versa. The third model consisted of two linked hyperbolic equations derived from a hyperbolic model of Cousens (1985) (Jasieniuk et al. 2001).

The third model used bluebunch wheatgrass density and spotted knapweed biomass to predict bluebunch wheatgrass biomass, and vice versa.

Table 4.3 Competition models used for predicting species biomass.

Competition model	Parameter explanation
1) $y_x = Y_{max_x} / (1 + \beta_{xx}N_x + \beta_{xy}N_y)$ (Spitters 1983)	$Y_{max_x}$ =maximum biomass of species x in absence of competition; $N_x$ =density of species x; $N_y$ =density of species y; $\beta_{xx}$ =intraspecific competition coefficient; $\beta_{xy}$ =interspecific competition coefficient
2) $y_x = Y_{max_x} / (1 + \beta_{xx}N_x + \beta_{xy}B_y)$ (Spitters 1983)	$Y_{max_x}$ =maximum biomass of species x in absence of competition; $N_x$ =density of species x; $B_y$ =biomass per unit area of species y; $\beta_{xx}$ =intraspecific competition coefficient; $\beta_{xy}$ =interspecific competition coefficient
3) $y_x = [(\beta_{xx}N_x)/(1 + \beta_{xx}N_x/Y_{max_x})] \times [(1 - (\beta_{xy}B_y/(1 + \beta_{xy}B_y/a)))]$ (Cousens 1985, Jasieniuk et al. 2000)	$Y_{max_x}$ =maximum biomass of species x in absence of competition; $N_x$ =density of species x; $N_y$ =biomass per unit area of species y; $\beta_{xx}$ =intraspecific competition coefficient; $\beta_{xy}$ =interspecific competition coefficient; $a$ =maximum yield loss of species x as biomass of species y becomes very large (=1 for analysis)

Microsoft Excel solver tool was used to fit data to competition models and provide preliminary estimates of regression coefficients and coefficients of determination (Wraith and Or 1998). The Excel solver allowed data to be fit to a model by iteratively estimating parameters until the error sum of squares was minimized. The maximum iterations, precision, and tolerance were set at 100 iterations,  $1 \times 10^{-5}$ , and 5%, respectively. Estimated parameters included maximum yield of species x in the absence of competition ( $Y_{max_x}$ ), intraspecific competition coefficient ( $\beta_{xx}$ ), and interspecific

competition coefficient ( $\beta_{xy}$ ). Data from each treatment were fit to the models to generate parameter estimates for each treatment at both sites. Following preliminary estimation of regression coefficients and adjusted coefficients of determination ( $r^2$ ) from the three competition models, the first model (Spitters 1983) using density of both species was chosen as the most appropriate model because it produced the minimum error sum of squares and highest, most consistent  $r^2$ s (Table 4.4).

Table 4.4. Adjusted coefficients of determination ( $r^2$ ) from three models for predicting bluebunch wheatgrass and spotted knapweed biomass using density (N) and biomass (B) at Red Bluff and Story Hills.

Species and Treatment	1) $y_x = Y_{max_x} / (1 + \beta_x N_x + \beta_y N_y)$		2) $y_x = Y_{max_x} / (1 + \beta_x N_x + \beta_y B_y)$		3) $y_x = [(\beta_x N_x) / (1 + \beta_x N_x / Y_{max_x})] \times [(1 - (\beta_y B_y / (1 + \beta_y B_y / a)))]$	
	Red Bluff	Story Hills	Red Bluff	Story Hills	Red Bluff	Story Hills
Bluebunch wheatgrass						
Control	0.79	0.70	0.44	0.66	0.10	0.79
Nitrogen	0.87	0.77	0.87	0.56	0.76	0.82
Sucrose	0.74	0.76	0.74	0.66	0.74	0.90
Spotted knapweed						
Control	0.05	0.06	0.06	0.05	0.06	0.01
Nitrogen	0.05	0.01	0.08	0.01	0.12	0.01
Sucrose	0.03	0.04	0.03	0.04	0.03	0.02

Regression Analysis. Multiple linear regression models were fit using densities of bluebunch wheatgrass and spotted knapweed as the independent variable and biomass of bluebunch wheatgrass or spotted knapweed as the dependent variable. Models were of the form:

$$\text{bluebunch wheatgrass: } y_b = \beta_{b0} + \beta_{bb}N_b + \beta_{bs}N_s$$

$$\text{spotted knapweed: } y_k = \beta_{k0} + \beta_{ss}N_s + \beta_{sb}N_b$$

where  $y_b$  is bluebunch wheatgrass mean biomass per plant,  $y_s$  is spotted knapweed mean biomass per plant,  $N_b$  is bluebunch wheatgrass density,  $N_s$  is spotted knapweed density, and  $\beta_{b0}$ ,  $\beta_{s0}$ ,  $\beta_{bb}$ ,  $\beta_{ss}$ ,  $\beta_{bs}$ ,  $\beta_{sb}$  are regression coefficients. The regression coefficients are interpreted as:  $\beta_{b0}$  and  $\beta_{s0}$  = biomass of an individual bluebunch wheatgrass or spotted knapweed plant grown in isolation,  $\beta_{bb}$  and  $\beta_{ss}$  = intensity of intraspecific competition and,  $\beta_{bs}$  and  $\beta_{sb}$  = intensity of interspecific competition. Data from each treatment were fit to the model to generate regression coefficients for each treatment at both sites (SAS Institute Inc. 1990).

Slope of the regressions were compared between treatments by calculating variance ratios using the equation:

$$\text{Variance Ratio}_i = [(RSS_i - RSS_1) / (df_i - df_1)] / (RSS_1 / df_1)$$

Where  $RSS_i$  is the residual sums of squares from pooling data from the two treatments being compared,  $RSS_1$  is the residual sums of squares of one treatment plus the residual sums of squares of the other treatment,  $df_i$  is the error degrees of freedom from the pooled treatments, and  $df_1$  is the error degrees of freedom of one treatment plus the error degrees of freedom for the other treatment. A variance ratio larger than the critical

$F_{(\alpha, df_{\text{numerator}}, df_{\text{denominator}})}$  value rejects the null hypothesis that the slopes are the same (Ratkowski 1983).

The ratio of the intraspecific competition coefficient and interspecific competition coefficient was used to determine the relative influence of each species on the response variable. For example, if  $\beta_{bb}/\beta_{bs} = 2$ , then bluebunch wheatgrass has twice the influence on bluebunch wheatgrass biomass than spotted knapweed has on bluebunch wheatgrass



biomass. Zero was used for all non-significant coefficients and a constant of 0.0001 was used for ratio calculations (Roush 1988, Jacobs et al. 1996). The  $[\beta_{bb}:\beta_{bs}/\beta_{ss}\beta_{sb}]$  double ratio was used to determine partitioning of resources between species (Spitters 1983). Deviations from unity (1.0) indicated increased resource partitioning (niche differentiation).

Soil N Concentration and Species Biomass. Analysis of variance (ANOVA) was used to determine the effects of site, replication, and soil amendment (control, N, and sucrose) on soil  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$  and total available N concentrations (SAS Institute Inc. 1990). Regression analysis did not always yield significant models, so bluebunch wheatgrass and spotted knapweed absolute biomass were also analyzed with ANOVA in a similar manner to soil N concentration. Each subplot within a rep was included as an observation for analysis. For example, when considering the effect of soil amendment on soil  $\text{NO}_3\text{-N}$  concentration at Story Hills, the total number of observations used in analysis equaled 377 (64 subplots times two reps minus missing values). Power equaled 1.00 in this example, which means that when differences were detected between mean soil  $\text{NO}_3\text{-N}$  for the three treatments, there was a 100% chance that the differences between means were true (Neter et al. 1996). Detection of treatment differences was conservative and there was a higher probability of committing type II errors than type I errors. Transformations of absolute biomass and soil N concentrations were performed to normalize the data and homogenize variances. When significant models were found ( $P \leq 0.05$ ), mean separations were achieved using Fisher's protected least significant

difference ( $LSD_{\alpha=0.05}$ ) comparisons (Peterson 1985). Non-transformed means are presented. Separation of actual means was based on the LSD from transformed data.

## Results

### Regression Analysis

Regression analysis provided significant models for predicting bluebunch wheatgrass biomass per plant at Story Hills, but not at Red Bluff (Table 4.5). Models for predicting spotted knapweed biomass per plant were significant for all treatments at both sites.

Table 4.5. Model P-values for regressions predicting bluebunch wheatgrass/spotted knapweed biomass per tiller or plant from bluebunch wheatgrass and spotted knapweed densities.

Species	Red Bluff			Story Hills		
	Control	Nitrogen	Sucrose	Control	Nitrogen	Sucrose
Bluebunch wheatgrass	0.07	0.38	0.49	<0.01	<0.01	0.03
Spotted knapweed	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

At Story Hills, bluebunch wheatgrass density influenced its biomass in the control only, and the effect was positive (Table 4.6, Figure 4.1). Spotted knapweed density negatively influenced bluebunch wheatgrass biomass in the control and amended plots. Based upon this model, every increase of 10 spotted knapweed plants decreased bluebunch wheatgrass biomass per tiller by one or two milligrams. The adjusted  $r^2$  for the models ranged from 0.07 to 0.27. Soil amendments had no effect on the slopes of the regressions (Table 4.7).

Table 4.6. Regression coefficients and adjusted coefficients of determination ( $r^2$ ) for predicting bluebunch wheatgrass biomass ( $\text{mg tiller}^{-1}$ ) at Story Hills.

Treatment	$\beta_{b0}$	$\beta_{bb}$	$\beta_{bs}$	$\beta_{bb}/\beta_{bs}$	$r^2$
Control	7.0 (10.0)	0.04 (0.01)	-0.09 (0.04)	0.44	0.27
Nitrogen	9.0 (10.0)	0.01 (NS)	-0.19 (0.06)	$5.0 \times 10^{-4}$	0.16
Sucrose	8.0 (10.0)	0.02 (NS)	-0.08 (0.04)	$1.3 \times 10^{-3}$	0.07

$\beta_{b0}$ =mean biomass of an individual bluebunch wheatgrass tiller grown in isolation,  
 $\beta_{bb}$ =effect of bluebunch wheatgrass density on bluebunch wheatgrass biomass per tiller,  
 $\beta_{bs}$ =effect of spotted knapweed density on bluebunch wheatgrass biomass per tiller.  
 Numbers in parentheses are standard errors for coefficients significantly different from zero ( $P=0.05$ ).

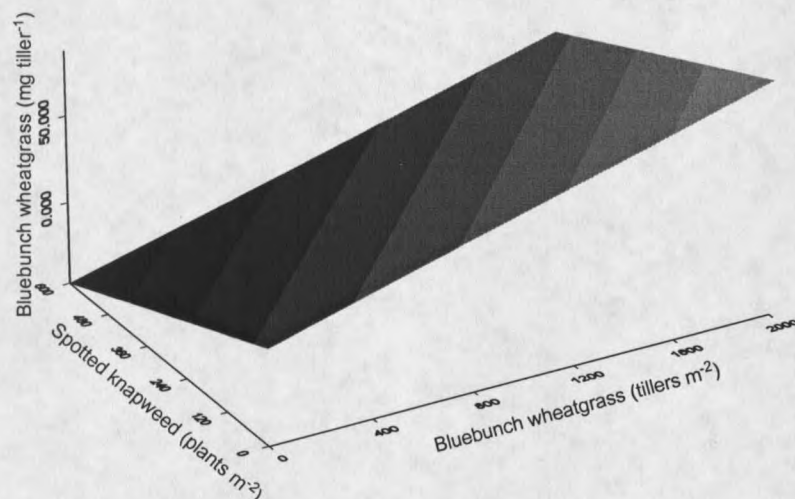


Figure 4.1. Response surface of bluebunch wheatgrass biomass per tiller versus bluebunch wheatgrass and spotted knapweed densities at Story Hills in non-amended plots.

Table 4.7. Calculated variance ratios and critical F values for accepting null hypothesis.

	Red Bluff	Story Hills	
	Spotted knapweed	Bluebunch wheatgrass	Spotted knapweed
Control vs. N	1.46	1.31	2.00
Control vs. S	0.72	0.63	0.19
N vs. S	0.79	0.70	2.54
Critical			
F-value( $\alpha=0.05$ )	2.60	2.21	2.60 (2.13 at $\alpha=0.10$ )

Spotted knapweed biomass per plant was negatively influenced by spotted knapweed density in the control and with soil amendments at both sites (Tables 4.8 and 4.9). The negative influence of spotted knapweed density on its biomass was nearly an order of magnitude greater at Story Hills than at Red Bluff. At Red Bluff, an increase of one spotted knapweed plant was associated with a four to six milligram decrease in spotted knapweed biomass per plant across treatments. At Story Hills, an increase of one spotted knapweed plant was associated with a 20 to 30 milligram decrease in spotted knapweed biomass per plant across treatments. Bluebunch wheatgrass density influenced spotted knapweed biomass in the control and N amended plots at Red Bluff, where an increase of three to six bluebunch wheatgrass tillers decreased spotted knapweed biomass by one milligram (Figure 4.2). Red Bluff adjusted  $r^2$ s were 0.17 to 0.22. Story Hills adjusted  $r^2$ s were 0.24-0.32. The slope of the regressions were not affected by soil amendments at either site (Table 4.6). At Story Hills, the slope of the N and S amended regressions differed at the  $\alpha=0.10$  level.

Table 4.8. Regression coefficients and adjusted coefficients of determination ( $r^2$ ) for predicting spotted knapweed biomass ( $\text{mg plant}^{-1}$ ) at Red Bluff.

Treatment	$B_{s0}$	$B_{ss}$	$B_{sb}$	$B_{ss}/\beta_{sb}$	$r^2$
Control	2880 (350)	-3.8 (1.0)	-5.7 (3.0)	0.67	0.17
Nitrogen	3560 (363)	-4.7 (1.0)	-3.3 (2.0)	1.42	0.22
Sucrose	3490 (393)	-5.8 (1.0)	-3.4 (NS)	$5.8 \times 10^4$	0.18

$B_{s0}$ =mean biomass of an individual spotted knapweed plant grown in isolation,  $\beta_{ss}$ =effect of spotted knapweed density on spotted knapweed biomass per plant,  $\beta_{sb}$ =effect of bluebunch wheatgrass density on spotted knapweed biomass per plant. Numbers in parentheses are standard errors for coefficients significantly different from zero ( $P=0.05$ ).

Based on ratios of competition coefficients, spotted knapweed influenced spotted knapweed biomass more than bluebunch wheatgrass influenced spotted knapweed

biomass (Table 4.8 and 4.9). This influence was especially large at Story Hills where spotted knapweed was almost 200 to 300 times more influential than bluebunch wheatgrass in determining spotted knapweed biomass per plant. The relative influence of spotted knapweed was greatest when N was added. At Red Bluff, the relative influence of spotted knapweed compared to bluebunch wheatgrass for predicting spotted knapweed biomass was 0.67, 1.42, and  $5.8 \times 10^4$  in the non-amended, N amended, and S amended models, respectively.

Table 4.9. Regression coefficients and adjusted coefficients of determination ( $r^2$ ) for predicting spotted knapweed biomass ( $\text{mg plant}^{-1}$ ) at Story Hills.

Treatment	$B_{s0}$	$B_{ss}$	$B_{sb}$	$B_{ss}/\beta_{sb}$	$r^2$
Control	8800 (788)	-17.7 (3.0)	-3.4 (NS)	$1.8 \times 10^5$	0.32
Nitrogen	11900 (1179)	-31.4 (6.0)	-6.4 (NS)	$3.1 \times 10^5$	0.24
Sucrose	8090 (802)	-16.9 (2.0)	-1.3 (NS)	$1.7 \times 10^5$	0.24

$B_{s0}$ =mean biomass of an individual spotted knapweed plant grown in isolation,  $\beta_{ss}$ =effect of spotted knapweed density on spotted knapweed biomass per plant,  $\beta_{sb}$ =effect of bluebunch wheatgrass density on spotted knapweed biomass per plant. Numbers in parentheses are standard errors for coefficients significantly different from zero ( $P=0.05$ ).

The  $[\beta_{bb}:\beta_{bs}/\beta_{ss}\beta_{sb}]$  double ratio used to determine partitioning of resources between species was calculated at Story Hills where significant models were available for both species. Strong deviations from unity occurred in all treatments. Double ratios equaled  $2.4 \times 10^{-6}$ ,  $1.6 \times 10^{-9}$ , and  $7.6 \times 10^{-10}$  for the non-amended, N amended, and sucrose amended models, respectively, suggesting strong resource partitioning between bluebunch wheatgrass and spotted knapweed.

### Absolute Biomass

Absolute biomass differed between sites, therefore sites were analyzed separately ( $P < 0.001$ ). Absolute biomass was lower at Red Bluff than Story Hills. Spotted knapweed absolute biomass was  $358.2 \text{ g m}^{-2}$  at Red Bluff and  $487.9 \text{ g m}^{-2}$  at Story Hills. Bluebunch wheatgrass absolute biomass was  $2.6 \text{ g m}^{-2}$  at Red Bluff and  $27.1 \text{ g m}^{-2}$  at Story Hills.

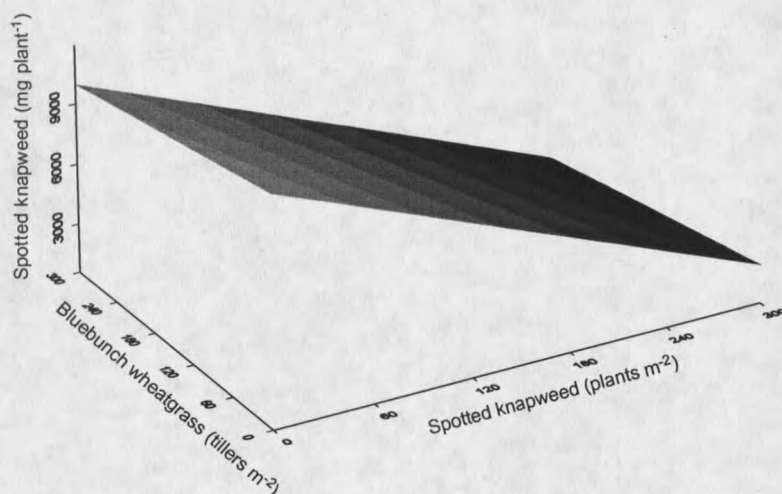


Figure 4.2. Response surface of spotted knapweed biomass per plant versus spotted knapweed and bluebunch wheatgrass densities at Story Hills in N amended plots.

Soil amendments affected absolute biomass of spotted knapweed at both sites, but bluebunch wheatgrass absolute biomass remained unaffected (Table 4.10). At both sites spotted knapweed absolute biomass was highest with N amendment and lowest with sucrose or no soil amendment (Table 4.11). Nitrogen amendment increased biomass by about 40% at Red Bluff and 30% at Story Hills.

Soil NO<sub>3</sub>-N, NH<sub>4</sub>-N, and Total Plant Available N Concentration

Soil NO<sub>3</sub>-N (P<0.01), NH<sub>4</sub>-N (P<0.01), and total plant available N concentration (P<0.01) were different at the two sites, therefore sites were analyzed separately. Soil N concentrations were lower at Red Bluff than Story Hills. Soil NO<sub>3</sub>-N concentration was 1.2 ppm at Red Bluff and 2.3 ppm at Story Hills. Soil NH<sub>4</sub>-N concentration was 2.8 ppm at Red Bluff and 4.1 ppm at Story Hills. Total plant available N concentration was 4.1 ppm at Red Bluff and 6.4 ppm at Story Hills.

Table 4.10. P-values from ANOVA for spotted knapweed and bluebunch wheatgrass absolute biomass at Red Bluff and Story Hills. Spotted knapweed data were square root transformed for Story Hills and bluebunch wheatgrass data were log<sub>10</sub> transformed.

Source	Df	Spotted knapweed Red Bluff	Spotted knapweed Story Hills	Bluebunch wheatgrass Red Bluff	Bluebunch wheatgrass Story Hills
Rep	2	0.92	0.59	0.70	0.72
Treatment	2	<0.01	<0.01	0.46	0.82

Table 4.11. Treatment effect on spotted knapweed absolute biomass (square root transformation). Actual lsmeans are presented. Different letters separate lsmeans that are significantly different.

Treatment	Spotted knapweed biomass (g m <sup>-2</sup> ) Red Bluff	Spotted knapweed biomass (g m <sup>-2</sup> ) Story Hills
Control	326.4 a	455.5 a
Nitrogen	438.9 b	577.5 b
Sucrose	310.3 a	428.1 a

Soil N concentrations were affected by soil amendments at both sites (Table 4.12). At Red Bluff, the N amendment increased NO<sub>3</sub>-N concentration by about 90% over that of the control and sucrose amendment. Nitrogen amendment increased NH<sub>4</sub>-N and total plant available N concentration by about 15% and 9% over that of the control

and sucrose amendment, respectively. The control and sucrose amendment did not differ in soil N concentration (Table 4.13).

Table 4.12. P-values from ANOVA for soil NO<sub>3</sub>-N, NH<sub>4</sub>-N, and total plant available N concentration at Red Bluff and Story Hills. Red Bluff data were square root transformed and Story Hills data were reciprocal transformed for analysis.

Source	df	Red Bluff			Story Hills		
		NO <sub>3</sub> -N	NH <sub>4</sub> -N	Total Plant Available N	NO <sub>3</sub> -N	NH <sub>4</sub> -N	Total Plant Available N
Rep	2	0.01	0.01	<0.01	0.84	<0.01	<0.01
Treatment	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

Table 4.13. Effect of treatment on Red Bluff soil NO<sub>3</sub>-N, NH<sub>4</sub>-N, and total plant available N concentrations (square root transformation). Actual lsmeans are presented. Different letters separate lsmeans that are significantly different.

Treatment	NO <sub>3</sub> -N (ppm)	NH <sub>4</sub> -N (ppm)	Total Plant Available N (ppm)
Control	0.04 a	0.97 a	1.06 a
Nitrogen	3.69 b	6.76 b	10.5 b
Sucrose	0.03 a	1.00 a	1.09 a

At Story Hills, soil N concentrations increased with N amendment (Table 4.14).

Nitrogen amendment increased NO<sub>3</sub>-N concentration by about 35%, NH<sub>4</sub>-N concentration by about 6%, and total plant available N concentration by about 10% over that of the control and sucrose amendment. Sucrose amendment decreased NO<sub>3</sub>-N concentration by about 40% below that of the control, but had no effect on NH<sub>4</sub>-N and total plant available N concentration (Table 4.14).

Table 4.14. Effect of treatment on Story Hills soil NO<sub>3</sub>-N, NH<sub>4</sub>-N, and total plant available N concentrations. Data were reciprocal transformed for analysis. Actual lsmeans are presented. Different letters separate lsmeans that are significantly different.

Treatment	NO <sub>3</sub> -N (ppm)	NH <sub>4</sub> -N (ppm)	Total Plant Available N (ppm)
Control	0.19 b	1.43 a	1.61 a
Nitrogen	6.68 c	9.61 b	16.30 b
Sucrose	0.12 a	1.38 a	1.50 a



## Discussion

### Competitive Dynamics

Competition importance describes the role of competition in relation to other processes that may influence plant community dynamics (Radosevich and Roush 1990). The adjusted  $R^2$  of a Spitters (1983) model are used to interpret the importance of competition (Weldon and Slauson 1986). Competition importance is useful for forecasting densities and species shifts at the community level (Radosevich et al. 1997). Competition importance was low in this study, typically accounting for less than one third of the variation. Competition appeared to be more important for explaining spotted knapweed biomass per plant than bluebunch wheatgrass biomass per tiller. As expected, intraspecific competition was more important than interspecific competition for spotted knapweed. This supports the findings of Jacobs and Sheley (1999) who found intraspecific competition was more important in determining spotted knapweed shoot weight than interspecific competition. Also, Lindquist et al. (1996) found that bluebunch wheatgrass had no effect on spotted knapweed growth when the two species were grown together.

In this study, abiotic factors influencing establishment of bluebunch wheatgrass may have been more important than competition, especially at Red Bluff. In another study conducted at Red Bluff, grass establishment was low and may have lowered the importance of competition with spotted knapweed (Carpinelli 2000). Spotted knapweed possesses traits typical of colonizing species (Bazzaz 1986), and appeared to overcome

establishment barriers created by harsh environments more effectively than the late successional bluebunch wheatgrass. Annual sunflower, an early successional, colonizing species initially established, but did not persist. The discrepancy in persistence between annual sunflower and spotted knapweed suggests spotted knapweed may possess traits that allow it to colonize and remain in the plant community even in the presence of competitors. Blicker et al. (2002) found that spotted knapweed may be tolerant of low nutrient conditions in addition to exploiting readily available resources following a disturbance, which may provide some explanation of its success.

The intensity of competition is the negative effect of a neighbor on the performance of an individual or population (Keddy 1990). Regression coefficients estimate the intensity of competition (Weldon and Slauson 1986). Competition intensity is useful for understanding specific physiological mechanisms influencing plant population dynamics (Radosevich et al. 1997). Competition intensity was not very high in this study. The two species experienced a high degree of resource partitioning, suggesting that spotted knapweed and bluebunch wheatgrass avoided competition. Niche differentiation may have occurred through germination behavior, root depth, temperature thresholds, phenology, and many other factors (Crawley 1997). Terrestrial plants occur as discrete individuals with each individual consuming resources in its immediate neighborhood (Tilman 1997). Because this study was limited to the first three years of establishment and followed a disturbance created by plowing, occupation of space may have influenced community dynamics more than competition for soil resources (Carpinelli 2000). Spotted knapweed may have a higher  $R^*$  for N than bluebunch

wheatgrass, but the two species coexisted with little competition because their "neighborhoods" may not have overlapped.

The intensity of competition may increase with increasing productivity (Grime 2001). Competition intensity at Story Hills, the more productive of the two study sites, was an order of magnitude greater than at Red Bluff. At Story Hills, amending the soil with N increased competition intensity and predicted maximum yield per plant for spotted knapweed. I had hypothesized that increasing soil N availability would increase the biomass and relative competitive ability of spotted knapweed. Amending the soil with N appeared to favor spotted knapweed at the more productive site, but had no effect at the less productive site.

#### Absolute Plant Biomass and Soil N Availability

Increased nitrogen availability consistently increased spotted knapweed absolute biomass. Results for spotted knapweed are supported by those of Story et al. (1989) who found applications of N fertilizer increased spotted knapweed biomass in western Montana. In other systems, high N availability has been found to facilitate invasion by nonindigenous, weedy species (Huenneke et al. 1990, Maron and Connors 1996, Alpert and Maron 2000, Blumenthal et al. 2003). Spotted knapweed and other invasive plants may respond to increased N availability because they possess traits characteristic of early succession species, such as rapid growth rate, high nutrient uptake rates, copious seed production, and short tissue longevity relative to late successional species (Bazzaz 1986). Species with these traits should have relatively high  $R^*$ s and be most successful in high nutrient environments (Tilman 1984).

Results for spotted knapweed absolute biomass support  $R^*$  theory (Tilman 1982, 1984, 1988). The  $R^*$  of spotted knapweed estimated in a companion study was between 0.4 and 0.6 ppm  $\text{NO}_3\text{-N}$ . Soil  $\text{NO}_3\text{-N}$  concentration in the N treatment was well above the estimated  $R^*$  and spotted knapweed absolute biomass increased above that of the control. However, spotted knapweed absolute biomass did not decrease when soil N availability was decreased by the sucrose treatment at Story Hills, even though soil  $\text{NO}_3\text{-N}$  concentration was lower than the estimated  $R^*$  for spotted knapweed. This result lends support to the suggestion that spotted knapweed's success may be explained by its genetic variation and plasticity; it can colonize disturbed sites by rapidly acquiring surplus nitrogen, and yet compete with late successional species for limited N on undisturbed sites (Blicker et al. 2002).

In contrast to spotted knapweed, bluebunch wheatgrass absolute biomass was not affected by increased N availability. Increases in available N have resulted in various responses by late successional, native species. In some cases, the application of N fertilizer increased late successional, native grass biomass (Owensby et al. 1972, Krueger-Mangold et al. 2004). Other studies have found an increase in late successional, native grass biomass when N availability is decreased (Paschke et al. 2000, Ewing 2002, Blumenthal et al. 2003). Additionally, nitrogen availability has been found to have no effect on late successional, native grass biomass (Morgan 1994, Alpert and Maron 2000). Differences in response may be due to the timing or level of N addition, species composition and life form, and past and current management (Huberty et al. 1998).

In this study, soil N concentration was low. Bluebunch wheatgrass is a perennial bunchgrass adapted to persist under N-limited conditions (Charley 1977). Late successional native species with low nutrient supply often show a limited response to increase in soil nutrients as a consequence of adaptations which promote conservative nutrient use, loss, and uptake (Chapin 1991, Chapin et al. 1993). Species with these traits should have relatively low  $R^*$ s and be most successful in low nutrient environments (Tilman 1984). Like spotted knapweed, bluebunch wheatgrass data are consistent with  $R^*$  theory (Tilman 1982, 1984, 1988). The estimated  $R^*$  of bluebunch wheatgrass was less than 0.05 ppm  $\text{NO}_3\text{-N}$ . Nitrate concentrations were well above the estimated  $R^*$ , even when sucrose was added. Therefore, soil  $\text{NO}_3\text{-N}$  concentration was not low enough to promote the dominance of bluebunch wheatgrass over that of spotted knapweed.

Annual sunflower did not persist throughout the duration of the study. This was not surprising considering the estimated  $R^*$  of annual sunflower from the previous chapter was at least 0.6 ppm  $\text{NO}_3\text{-N}$ . Annual sunflower was not present during the third year of the study when soil amendments were applied. Ambient soil  $\text{NO}_3\text{-N}$  concentration during the first and second years of the study, based on the control, was less than the  $R^*$  of annual sunflower. The lack of performance of annual sunflower further supports  $R^*$  theory (Tilman 1982, 1984, 1988).

#### Effectiveness of Sucrose Amendments as a Method for Lowering N Availability

Soil N availability was increased when N was added to the plots, but only decreased with sucrose addition at Story Hills. In other studies, the effectiveness of carbon additions and the amount of carbon necessary to decrease soil N availability

varied (Morgan 1994, Wilson and Gerry 1995, Reeve Morghan and Seastedt 1999, Alpert and Maron 2000, Blumenthal et al. 2003, Brockington 2003). Brockington (2003) applied varying amounts of sucrose at three frequencies to pots of spotted knapweed in the greenhouse. She found that soil  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$  increased with increasing amounts and frequencies of application of sucrose. The effects of sucrose on microbial immobilization may be highly ephemeral (Stevenson 1982, Brockington 2003). With time, soil microbial populations may decline and release previously immobilized  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$  (Jonasson et al. 1999, Reeve-Morghana and Seastedt 1999, Brockington 2003).

Sucrose may have been more effective at Story Hills than at Red Bluff because Story Hills soil contained more clay than Red Bluff soil. Clay particles are highly absorptive of water, gas, and dissolved substances (Kohnke and Franzmeier 1995) and are positively correlated with mineralized N, microbial biomass, and non-exchangeable  $\text{NH}_4\text{-N}$  content (Wardle 1992, Liang et al. 1999, Patra et al. 1999). Clay has a superior ability to hamper turnover of organic products and thus enhance retention of microbial biomass (Wardle 1992). Because soil from Story Hills had higher clay content, initial microbial biomass and its subsequent retention may have been greater than at Red Bluff. If so, greater microbial biomass would have resulted in greater N immobilization in response to carbon amendments (Wardle 1992).

### Conclusion and Management Implications

The first objective of this study was to determine the potential to predict the outcome of succession within an Idaho fescue/bluebunch wheatgrass (Mueggler and

Stewart 1980) plant association using  $R^*$  theory. Annual sunflower disappeared by the third year of the study, thereby confirming my expectation that the species with the highest  $R^*$  would diminish in dominance over time as long as soil N concentration continued to decrease (Tilman and Wedin 1991a, 1991b). After three years, I was unable to conclude whether the species with the lowest estimated  $R^*$ , bluebunch wheatgrass, would dominate as soil N concentration decreased. Bluebunch wheatgrass did not establish well at either site compared with spotted knapweed. Initial establishment and dominance may largely influence transient successional dynamics (Gleeson and Tilman 1990). Observation of the plots in upcoming years, especially the third replication at Story Hills that was not sampled for this study, may provide a more accurate prediction of successional dynamics.

The second objective of this study was to determine the influence of modifying soil N concentration on successional dynamics, to further test the  $R^*$  theory, and to test the potential of soil N alteration with sucrose amendment as a modifying factor to direct plant communities toward desired species. Further research on the effectiveness of carbon amendments is necessary. Longevity of effectiveness, amount of labor involved in application, and cost of carbon amendments currently prevent large-scale application (Reever Morghan and Seastedt 1999). Future research should investigate how the quantity and frequency of application and site characteristics will influence the effectiveness of sucrose amendments in management of nonindigenous, invasive plants. In addition, future research should strive to identify and evaluate practical sources of carbon, such as waste products like sawdust or sugar beet pulp (Reever Morghan and

Seastedt 1999). In addition, other less intrusive methods of decreasing soil N concentration, such as seeding cover crops (Herron et al. 2001), should be further investigated.

My results suggest that competitive relationships between bluebunch wheatgrass and spotted knapweed may be affected by soil N concentration at sites with higher productivity. Spotted knapweed absolute biomass increased as N availability increased, suggesting spotted knapweed may dominate when soil N concentrations are high.

Results concerning successional dynamics when soil N concentration is decreased are less clear. If soil N concentration could have been lowered closer to the estimated  $R^*$  of bluebunch wheatgrass through either increased quantities of sucrose additions or more frequent sucrose applications, bluebunch wheatgrass may have increased in dominance.

Increased soil N availability enhanced the performance of spotted knapweed. In areas currently infested with spotted knapweed, land managers should prevent activities that increase soil N availability, such as direct fertilization, burning, and cultivation. During restoration of weed-infested lands, seeding a cover crop along with desirable species that will sequester N and facilitate establishment of late successional, desirable species (Herron et al. 2001).



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## SUMMARY AND IMPLICATIONS OF RESEARCH

This body of research focused on expanding the successional management framework for nonindigenous plant invasions. I concentrated on controlling species performance through competition for a resource in limited supply. The overall research objective was to investigate the applicability of  $R^*$  theory on western range and wild lands currently infested by invasive plants.  $R^*$  theory is a model of plant community dynamics that addresses competition for limited resources. It states that the plant population with the lowest  $R^*$ , the amount of an essential resource required for an equilibrium population (birth rate = mortality rate), will ultimately dominate the community as succession progresses.

The first study identified the primary limiting resource within the Idaho fescue (*Festuca idahoensis* Elmer)/bluebunch wheatgrass (*Agropyron spicatum* Pursh) plant association typical of western Montana. I hypothesized that nitrogen (N) would be more limiting to plant growth than water, light, phosphorus, potassium, or sulfur. Nitrogen was found to increase aboveground biomass of the dominant functional group (native bunchgrasses) over that of the untreated control. No other resource tested increased aboveground biomass. I concluded that N was the primary limiting resource within the Idaho fescue/bluebunch wheatgrass plant association. Nitrogen should be the focus when attempting to control species performance through competition for resources in limited supply.

The second study, conducted in the greenhouse, compared  $R^*$ s for N for three species found within the Idaho fescue/bluebunch wheatgrass plant association.  $R^*$ s were

estimated for annual sunflower (early successional), bluebunch wheatgrass (late successional), and spotted knapweed (nonindigenous invader) by growing them in monoculture. Estimated  $R^*$ s were then used to predict the outcome of competition when the three species were grown in polyculture. I hypothesized that annual sunflower would have the highest  $R^*$ , bluebunch wheatgrass would have the lowest  $R^*$ , and the  $R^*$  of spotted knapweed would be greater than bluebunch wheatgrass but less than annual sunflower. I further hypothesized that  $R^*$ s from the monocultures could predict the outcome of competition in polyculture. Therefore, as N availability decreased, the biomass of a species with a higher  $R^*$  would decrease below that of the monoculture when grown in polyculture with a species that had a lower  $R^*$ .

Results from the second study confirmed my hypothesis that the  $R^*$  of annual sunflower  $>$   $R^*$  of spotted knapweed  $>$   $R^*$  of bluebunch wheatgrass. Estimated  $R^*$ s also successfully predicted the outcome of competition between annual sunflower and bluebunch wheatgrass and annual sunflower and spotted knapweed. Estimated  $R^*$ s did not successfully predict the outcome of competition between bluebunch wheatgrass and spotted knapweed. Spotted knapweed biomass increased when growing with bluebunch wheatgrass and bluebunch wheatgrass biomass decreased when growing with spotted knapweed, even though the estimated  $R^*$  for spotted knapweed was higher than that of bluebunch wheatgrass. I concluded that processes other than competition, such as allelopathy or mycorrhizal associations, may have allowed spotted knapweed to outperform bluebunch wheatgrass. Alternatively, bluebunch wheatgrass may be the superior competitor for N, but spotted knapweed may be a better competitor for a limiting

resource other than N, such as P. The ratio of N availability to P availability may have explained the outcome of competition when the two species grew together.

The final study expanded the greenhouse study to the field. I seeded annual sunflower, bluebunch wheatgrass, and spotted knapweed in an addition series. During the third growing season, soil N availability was increased by adding N, decreased by adding sucrose, or left unmodified. The objective of the final study was to predict the outcome of succession under varying soil N availability based upon estimated  $R^*$ s of annual sunflower, bluebunch wheatgrass, and spotted knapweed. I hypothesized that under increased N availability spotted knapweed or annual sunflower would increase its biomass and competitive ability relative to the other two species, and under decreased N availability bluebunch wheatgrass would increase its biomass and competitive ability relative to the other two species.

Annual sunflower did not persist throughout the three years of the final study. At both sites, the importance and intensity of competition were not very high. The intensity of competition increased at the more productive study site and in the N amended plots, suggesting competition intensity increased with increasing productivity. Spotted knapweed appeared to be favored by increased nitrogen availability relative to bluebunch wheatgrass.

Bluebunch wheatgrass absolute biomass was not affected by N availability. When soil N concentration was compared to the estimated  $R^*$  of bluebunch wheatgrass, results supported  $R^*$  theory. Even with sucrose addition, soil N concentration never fell below the  $R^*$  of bluebunch wheatgrass to cause a decrease in bluebunch wheatgrass

biomass. Spotted knapweed absolute biomass increased when soil N increased, but did not decrease when soil N was decreased. Spotted knapweed absolute biomass did not decrease even though soil N concentration fell below its  $R^*$  when sucrose was added.

The effectiveness of sucrose in lowering soil N concentration was variable. At one site sucrose successfully lowered soil  $\text{NO}_3^-$  concentration below that of the control. At the other site, however, sucrose did not lower soil  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , or total N concentration below that of the control. I concluded that soil characteristics, such as clay content, were influential in determining sucrose effectiveness.

This research has implications for understanding and managing succession on western range and wild land that includes nonindigenous, invasive plants.  $R^*$  theory may be applicable to native species as estimated  $R^*$ s successfully predicted the outcome of competition between annual sunflower and bluebunch wheatgrass. When nonindigenous, invasive plants are included in the mix, however,  $R^*$  theory was not as effective in predicting the outcome of competition. Bluebunch wheatgrass was estimated to be a better competitor for N than spotted knapweed, but was outperformed by spotted knapweed when grown together. Additionally, complex processes may allow spotted knapweed to invade and persist in low N systems. Based on my results, competition for N contributes to successional dynamics in native systems. My results suggest invasive species may have other mechanisms at their disposal, however, that mediate competitive relationships with natives such as allelopathy and mycorrhizal associations.

Spotted knapweed appeared to capitalize on increased N availability by increasing its biomass, whereas bluebunch wheatgrass did not increase its biomass when N

availability was increased. Furthermore, spotted knapweed was persistent even when N availability was decreased. My research suggests spotted knapweed exhibits plasticity in its response to N availability. Spotted knapweed responds to increased N availability by increasing its growth but is not necessarily hindered by decreased N availability.

Plasticity may help explain the success of spotted knapweed, but also complicates the search for effectual management strategies.

The practicality of sucrose or other carbon amendments as a management tool for nonindigenous plant invasions is still in question. The impact of sucrose amendment on soil N concentration was variable. When soil N was lowered, bluebunch wheatgrass did not become more competitive and spotted knapweed biomass did not decrease. My results suggest the effectiveness of carbon amendments may be site specific, suggesting the need for tests of carbon amendments prior to broad application. Less expensive carbon sources than sucrose would have to be identified before large scale application could be feasible. More importantly, high N availability appears to increase the success of spotted knapweed and action should be taken to limit N enrichment on western range and wild land currently infested or under the threat of invasion.

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