Directing succession by altering nutrient availability
by Gretchen J Herron

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Land Rehabilitation
Montana State University
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Abstract:
Spotted knapweed reduces wildlife and livestock habitat, biodiversity, and increases erosion. Manipulating nutrient availability may be used to accelerate succession away from spotted knapweed. Early successional plant communities often thrive in sites with high nutrient availability, whereas late-successional communities are often found on lower nutrient availability. This study tested the ability to direct succession by altering nutrient availability in a growth chamber experiment and in the field. My hypotheses were: removal of nutrients changes the competitive advantage from spotted knapweed to bluebunch wheatgrass (late-seral), and nutrient addition will favor spotted knapweed in a growth chamber study. The field study tested the hypothesis that using either mid-seral species or annual rye would direct succession away from a weedy plant community.

In addition series matrices (densities ranging from 100 seeds m-2 to 5,000 seeds m-2), background densities of rye and bottlebrush squirreltail (3,000 seeds m-2) were used to remove nutrients from the soil in the growth chamber. Nitrogen or phosphorus (33 kg ha⁻¹) were added to the soil. The field study applied annual rye, bottlebrush squirreltail, nitrogen (31 kg ha⁻¹), and bluebunch wheatgrass as a completely randomized incomplete factorial design.

In the growth chamber, nutrient analysis of soil and vegetation indicated that rye and bottlebrush squirreltail reduced nutrient availability in soils. Data were fit to Watkinson’s curvilinear model to determine the competitive relationship between bluebunch wheatgrass and spotted knapweed. Competition coefficients indicated that without nutrient manipulation, spotted knapweed was more competitive than bluebunch wheatgrass. Annual rye changed the competitive balance in favor of bluebunch wheatgrass (equivalence ratio = 9.9). Addition of nitrogen, phosphorus, or the mid-seral species did not change the competitive relationship between the two species. The field study, demonstrated that the application of nitrogen and rye increased spotted knapweed density over rye alone. Bluebunch wheatgrass tended to enhance spotted knapweed establishment and growth. However, bottlebrush squirreltail and rye had negative effects on spotted knapweed without affecting bluebunch wheatgrass. The growth chamber study and the field study suggest that succession from spotted knapweed to late-seral bluebunch wheatgrass community may be accelerated by altering resource availability.
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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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CHAPTER 1

INTRODUCTION

Spotted knapweed (*Centaurea maculosa* L.) is a perennial forb native to central Europe and Russia (Rees *et al.*, 1996). Spotted knapweed currently infests every county in Washington, Idaho, Montana, and Wyoming (Sheley *et al.*, 1998). In Montana, spotted knapweed infests over 2.2 million hectares and is spreading at a rate of 27% per year (Lacey *et al.*, 1989; Chicoine *et al.*, 1985). The environmental impacts of spotted knapweed include reduced forage production (Watson and Renney 1974; Harris and Cranston 1979), reduced plant species diversity (Tyser and Key 1988), reduced wildlife habitat (Bedunah and Carpenter 1989) as well as increased erosion and stream sedimentation (Lacey *et al.*, 1989). The economic impact of spotted knapweed to the Montana livestock industry has been estimated at about $11 million each year (Hirsch and Leitch 1996).

Spotted knapweed is well-adapted to a wide range of environmental and climatic conditions (Watson and Renney 1974; Chicoine *et al.*, 1985). Spotted knapweed is highly competitive and relatively drought tolerant (Berube and Myers 1982). The weed displays germination and emergence polymorphism, allowing it to avoid intraspecific competition and occupy all available safe-sites by developing a hierarchy of age classes within a population (Sheley and Larson 1996). In addition, early establishment and rapid growth
rates enable knapweed to capture resources prior to neighboring species (Sheley et al., 1993). These characteristics allow spotted knapweed to establish and out compete established native species (Harris and Cranston 1979; Watson and Renney 1974).

Large scale spotted knapweed infestations become intractable due to their size. Cultural, mechanical, and chemical means of management have not proved sustainable and are not cost effective on most lands (Griffith and Lacey 1991). Development of sustainable cost-effective weed management is imperative to rehabilitate and preserve native plant communities. Sustainable methods for weed management focus on natural processes that govern plant community dynamics (Sheley et al., 1996). It is a reasonable assumption that mechanisms which control community dynamics could be used to manage weed invasion and spread (Sheley et al., 1996). Mechanisms that influence plant establishment and competitive ability such as disturbance, nutrient availability, growth rate and resource use efficiency are potential factors to sustainably manage invasive plants.

**Successional Introduction and History**

The process of succession occurs as plant populations within a community change over time. If the environment remains relatively constant, the change in composition becomes very slow or even ceases. Environmental stasis may occur when disturbance is removed (e.g. a stream meanders away from original site) or an exotic species creates a monoculture. Succession is divided into two parts, pertaining to the conditions of disturbance, primary and secondary. Primary succession occurs when plants establish on substrate that was not previously vegetated. An example of primary succession could
include a lava flow or a desiccated lake bed. Secondary succession is the pattern of establishment that follows a disturbance on vegetated land. An example of secondary succession is when a plant community establishes after a fire or clear-cut logging event. If undisturbed, secondary succession plant community composition will transition toward its predisturbance community structure and composition. Three successional stages (early, mid, and late) are recognized as containing unique species with distinct evolutionary characteristics. Late-succession communities are often idealized as a community having constant species composition. This plant community is associated with the efficient capture of resources by late-successional species creating a resilient community.

The theory of plant community change over time was originally discussed by Clements (1916) in the early 20th century. Clementian ecology focuses on a singular "climax" community. His successional theory is unidirectional and determined by individual performance. Clements brought an element of individual species influence to the pervasive landscape theory of the era. He emphasized vegetational homogeneity, dynamic nature of plant communities, and recognized that each species requires particular conditions to become established in the community. Clements theorized that over large tracts of land, vegetation can be characterized by a single climate-determined mature phase. All other populations reflect immature stages of the self-sustaining climatic climax vegetation (Allen and Hoekstra 1992).

Gleason expanded (1917; 1926) upon previous theories by introducing seed source, habitat condition, and dispersal's effect on species composition. Gleason (1926) also theorized that multiple steady states or climax communities exist and abiotic/biotic
processes select for organisms on a site. His approach expanded on the organismal concept Clements had developed. However, Gleason did not refute Clement's theory; he focused on the underlying processes that select individual organisms for a community rather than emphasizing Clement's community constraints on a large scale (Allen and Hoekstra 1992).

According to Gause's (1934) competitive exclusion principle, species that are in direct competition cannot coexist permanently on the same site. Therefore, the late-successional stage must be comprised of species that complement, rather than directly compete, with each other. Initial stages of succession include early-successional (pioneer) and mid-successional (intermediate) phases. However, currently, this principle is not accepted as the best explanation of species diversity and coexistence (Silvertown 1987).

Recent theories claim that plant species have various life cycle characteristics that allow them to succeed other species in a niche. Resource allocation is the term used to denote plant traits that allow species to survive (Radosvich et al., 1997). The theory addressing patterns of evolutionary development is that of r- and K-selection. This theory is based on carrying capacity limits. A resource limitless environment would increase exponentially whereas in a real environment growth levels off as the population approaches the carrying capacity. MacArthur (1962) and Pianka (1970; 1994) developed the theory of r- and K-selection. The theory hypothesizes that within the range of resource availability, species develop two contrasting strategies for survival. Extreme K-strategists tend to be long lived, have prolonged vegetative stages, allocate a small portion of biomass to reproduction, are nutrient competitive, and occupy late stages of succession
Extreme r-selection species are often short-lived, colonize open spaces, allocate resources to reproduction, possess high growth rates, and occupy early successional stages.

Connell and Slatyer (1977) described several alternative mechanisms through which species replace each other via successional changes in the community. After a disturbance in the environment, opportunistic species classified as early-seral species colonize. Seeds of early-seral species are abundant in the seed bank or are adapted to migrate to disturbances. These species have the ability to first colonize a disturbed site because they allocate resources to rapid growth rates, dispersal mechanisms, and seed production (Tilman 1991). Early-seral species are most often annuals that occupy safe-sites becoming less competitive in sites where mature species are already established. Allocation of resources to above ground biomass decreases competitive ability for soil nutrients (Radosevich et al., 1997). According to Connell and Slatyer, (1977) the species that replace these early communities may be influenced by one of three mechanisms. Early-seral species may be replaced through facilitation, tolerance, or inhibition. Facilitation, requires early-seral species to change the soil and above ground environment prior to the establishment of mid- or late-seral species. The second mechanism emphasizes species tolerance. A predictable successional sequence occurs because of the existence of species that have evolved different strategies for exploiting environmental resources. Late-seral species are able to tolerate lower levels of resources than early-seral species. The third mechanism thought to be associated with successional changes is inhibition, whereby, all species resist invasion by competitors. The first occupants pre-
empt the space and continue to exclude or inhibit later colonists until the inhibitor species
die or are damaged; releasing environmental resources. When resources are released later
colonizers establish and reach maturity. This model has not been thoroughly investigated.

Grime (1979) expanded on the r and K theory of resource allocation developed by
Pianka (1970) and MacArthur (1962) to include stress and disturbance. He defined stress
as an external factor that limits production when resources (light, nutrients, water) are
limited. Disturbance is perturbation of plant biomass. If the extremes of high and low
stress and disturbance are considered, four possible combinations occur. These
combinations allow four evolutionary strategies: 1) ruderals: low stress, high disturbance
2) stress tolerators: high stress, low disturbance and 3) competitors: low stress, low
disturbance. The fourth combination of high stress and high disturbance are intolerable for
plant establishment (Radosevich et al., 1997). Grime arranges the three evolutionary
strategies depicting various degrees of stress, disturbance, and competition. Model
arrangement of various strategies provides categorical information about plant life cycles.

More recently, Tilman theorized that regardless of which species colonizes first the
species which is most competitive for the limiting resource(s) will eventually dominate the
site (Wedin and Tilman 1993). This theory of succession is termed the "resource-ratio"
hypothesis (Tilman 1985). This hypothesis suggests that succession results from a
gradient over time in the relative availabilities of limiting resources on a site. Resources
emphasized are soil nutrient availability and light at the soil surface. It is assumed that
these resources are inversely related. In addition, each plant species is assumed to be a
superior competitor for a particular proportion of the limiting resources. Therefore,
community composition should change when the ratio of the two limiting resources changes. The resource-ratio theory suggests that competition drives succession.

Tilman (1990) introduced a supporting theory to the resource-ratio hypothesis termed the R* theory. The R* theory delineates a basic mechanism of competition for a soil resource. The level that a soil limiting resource is reduced by a monoculture of a species is called R*. R* is the resource level a species requires for it to be able to persist in that environment. The species with the lowest R* for a limiting soil resource is predicted to be the superior competitor for the resource (Tilman 1980; 1990) and will displace less competitive species. R* is predicted to depend on plant traits (root mass, nutrient conservation abilities, photosynthetic rates, and maximal growth rate).

Study of successional catalysts has indicated that there may be a relationship between nutrient availability and successional stages (Wedin and Tilman 1993; Tilman 1990). Reflecting on what is known regarding plant seral stages and their characteristics, it is logical to assume that early-successional species that colonize open disturbed sites are poor competitors for nutrients. In these systems nutrient availability is not limiting. The limiting resources are often propagules, light, or space. This theory is reinforced by examining life cycle traits of early-seral species. Early-seral species have evolved to deseminate seeds, establish, and grow quickly to capture light resources and exclude slower growing species through development of above-ground biomass. Resource allocation for early-seral species includes prolific seed production increasing the probability that the species will be represented on site in the event of a disturbance. In addition, the evolution of high above-ground biomass enables early-seral species to
exclude neighboring species. Resources are not limited in disturbed sites because of the rerelease of nutrients previously constrained in plant biomass. Alternatively, late-seral species have highly developed root systems that, although decreases their ability to grow quickly, allows them to be highly competitive for nutrients and deplete the soil of available N (Wedin and Tilman 1993). Late-seral species have the ability to capture and hold nutrients present at low levels. High competitiveness allows late-seral species to displace earlier-seral stages over the course of time as nutrient levels decline. Wedin and Tilman (1993) identified lower levels of soil NO$_3^-$ and NH$_4^+$ in stands of late-seral *Agropyron*. Late-seral species are highly competitive in low nutrient soils but are inferior competitors under highly productive light limited habitats. (Wedin and Tilman 1993; Tilman 1988; 1990).

Weed scientists have begun to develop management methods based upon ecological principles. Maxwell *et al.* (1988) have developed a weed population model that serves as a framework to organize weed population biology information and develop weed control strategies. The model distinguishes stages in a weed’s life cycle when it is most susceptible to management efforts. These models are used to identify information gaps, set research priorities, develop hypotheses pertinent to weed population regulation, and suggest management strategies. Modeling work depicting weed/crop interactions have also been developed by Wilkerson *et al.* (1991), Shribbs *et al.* (1990), and Kropff and van Laar (1993). These models focus on weed threshold levels and give insight into when to employ control measures. Models were developed under various crop environments and are individually based upon factors such as abiotic influence, timing of herbicide
application, seed bank content, biomass, and plant interaction (Radosevich et al., 1997).

Resource management models developed by Rosenberg and Freedman (1984) and Pickett et al. (1987) have been utilized as the basis for a conceptual successional management model for weed infested rangelands (Sheley et al., 1996). The approach used by Sheley et al. (1996) incorporates successional components in managing exotic weed infestations. Successional weed management recognizes that plant communities are dynamic and employs technology to enhance natural processes that regulate vegetation change (Sheley et al., 1996). The conceptual model is based upon three components of succession (i.e. disturbance, colonization, and species performance).

**Objectives**

Our objective was to test early- and late-seral species response to nutrient addition and reduction. It may be possible to use species with demonstrated abilities to sequester nitrogen, such as annual rye (*Secale cereale* L.) or mid-seral species, to reduce resource availability during seedling establishment in order to favor late-seral species. The objective of the growth chamber study was to determine the effect of additions and reductions of nitrogen (N) and phosphorus (P) on the relationship between spotted knapweed and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Scribn and Smith). We hypothesized that nutrient additions would favor spotted knapweed, while nutrient reductions would favor bluebunch wheatgrass. In addition, resource additions or extractions may also be used to direct plant community succession. The objective of the field study was to determine the potential for directing weed dominated plant communities
along a trajectory toward more desirable communities by altering resource availability. The specific objective was to determine the effects of applied N, annual rye, and bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J. G. Smith) on the establishment and growth of spotted knapweed and the late-seral species, bluebunch wheatgrass. Annual rye and bottlebrush squirreltail, considered a mid-seral species, were seeded in an attempt to reduce the availability of nutrients to other species. We hypothesized that annual rye and bottlebrush squirreltail would decrease establishment and growth of spotted knapweed and favor the establishment and growth of bluebunch wheatgrass. The value of this work is to create an example of using successional principles to disturbed weed infested sites and direct a plant community change from weed dominated to desirable species dominated.
CHAPTER 2

INFLUENCE OF NUTRIENT AVAILABILITY ON THE INTERACTION BETWEEN SPOTTED KNAPWEED AND BLUEBUNCH WHEATGRASS

Introduction

Invasion of rangelands by spotted knapweed (*Centaurea maculosa* Lam.) in the northwestern United States and Canada has altered plant community composition and reduced forage value (Watson and Renney 1974), wildlife habitat (Bedunah and Carpenter 1989), and species diversity (Tyser and Key 1988). Spotted knapweed displaces perennial grasses and increases bare-ground (Tyser and Key 1988), surface water runoff, and stream sedimentation (Lacey *et al.*, 1989). Spotted knapweed infests over 7 million hectares in North America (Sheley *et al.*, 1998). Early germination, rapid growth, and allocation of resources to above ground biomass enable knapweed to preempt resource use by its competitors (Sheley *et al.*, 1993). Typically, knapweeds are more competitive than perennial grasses in high nutrient environments (Prather and Callihan 1991; Velagala *et al.*, 1997).

Over the past several decades, spotted knapweed management has focused mainly on chemical control. Because of environmental, ecological, and economic concerns, the appropriateness and effectiveness of chemical weed control strategies are being questioned (Sheley *et al.*, 1996). There has been an increasing call for weed management strategies that are based on an understanding of ecology (Radosevich *et al.*, 1997). Understanding
the mechanisms and processes associated with plant community dynamics is central to developing sustainable weed management strategies on rangeland (Maxwell et al., 1988; Sheley et al., 1996).

Nutrient availability may be a driving force in grassland community composition dynamics (Seastadt et al., 1991; Wedin and Tilman 1996; Vitousek et al., 1997). In disturbed, semiarid steppe, the rate of species replacement was more rapid on plots with less available soil nitrogen (N) and slowest on plots with more available N (McLendon and Redente 1992). Similarly, Tilman and Wedin (1991) studied a range of species with different successional niches and found that late-seral species were very competitive for N. Late-seral species had high below-ground biomass and created soils with high C:N, and consequently low N mineralization. Early-seral species were poor competitors for nitrogen, but persisted by maintaining rapid growth rates and high seed production. When grown in pairwise competition experiments, the late-seral species displaced early and mid-seral species (Tilman and Wedin 1991). The ability of a late-seral species to lower available ammonium and nitrate accounted for the change to a late-seral plant community.

Although Story et al. (1989) found that increasing available N increased the biomass of spotted knapweed, few studies address the influence of nutrient availability on the interactions of invasive non-indigenous plants and indigenous plants. It may be possible to use species with demonstrated abilities to sequester N, such as annual rye (Secale cereale L.) or mid-seral species, to reduce resource availability during seedling establishment in order to favor late-seral species. The objective of this study was to determine the effect of additions and reductions of N and phosphorus (P) on the
relationship between spotted knapweed and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Scribn and Smith). We hypothesized that nutrient additions would favor spotted knapweed, while nutrient reductions would favor bluebunch wheatgrass.

**Materials and Methods**

**Interference**

Spotted knapweed, bottlebrush squirreltail (*Sitanion hystrix* [Nutt.] J. G. Smith), and bluebunch wheatgrass were used as a model plant community to test the hypothesis that succession from a weedy plant community toward a desired late-seral plant community could be accelerated by altering nutrient availability. This study examined the effect of additions of N and P; annual rye; and bottlebrush squirreltail (mid-seral) on the interaction between spotted knapweed and bluebunch wheatgrass. Annual rye is reported to reduce nutrient availability in the soil (Mugwira et al., 1980). Densities and proportions of spotted knapweed (early-seral) and bluebunch wheatgrass (late-seral) were arranged to provide five addition series matrices (Radosevich 1987). Seeding densities of spotted knapweed:bluebunch wheatgrass in each matrix were 100:100, 100:1000, 100:3000, 100:5000, 1000:100, 1000:1000, 1000:3000, 1000:5000, 3000:100, 3000:1000, 3000:3000, 3000:5000, 5000:100, 5000:1000, 5000:3000, and 5000:5000 m⁻². Five treatments that alter nutrient availability were applied to each addition series matrix. Treatments consisted of (1) 0.65g N/pot, in the form of urea (2) 0.2004g P₂O₅/pot (3) an annual rye covercrop (3,000 seeds m⁻²), (4) bottlebrush squirreltail (mid-seral species) (3,000 seeds m⁻²), and (5) no nutrient manipulation (control). Each treatment matrix was
replicated three times. Nutrients were applied in liquid form. Experiments were conducted in pots (15 cm x 15 cm x 38 cm) which were filled with a low nutrient soil mixture collected from a grassland dominated by late successional species, including bluebunch wheatgrass and Idaho fescue (*Festuca idahoensis* Elmer) (Mueggler and Stewart 1980). Soil was sieved, mixed at a rate of 1:3 sand to soil, and pasteurized. Sand was used to simulate a nutrient poor soil. The soil mixture was saturated with water and allowed to equilibrate to field capacity. Seeds were broadcast on the soil surface and manually arranged until a uniform distribution was achieved. A small amount (<2mm depth) of dry soil was used to cover the seeds. The soil surface was periodically moistened with a fog mister and covered with plastic until seedlings emerged. Pots within each matrix were randomly placed in an environmental chamber (12 C, 12-h day length; 200 uE/m²/s, spectral light). Conditions of this study were within the range of those found during establishment of bluebunch wheatgrass populations. Plants were allowed to grow for 60 days.

In 1997, additional densities of bluebunch wheatgrass and spotted knapweed were seeded in combination with annual rye in the environmental chamber under identical environmental conditions (12 C, 12-h day length; 200uE/m²/s, spectral light). Additional densities of bluebunch wheatgrass and spotted knapweed were created to quantify annual rye’s effect on these species at low densities. Densities of 1, 2, 3, and 4 seeds of bluebunch wheatgrass were seeded with annual rye (3,000 seeds m⁻²). Spotted knapweed densities of 1, 2, 3, and 4 seeds were sown in the presence of annual rye at the same density.
Sampling. The soil was sampled and analyzed prior to seeding to determine available levels of N and P (Page et al., 1982; Olsen et al., 1954). Soil analysis prior to mixing indicated that the soil contained about 31 mg kg\(^{-1}\) NH\(_4\), 138 mg kg\(^{-1}\) NO\(_3\), and 13 mg kg\(^{-1}\) of phosphorus. Organic matter was approximately 8%. Initial seedling densities were recorded two weeks after planting. All vegetation was harvested 60 days following seeding. Final harvest densities by species and above and below ground biomass were determined. At the end of the study, soil samples were collected and analyzed for available N (NO\(_3\) and NH\(_4\)) and P (PO\(_4\)) levels. Above ground biomass was collected and analyzed for N and P concentration. Total N and P uptake (concentration*plant biomass) was used to quantify nutrient dynamics. Analysis of variance was used to quantify nutrient addition and depletion effects on spotted knapweed and bluebunch wheatgrass N and P uptake and soil nutrient levels.

Analysis. Nonlinear regression analysis was used to determine the effect of the nutrient addition, annual rye, and a mid-seral species on equivalence ratios of spotted knapweed and bluebunch wheatgrass. Data were iteratively fit to models of the following forms (Firbank and Watkinson 1985):

\[
\text{bluebunch wheatgrass } W_w = W_{mw} \left[1 + A_w(N_w + C_{wk}N_k)\right]^{Bw} \\
\text{spotted knapweed } W_k = W_{mk} \left[1 + A_k(N_k + C_{kw}N_w)\right]^{Bk}
\]

where \(W_w\) and \(W_k\) are the weight per plant of bluebunch wheatgrass and spotted knapweed, respectively. \(W_{mw}\) and \(W_{mk}\) are the maximum weight of a plant grown in isolation, and \(A_w\) and \(A_k\) represents the area required by a plant to achieve \(W_m\). \(N_w\) and
\( N_k \) are the harvest densities of bluebunch wheatgrass and spotted knapweed, respectively. The parameters, \( C_{wk} \) and \( C_{kw} \), are the per-plant equivalence of \( w \) and \( k \) and can be interpreted as the ratio of intra:interspecific competition. The \( C \) parameters are also the equivalence ratio of the number of plants \( (N_k \) and \( N_w) \) it takes to have equivalent effect on bluebunch wheatgrass or spotted knapweed biomass. For example, in determining bluebunch wheatgrass biomass, if the \( C \) parameter is 0.5, then 0.5 unit of spotted knapweed density has the same ability to reduce biomass of bluebunch wheatgrass as one unit density of bluebunch wheatgrass. \( B_w \) and \( B_k \) may be used to estimate the efficiency of resource utilization by each population. The asymptotic 95\% confidence interval around fit values for \( C_{wk} \) and \( C_{kw} \) were used to determine the relative intensity of competition under the different nutrient and plant community treatments.

**Growth of Isolated Individuals**

Growth analysis was conducted at the same time and under the same environmental conditions as the addition series experiments. Absolute growth rate was used to compare inherent growth differences of each species. Individual species were seeded in pots 15 cm x 15 cm x 38 cm. The soil used in the growth analysis experiment is same soil described in the interference study. Pots were filled with soil, saturated with water and allowed to equilibrate to field capacity. Each of the four species were seeded in individual pots. Five seeds of each individual species were broadcast on the soil surface and arranged in a uniform distribution. A small amount (<2 mm depth) of dry soil was used to cover the seeds. The soil surface was covered with plastic and moistened with a
fog mist until seedlings emerged. Upon emergence, plants were thinned to a single individual plant. Pots were randomly placed in a growth chamber. The experiment was replicated three times.

**Sampling.** Each pot was harvested for plant biomass every 12 days over 60 days. Above-ground biomass was harvested by clipping plants at the soil surface. Plants were dried (60°C, 48 hr) to a constant weight and weighed.

**Analysis.** Linear regression was used to quantify the absolute growth rate of each species. Regression lines were compared using the extra sums of squares procedure (Snedecor and Cochran 1980).

**Results**

**Nutrients**

**Soil Nitrogen and Phosphorus.** Analysis of variance indicated a difference in residual soil NO₃ and P (p<0.05) among treatments imposed on the addition series of spotted knapweed and bluebunch wheatgrass (Table 1). Available soil N was 0.40 mg N kg⁻¹ soil in the control addition series. Annual rye, P, and bottlebrush squirreltail decreased available N to 0.11, 0.18, 0.31 mg N kg⁻¹ of soil, respectively. N addition increased final N levels in the soil (0.64 mg N kg⁻¹). Soil P was 21.67 mg P kg⁻¹ in the control. P addition increased soil P to about 143 mg P kg⁻¹. No other treatments affected soil P levels.
Nitrogen and Phosphorus Uptake by Bluebunch Wheatgrass. N and P uptake by bluebunch wheatgrass differed among treatments \((p<0.05)\). Without nutrient manipulation, N uptake by bluebunch wheatgrass was 10.5 mg N of plant material per pot (Table 2).

Table 1. Residual soil N and P content following the plant growth study.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Soil NO\textsubscript{3}N (mg/kg)(standard deviation)</th>
<th>Soil P (mg/kg)(standard deviation)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.40 (+0.064)</td>
<td>21.7 (+13.43)</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>0.64 (+0.062)</td>
<td>9.0 (+13.10)</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>0.18 (+0.061)</td>
<td>143.0 (+12.80)</td>
</tr>
<tr>
<td>Squirreltail</td>
<td>0.31 (+0.061)</td>
<td>12.7 (+12.80)</td>
</tr>
<tr>
<td>Rye</td>
<td>0.11 (+0.060)</td>
<td>9.8 (+12.57)</td>
</tr>
<tr>
<td>LSD (0.05)</td>
<td>0.09</td>
<td>18.3</td>
</tr>
</tbody>
</table>

N uptake was unaffected by addition of N or P. Bottlebrush squirreltail and annual rye decreased N uptake by bluebunch wheatgrass when grown in the addition series mixture. Annual rye reduced N uptake 5 times more than did bottlebrush squirreltail. P uptake by bluebunch wheatgrass in the control was 0.71 mg P of plant material per pot, which was similar to the N and bottlebrush squirreltail nutrient manipulations. P application dramatically increased uptake to 1.63 mg P of plant material per pot. Annual rye decreased P uptake to the lowest level by bluebunch wheatgrass at 0.12 mg of plant material per pot.
Nitrogen and Phosphorus Uptake by Spotted Knapweed. N uptake by spotted knapweed ranged from 1.43 to 6.42 mg N of plant material per pot (Table 2). N or P addition did not affect N uptake by knapweed as compared to the control. Bottlebrush squirreltail increased N uptake by spotted knapweed, while annual rye decreased uptake of N in spotted knapweed more than all other treatments. Annual rye and bottlebrush squirreltail dramatically decreased P uptake by knapweed. N addition did not alter P uptake by spotted knapweed, while P addition increased P uptake nearly 3-fold that of the control.

Table 2. Nitrogen and phosphorus uptake by bluebunch wheatgrass and spotted knapweed.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Nitrogen Bluebunch Wheatgrass</th>
<th>Spotted Knapweed</th>
<th>Phosphorus Bluebunch Wheatgrass</th>
<th>Spotted Knapweed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(mg/kg)</td>
<td></td>
<td>(mg/kg)</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>10.49 (±1.16)</td>
<td>4.49 (±0.90)</td>
<td>0.71 (±0.12)</td>
<td>0.19 (±0.04)</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>10.22 (±1.20)</td>
<td>5.49 (±0.94)</td>
<td>0.65 (±0.12)</td>
<td>0.14 (±0.04)</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>11.49 (±1.10)</td>
<td>3.70 (±0.87)</td>
<td>1.63 (±0.11)</td>
<td>0.54 (±0.04)</td>
</tr>
<tr>
<td>Squirreltail</td>
<td>6.34 (±1.16)</td>
<td>6.42 (±0.74)</td>
<td>0.63 (±0.12)</td>
<td>0.01 (±0.04)</td>
</tr>
<tr>
<td>Rye</td>
<td>1.26 (±2.14)</td>
<td>1.43 (±0.98)</td>
<td>0.12 (±0.22)</td>
<td>&lt;0.01 (±0.05)</td>
</tr>
<tr>
<td>LSD (0.05)</td>
<td>1.76</td>
<td>1.24</td>
<td>0.18</td>
<td>0.06</td>
</tr>
</tbody>
</table>
Interference

**Bluebunch Wheatgrass Biomass.** Nonlinear regression coefficient predicting bluebunch wheatgrass mean plant biomass from spotted knapweed and bluebunch wheatgrass densities indicated that 0.17 spotted knapweed plants was competitively equivalent to 1.0 bluebunch wheatgrass when no addition of nutrients or other species were included in the experiment (Table 3). N addition to the system had no effect on the equivalence of spotted knapweed and bluebunch wheatgrass in determining individual bluebunch wheatgrass biomass. P addition or a background of bottlebrush squirreltail reduced the equivalence influence of spotted knapweed with bluebunch wheatgrass when predicting individual bluebunch wheatgrass biomass. Annual rye shifted the competitive advantage from spotted knapweed to bluebunch wheatgrass where it took 9.9 units of spotted knapweed to have an equivalent impact as 1.0 unit of bluebunch wheatgrass. Based on R², competition became more important in the annual rye (R²= 0.40) and bottlebrush squirreltail (R²=0.33) treatments than the other treatments (Weldon and Slauson 1986).

**Spotted Knapweed Biomass.** It took 0.38 bluebunch wheatgrass plants to have an equivalent impact on spotted knapweed mean individual plant biomass in the control addition series where no N or P were added and no other species were added as background (Table 4). Addition of N, P, bottlebrush squirreltail, or annual rye did not alter the competitive balance from that of the control. R² for the nonlinear regression were relatively low in all treatments. However, the system with the P addition showed a
trend of increasing the equivalence impact of bluebunch wheatgrass biomass on spotted knapweed and increased the importance ($R^2$) of competition.

Table 3. Equivalence ratios generated from the prediction of bluebunch wheatgrass biomass.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Equivalence ratio</th>
<th>Confidence Interval</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.17</td>
<td>0.03 - 0.30</td>
<td>0.13</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>0.14</td>
<td>0.03 - 0.24</td>
<td>0.12</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>0.64</td>
<td>0.21 - 1.06</td>
<td>0.07</td>
</tr>
<tr>
<td>Squirreltail</td>
<td>0.82</td>
<td>0.27 - 1.36</td>
<td>0.33</td>
</tr>
<tr>
<td>Rye</td>
<td>9.90</td>
<td>2.57 - 17.4</td>
<td>0.40</td>
</tr>
</tbody>
</table>

Table 4. Equivalence ratios generated from the prediction of spotted knapweed.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Equivalence ratio</th>
<th>Confidence Interval</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.38</td>
<td>0.17 - 0.57</td>
<td>0.10</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>0.23</td>
<td>0.07 - 0.39</td>
<td>0.05</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>0.54</td>
<td>0.10 - 0.97</td>
<td>0.27</td>
</tr>
<tr>
<td>Squirreltail</td>
<td>0.59</td>
<td>0.10 - 1.0</td>
<td>0.13</td>
</tr>
<tr>
<td>Rye</td>
<td>0.85</td>
<td>-1.05 - 2.75</td>
<td>0.07</td>
</tr>
</tbody>
</table>
Growth Rate of Isolated Individuals

Linear regression equations determining change in plant weight over time indicate that all species grew at different rates when compared using the extra sums of squares procedure (Figure 1). Annual rye had the fastest growth rate, followed by bluebunch wheatgrass, then spotted knapweed, and lastly, bottlebrush squirreltail.

Discussion

Many members of the knapweed genus are reported to grow rapidly (Sheley and Larson 1994, 1995; Velagala et al., 1997), whereas late-seral species, such as bluebunch wheatgrass, typically have slower growth rates, but are more competitive (Grime 1979). Species with high intrinsic growth rates are generally favored in high N environments (Heil and Bruggink 1987; Aerts and Benende 1988). In this study, bluebunch wheatgrass seedlings grew faster than spotted knapweed seedlings. Furthermore, N uptake was unaffected by N addition. We believe this was because of the low N level in the soil, which was collected from a bluebunch wheatgrass/Idaho fescue community type dominated by late-seral species. Soil low in N may not support the high production requirements of early-seral species, thus the species with the lower nutrient requirement should have a more rapid growth rate (Grime 1979; McGraw and Chapin 1989). It is also possible that the growth rate of seedlings is different than that of mature plants.

N is a major determinant of successional patterns in many ecosystems (Parrish and Bazzaz 1982; Tilman 1984, 1986; Wedin and Tilman 1996). Plant community shifts are attributed to changes in the competitive relationships among species as the level of N
Figure 1. Growth rate of isolated individuals
availability changes (Parrish and Bazzaz 1982; Tilman 1982, 1986; McLendon and Redente 1991; Miller and Werner 1987; Carson and Barrett 1988). It has been shown that increasing N availability facilitates establishment and persistence of species with high growth rates such as early-seral weed species (Bernese and Aerts 1984; Heil and Bruggink 1987). N amendments of 56 kg N ha$^{-1}$, 112 kg N ha$^{-1}$, and 224 kg N ha$^{-1}$ favored spotted knapweed in field trials in Montana (Story et al., 1989). In our study, increasing N did not alter the competitive relationship between spotted knapweed and bluebunch wheatgrass. Either the soil was so low in N that adding low amounts of N may not have been sufficient to alter the competitive relationship between the species, or N was not limiting. Leaching was not a factor in soil available N because pots were not watered after emergence.

Addition of P decreased soil N below that of the control. Reduction of available N by P may be explained using the resource-ratio hypothesis. N and P are essential resources for these plants, with their growth rates determined solely by the one resource in lower supply relative to their requirements (Tilman 1980, 1982). In this case, if P is the most limited resource it would limit growth in unamended soil. We believe addition of P allowed increased plant growth which, in turn, increased N uptake and decreased N availability at the end of the study. Reduction of available N by P shifted the competitive balance in favor of bluebunch wheatgrass.

Species composition can directly influence nutrient dynamics. Wedin and Tilman (1993) studied a range of species and found that the later the successional niche, the more competitive the species was for N. Late-seral species had high below-ground biomass. This creates soils with high C:N and low N mineralization. In this study, addition of the
mid-seral bottlebrush squirreltail reduced the N availability and correspondingly reduced the effect of spotted knapweed on bluebunch wheatgrass (Table 2). It is possible that mid-seral species persist by maintaining rapid growth rates and high seed production and begin to lower the availability of N in the root zone of surrounding species (Tilman 1991). This would create an environment that facilitates the establishment of late-seral species like bluebunch wheatgrass (Tilman 1991).

In restoration of spotted knapweed infested rangeland, establishment of late-seral species is often difficult because of weed competition during the establishment phase (Velagala et al., 1996). Sheley et al. (1996) proposed that it may be possible to use species with demonstrated abilities to sequester N, such as annual rye, to reduce resource availability. In this study, annual rye dramatically lowered N and shifted the competitive relationship from spotted knapweed to bluebunch wheatgrass. We believe that bluebunch wheatgrass has a lower N requirement than spotted knapweed and, therefore, has the ability to out-compete spotted knapweed at lower N levels (Tilman 1996). The shift in competitive balance from spotted knapweed to bluebunch wheatgrass when N levels were reduced is consistent with McLendon and Redente (1992) who demonstrated that reductions in N availability by adding sucrose accelerated succession in a sagebrush steppe site in northwestern Colorado.

Results for the prediction of spotted knapweed biomass indicate that no treatments effected the competitive ability of spotted knapweed. Low R² for the nonlinear regression indicate that competition under these treatments was not an important factor.
Our study provides initial evidence supporting the theory that nutrient levels can be altered to accelerate successional change from a weedy plant community toward a desired plant community. Ephemeral cover crops or mid-seral species could be used in restoration projects to lower N availability. Lower N availability could accelerate the establishment and domination of late-seral species over earlier successional weedy species. Because the growth chamber experiment studied seedlings that were not grown to reproduction, these results need to be tested in a long-term field study.
CHAPTER 3

DIRECTING SUCCESSION BY ALTERING NUTRIENT AVAILABILITY

Introduction

Over the past several decades, rangeland managers have focused weed management on controlling weeds, with limited regard for existing or resulting plant communities. While the appropriateness and effectiveness of weed management practices are being questioned, it is becoming increasingly clear that weed management decisions must consider ecological, environmental, and economic principles. The development of future rangeland weed management practices must be based on our understanding of the biology and ecology of rangeland ecosystems (MacMahon 1987; Allen and Allen 1988; Call and Roundy 1991; Pyke and Archer 1991).

Ecologically-based weed management will require scientists and managers to develop strategies based on an understanding of succession. Successional weed management depends on the principle that plant communities are dynamic and technology can be used to enhance natural processes and mechanisms that regulate vegetation change (Sheley et al., 1996). Ultimately, the goal is to direct weed-infested communities along a trajectory toward more desirable plant communities.

Resource availability may be one factor that can be regulated in successional management. In some cases, changes in plant communities are related to resource availability, and the relative ability of the species to use those resources at particular levels
(Sheley and Larson 1996). To quote Tilman (1988), "Because each plant species is constrained to being a superior competitor for particular resource levels, the forces that determine resources are critically important in determining vegetation pattern".

Researchers generally agree that the availability of soil nutrients change during succession, but there is a lack of agreement on the direction and significance of such changes. One line of argument suggests that the availability of all major resources (e.g. light, water, nutrients) is elevated at the soil surface shortly after disturbance, and that succession thereafter involves a diminution in resource availability (Grime 1979). For example, McLendon and Redente (1991) demonstrated that additions of N inhibited succession from annual to perennial species in a sagebrush steppe site in northwestern Colorado. They concluded that dominance by annuals during the early stages of secondary succession was related to high nutrient availability. Similarly, Story et al. (1989) and Carter et al. (1999) found that increased nitrogen favored spotted knapweed (*Centaurea maculosa* Lam.). However, Myers and Berube (1983) found no effect of nitrogen on diffuse knapweed (*Centaurea diffusa* L.) on a dry site in Canada. Because little is known about the ecological role and successional status of perennial non-indigenous weeds in assemblages of native plants, directing and predicting successional trajectories based on resource availability will not be possible until more information is available.

The potential for altering nutrient availability to direct succession has not been adequately explored. Most of the emphasis in nutrient management has been on increasing availability. However, various crops and cropping systems have been used to reduce nitrate leaching on agricultural fields (Chaubey *et al.*, 1994; Coyne *et al.*, 1995). Tilman
and Wedin (1991) studied a range of species with different successional niches and found late-seral species were very competitive for nitrogen. Late-seral species had high below-ground biomass and created soils with high C:N, resulting in low nitrogen mineralization. Early-seral species were poor competitors for nitrogen, but persisted by maintaining rapid growth rates and high seed production. When grown in pairwise competition experiments, late-seral species displaced early to mid-seral species (Tilman and Wedin 1991). The ability of a species to lower plant available ammonium and nitrate accounted for the results of the competition trials. It may be possible to use species with demonstrated abilities to sequester nitrogen, such as annual rye (*Secale cereal* L.) or mid-seral species to reduce resource availability.

Resource additions or extractions may be used to direct succession. The overall objective of this study was to determine the potential for directing weed dominated plant communities along a successional trajectory toward more desirable communities by altering resource availability. The specific objective was to determine the effects of nitrogen (N), annual rye, and bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J. G. Smith) on the establishment and growth of spotted knapweed and the late-seral species, bluebunch wheatgrass (*Pseudoroegneria spicatum* [Pursh.] Scribn and Smith). Annual rye and bottlebrush squirreltail, considered a mid-seral species, were seeded in an attempt to reduce the availability of nutrients. We hypothesized that annual rye and bottlebrush squirreltail would favor the establishment and growth of bluebunch wheatgrass and have a negative impact on spotted knapweed.
Materials and Methods

Study Sites

The study was conducted during 1996, 1997 at site 1 and 1996, 1997, and 1998 at site 2. Site 1 was located 25 km southwest of Bozeman, Mont. (45°36'N, 111°11'W) at an elevation of 1524 m. Site 2 was located 11 km east-northeast of Hamilton, Mont. (46°17'N, 114°1'W) at an elevation of 1341 m. Site 1 lies on a Festuca idahoensis/Agropyron spicatum habitat type and site 2 lies on a Festuca scabrella/Agropyron spicatum habitat type (Mueggler and Stewart 1980). Soil at site 1 is a loamy-skeletal over sandy or sandy skeletal mixed typic Argiboroll. Site 2 soil is a Stecum stony-loamy coarse sand, moderately steep mixed typic Cryothents. Both sites were dominated by spotted knapweed with an understory of downy brome (Bromus tectorum L.) with few forbs present. Annual precipitation at both sites ranges from 406 to 457 mm. Mean annual temperature at site 1 is 6.1 °C and 6.6 °C at site 2.

Procedures

Treatments were N, annual rye, bottlebrush squirreltail, and bluebunch wheatgrass arranged in an incomplete factorial arrangement (2 X 2 X 2 X 2). Each treatment was applied as either with or without that treatment including a combination without any treatment (control). All bottlebrush squirreltail by annual rye combinations were omitted. Treatments were arranged in a completely-randomized-design and replicated 4 times at each site.

In the fall of 1996, both sites were disced to a depth of 25 cm, which did not kill existing plants. Each site was divided into 48, 2 by 3 m plots. Seeds were broadcast,
raked, compacted with a roller, and lightly watered once in the fall of 1996 to enhance seed germination. All species were seeded at rate of 32 kg ha\(^{-1}\) to ensure establishment. N (31 kg ha\(^{-1}\)) was broadcast via a hand-spreader at a rate of 67 kg ha\(^{-1}\) (46-0-0; N-P-K).

**Sampling**

Spotted knapweed, annual rye, bottlebrush squirreltail, and bluebunch wheatgrass density and cover were measured at peak standing crop (July) of 1997 using a 0.445 m\(^2\) circular hoop on both sites. Because site 1 was inadvertently destroyed by the landowner, the same data, plus biomass, were only collected on site 2 in 1998 at peak standing crop. Harvesting included clipping all plants within a single randomly placed hoop by species to ground level in each plot. Biomass samples were dried to a constant weight (60° C) and weighed.

**Analysis**

Each site was analyzed separately using analysis of variance. N, annual rye, bottlebrush squirreltail, bluebunch wheatgrass, and all interactions (except interactions with annual rye by bottlebrush squirreltail) were included in the model, and tested using the residual error term. When a significant F-test (P\(<0.05\)) was calculated, differences among means were tested using Fishers protected least significant difference LSD (0.05) comparisons (Peterson 1985). In cases where low numbers caused lack of variance homogeneity (i.e. annual rye and bottlebrush squirreltail), main effects (N, annual rye, bottlebrush squirreltail, and bluebunch wheatgrass) were tested using standard t-tests.
Results

Spotted Knapweed

Density. Spotted knapweed density was unaffected by any treatment at site 1 in 1997 (Table 5). At site 2, bluebunch wheatgrass decreased spotted knapweed by 22.2 plants m\(^{-2}\) from that of the control (73.7 plants m\(^{-2}\); P=0.02) in 1997. By 1998, N and annual rye interacted to affect spotted knapweed density at this site (Table 5). Treatments without annual rye and/or N produced 173 plants m\(^{-2}\) (Figure 2). Adding N alone did not affect spotted knapweed density. Adding annual rye reduced mean spotted knapweed density to 46 plants m\(^{-2}\), which was below that of all other treatments. Adding both N and annual rye increased spotted knapweed density over the annual rye treatment.

Cover. Annual rye, bluebunch wheatgrass, and N also interacted to affect spotted knapweed cover at site 1 in 1997 (Table 5). Within the three way interaction, (N by annual rye by bluebunch wheatgrass), N plus annual rye produced the lowest spotted knapweed cover (Figure 3). N, bluebunch wheatgrass, and annual rye combined had the highest spotted knapweed cover but was similar to bluebunch wheatgrass and to N treatments, and N plus bluebunch wheatgrass treatments. Bluebunch wheatgrass produced similar spotted knapweed cover to that of N. Without N, bluebunch wheatgrass increased spotted knapweed cover.
Table 5. P-values for spotted knapweed density, cover, and biomass (1998) as the dependant variables generated from ANOVA.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Density (P-value)</th>
<th>Cover (P-value)</th>
<th>Density (P-value)</th>
<th>Cover (P-value)</th>
<th>Density (P-value)</th>
<th>Cover (P-value)</th>
<th>Biomass (P-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>1</td>
<td>0.67</td>
<td>0.41</td>
<td>0.58</td>
<td>0.07</td>
<td>0.15</td>
<td>0.85</td>
<td>0.25</td>
</tr>
<tr>
<td>Rye</td>
<td>1</td>
<td>0.68</td>
<td>0.17</td>
<td>0.65</td>
<td>0.34</td>
<td>0.37</td>
<td>0.85</td>
<td>0.85</td>
</tr>
<tr>
<td>Squirreltail</td>
<td>1</td>
<td>0.37</td>
<td>0.15</td>
<td>0.13</td>
<td>0.20</td>
<td>0.37</td>
<td>0.40</td>
<td>0.83</td>
</tr>
<tr>
<td>Wheatgrass</td>
<td>1</td>
<td>0.63</td>
<td>0.02</td>
<td>0.02</td>
<td>0.36</td>
<td>0.25</td>
<td>0.56</td>
<td>0.48</td>
</tr>
<tr>
<td>Rye*N</td>
<td>1</td>
<td>0.63</td>
<td>0.96</td>
<td>0.75</td>
<td>0.37</td>
<td>0.03</td>
<td>0.06</td>
<td>0.01</td>
</tr>
<tr>
<td>Squirreltail*N</td>
<td>1</td>
<td>0.16</td>
<td>0.49</td>
<td>0.96</td>
<td>0.64</td>
<td>0.12</td>
<td>0.42</td>
<td>0.01</td>
</tr>
<tr>
<td>Wheatgrass*N</td>
<td>1</td>
<td>0.97</td>
<td>0.13</td>
<td>0.90</td>
<td>0.57</td>
<td>0.95</td>
<td>0.24</td>
<td>0.01</td>
</tr>
<tr>
<td>Squirreltail*Wheatgrass</td>
<td>1</td>
<td>0.60</td>
<td>0.01</td>
<td>0.56</td>
<td>0.62</td>
<td>0.46</td>
<td>0.68</td>
<td>0.97</td>
</tr>
<tr>
<td>Rye*Wheatgrass</td>
<td>1</td>
<td>0.60</td>
<td>0.15</td>
<td>0.16</td>
<td>0.48</td>
<td>0.60</td>
<td>0.94</td>
<td>0.18</td>
</tr>
<tr>
<td>Rye<em>Wheatgrass</em>N</td>
<td>1</td>
<td>0.15</td>
<td>0.01</td>
<td>0.31</td>
<td>0.42</td>
<td>0.99</td>
<td>0.32</td>
<td>0.03</td>
</tr>
<tr>
<td>Squirreltail<em>Wheatgrass</em>N</td>
<td>1</td>
<td>0.66</td>
<td>0.06</td>
<td>0.53</td>
<td>0.93</td>
<td>0.47</td>
<td>0.88</td>
<td>0.50</td>
</tr>
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</table>
Figure 2.
Interaction of annual rye and N on spotted knapweed density at site 2 in 1998
Figure 3.
Interaction of annual rye, N, and bluebunch wheatgrass on spotted knapweed cover at site 1 in 1997
Bottlebrush squirreltail and bluebunch wheatgrass interacted to affect spotted knapweed cover at site 1 in 1997 (Table 5). Treatments without bottlebrush squirreltail produced similar spotted knapweed cover as those including bluebunch wheatgrass (Figure 4). Adding bottlebrush squirreltail alone reduced spotted knapweed cover by approximately 20% below all other treatments; however, the effect of bottlebrush squirreltail was removed in the presence of bluebunch wheatgrass. In 1997 and 1998, spotted knapweed cover was not affected by any treatment at site 2 (Table 5).

**Biomass.** Annual rye, bluebunch wheatgrass, and N interacted to determine spotted knapweed biomass at site 2 in 1998 (Table 5). Without these treatments, mean spotted knapweed biomass was about 144 g m^-2 (Figure 5). Adding both bluebunch wheatgrass and N reduced spotted knapweed biomass to about 86 g m^-2. Adding annual rye and bluebunch wheatgrass yielded the lowest spotted knapweed biomass (49 g m^-2). Including all three (annual rye, bluebunch wheatgrass, and N) yielded the highest spotted knapweed biomass. Within the three way interaction, (annual rye, bluebunch wheatgrass, and N), the addition of N bluebunch wheatgrass, or annual rye alone had no effect on spotted knapweed biomass.
Figure 4.
Interaction of bluebunch wheatgrass and bottlebrush squirreltail on spotted knapweed cover at site 1 in 1997
Figure 5. Interaction of annual rye, N, and bluebunch wheatgrass on spotted knapweed biomass at site 2 in 1988.
Bluebunch Wheatgrass

Density. Bluebunch wheatgrass successfully established at site 1 and site 2 by 1997 (Table 6). Its density was 37 plants m\(^{-2}\) at site 1. At site 2, adding N to those plots with bluebunch wheatgrass increased density from 10 to about 25 plants m\(^{-2}\) (Table 6; Figure 6). In 1998, bluebunch wheatgrass increased its density from zero (without bluebunch wheatgrass) to 26 plants m\(^{-2}\) at site 2 (Table 6).

Cover. Plots receiving bluebunch wheatgrass had twice the bluebunch wheatgrass cover (31%) than those without the seeding (15%) at site 1 in 1997 (Table 6). Bluebunch wheatgrass cover interacted with N to affect bluebunch wheatgrass cover at site 2 in 1997 (P=0.04). Seeding bluebunch wheatgrass increased its cover from 0.0 to 0.6 percent (LSD=0.004). At site 2 in 1998, adding N increased bluebunch wheatgrass cover to 1.2 percent. Bluebunch wheatgrass cover was unaffected by any treatment (Table 6).

Biomass. N and bluebunch wheatgrass interacted to affect bluebunch wheatgrass biomass at site 2 in 1998 (Table 6). Including bluebunch wheatgrass increased its biomass to 3.2 g m\(^{-2}\) (Figure 7). Adding N with bluebunch wheatgrass more than doubled bluebunch wheatgrass biomass.

Bottlebrush Squirreltail

Density. Including bottlebrush squirreltail among treatments resulted in 5.6 (P=0.0001) and 0.4 (P=0.0001) plants m\(^{-2}\) at site 1 and site 2, respectively, in 1997. Including N with bottlebrush squirreltail increased its density to 9.9 plants m\(^{-2}\) (P=0.002) at
Table 6. P-values for bluebunch wheatgrass density, cover, and biomass (1998) as the dependant variables generated from ANOVA.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Site 1 1997 Density (P-value)</th>
<th>Site 1 1997 Cover (P-value)</th>
<th>Site 2 1997 Density (P-value)</th>
<th>Site 2 1997 Cover (P-value)</th>
<th>Site 2 1998 Biomass (P-value)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0.74</td>
<td>0.02</td>
<td>0.04</td>
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<td>0.19</td>
<td>0.32</td>
<td>0.21</td>
<td>0.82</td>
</tr>
<tr>
<td>Squirreltail</td>
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<td>0.58</td>
<td>0.42</td>
<td>0.26</td>
<td>0.40</td>
<td>0.85</td>
</tr>
<tr>
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<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.85</td>
</tr>
<tr>
<td>Rye*N</td>
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<td>0.70</td>
<td>0.06</td>
<td>0.67</td>
<td>0.85</td>
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<tr>
<td>Squirreltail*N</td>
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<td>0.87</td>
<td>1.00</td>
<td>0.26</td>
<td>1.00</td>
<td>0.64</td>
</tr>
<tr>
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<td>0.72</td>
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<td>0.37</td>
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</tr>
<tr>
<td>Rye*</td>
<td>1</td>
<td>0.14</td>
<td>0.19</td>
<td>0.43</td>
<td>0.21</td>
<td>0.79</td>
</tr>
<tr>
<td>Wheatgrass</td>
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</tr>
<tr>
<td>Rye*</td>
<td>1</td>
<td>0.27</td>
<td>0.70</td>
<td>0.07</td>
<td>0.67</td>
<td>0.82</td>
</tr>
<tr>
<td>Wheatgrass*N</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Squirreltail*</td>
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<td>0.87</td>
<td>1.00</td>
<td>0.29</td>
<td>1.00</td>
<td>0.62</td>
</tr>
<tr>
<td>Wheatgrass*N</td>
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<td></td>
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<td></td>
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</tbody>
</table>

* Variances were heterogenous, therefore main effect were analyzed using t-tests
Figure 6. Interaction of bluebunch wheatgrass and N on bluebunch wheatgrass density at site 2 in 1997

Figure 7. Interaction of bluebunch wheatgrass and N on bluebunch wheatgrass at site 2 in 1998
site 1. Including bluebunch wheatgrass with bottlebrush squirreltail increased bottlebrush squirreltail to 15.6 plants m\(^{-2}\). At site 2 including bottlebrush squirreltail among treatments resulted in 22 plants m\(^{-2}\) in 1998 (P=0.02). No other treatment affected bottlebrush squirreltail density.

**Cover and Biomass.** Based on individual t-tests comparing main effects of treatments, no treatment affected percent cover at either site or year. Addition of bottlebrush squirreltail did not affect its biomass (0.02 to 0.35 g m\(^{-2}\)) at site 2 in 1998 (P=0.003; LSD=1.2). Addition of bottlebrush squirreltail plus N increased bottlebrush squirreltail biomass from 0.35 to 2.9 g m\(^{-2}\) (P=0.04).

**Annual Rye**

**Density.** In 1997, seeding annual rye increased rye density from 0.0 plants m\(^{-2}\) to 22.7 plants m\(^{-2}\) (P=0.0008) and from 0.6 plants m\(^{-2}\) to 11.3 m\(^{-2}\) (P=0.034; main effect) at site 1 and site 2, respectively. Addition of bluebunch wheatgrass at site 1 increased annual rye from 22.7 plants m\(^{-2}\) to 60.4 plants m\(^{-2}\) (P=0.0008). No treatments affected annual rye at site 2 in 1998.

**Cover and Biomass.** Based on individual t-tests comparing main effects of treatments, no treatment affected percent cover at either site or year. No treatment affected annual rye biomass in 1998.
Discussion

Previous research has indicated that spotted knapweed may excel in the presence of high N concentrations (Papova 1960; Story et al., 1989). Spotted knapweed has the early-seral characteristics of rapid growth rates, high seed production, high above ground biomass, and enhanced establishment and growth in high nutrient environments. Story et al. (1989) found that increasing N significantly increased spotted knapweed biomass. McLendon and Redente (1991) found that dominance of a site by annuals in early stages of secondary succession was related to high nutrient availability. In addition, McLendon and Redente (1992) tested the supply of N on plant community dynamics and found N incorporation in perennial plant tissue was a primary mechanism in controlling the rate of succession. In our study, annual rye decreased spotted knapweed density and biomass, when combined with bluebunch wheatgrass, at site 2 in 1998. In addition, spotted knapweed cover was decreased 20% below all other treatments by seeding bottlebrush squirreltail at site 1 in 1997; however, spotted knapweed was unaffected by bottlebrush squirreltail at site 2. Although these responses could result from competition for various factors (e.g. light, moisture, nutrients), annual rye and bottlebrush squirreltail may have affected spotted knapweed by removing available N from the rooting zone. In a growth chamber experiment, annual rye and bottlebrush squirreltail reduced available soil N below that of other treatments (Herron et al., 1998). This supports the hypothesis that annual rye and bottlebrush squirreltail can sequester N and make it less available to spotted knapweed.
Addition of N and annual rye increased spotted knapweed density over that of annual rye at site 2 in 1998. Addition of N may have negated the N depleted conditions produced by annual rye. Species, such as annual rye with higher potential growth rates are favored over those with slower growth rates under conditions of high N availability (Berendse et al., 1987; Heil and Bruggink 1987; Aerts and Berendse 1988).

In many cases, including bluebunch wheatgrass enhanced spotted knapweed establishment and growth, and adding N exacerbated the response. Whitford (1986) found that both soil moisture and nutrients are often higher under a plant canopy than between canopies or in vegetation gaps in dry environments. Many other researchers have found a form of facilitation, rather than competition, resulting in higher biomass under plant canopies (Muller 1953; Halvorson and Patten 1975; Parker et al., 1982). It appeared that bluebunch wheatgrass enhanced spotted knapweed by altering the microenvironment to provide increased safe-sites for spotted knapweed.

It was not surprising that bluebunch wheatgrass and bottlebrush squirreltail density were increased with the addition of N, where they were seeded. Conversely, addition of N did not affect spotted knapweed. In our study, about 31 kg ha\(^{-1}\) of N were applied. We believe that low application only enhanced newly seeded species with young root systems by remaining in the upper portion of the soil profile. In addition, the winter-annual, cheatgrass, may have had a temporal advantage in sequestering N. They may have captured the applied N and preempted its use by the deeper rooted, spotted knapweed (Sheley et al., 1993). These results differ from previous research of Story et al. (1989) and Carter et al. (1999); however, neither study included newly seeded species simultaneously with N application.
The most important finding of this study is that bottlebrush squirreltail and annual rye had some negative effects on spotted knapweed without affecting bluebunch wheatgrass. If the impacts on spotted knapweed persist, they may confer an advantage to bluebunch wheatgrass in the future.

Therefore, we believe that using either cover crops that sequester N or mid-seral species to facilitate the establishment of late-seral species when revegetating weed infested rangeland has merit. Our results suggest that further work on altering nutrient availability to direct succession away from weed dominance is warranted.


Gause, G. F. 1934. The Struggle for Existence. Williams and Wilkens, Baltimore, MD


APPENDICES
Appendix A

SPOTTED Knapweed AND Bluebunch Wheatgrass Density, Cover, And Biomass Means Generated For Treatment Main Effects.
Table 7. Spotted knapweed means for density, cover, and biomass generated for treatment main effects.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Site 1 1997</th>
<th></th>
<th>Site 2 1997</th>
<th></th>
<th>Site 2 1998</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Density (Plants m$^{-2}$)</td>
<td>Cover (Percent)</td>
<td>Density (Plants m$^{-2}$)</td>
<td>Cover (Percent)</td>
<td>Density (Plants m$^{-2}$)</td>
<td>Cover (Percent)</td>
</tr>
<tr>
<td>N</td>
<td>1</td>
<td>109.53</td>
<td>0.25</td>
<td>60.18</td>
<td>0.22</td>
<td>168.42</td>
<td>0.30</td>
</tr>
<tr>
<td>Rye</td>
<td>1</td>
<td>101.23</td>
<td>0.20</td>
<td>60.53</td>
<td>0.16</td>
<td>121.55</td>
<td>0.30</td>
</tr>
<tr>
<td>Squirreltail</td>
<td>1</td>
<td>96.33</td>
<td>0.19</td>
<td>55.61</td>
<td>0.16</td>
<td>121.01</td>
<td>0.28</td>
</tr>
<tr>
<td>Wheatgrass</td>
<td>1</td>
<td>110.24</td>
<td>0.30</td>
<td>51.50</td>
<td>0.16</td>
<td>116.71</td>
<td>0.29</td>
</tr>
</tbody>
</table>
Table 8. Bluebunch wheatgrass means for density, cover, and biomass generated for treatment main effects.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Density (Plants m$^{-2}$)</th>
<th>Cover (Percent)</th>
<th>Density (Plants m$^{-2}$)</th>
<th>Cover (Percent)</th>
<th>Biomass (Grams m$^{-2}$)</th>
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</thead>
<tbody>
<tr>
<td>N</td>
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<td>22.70</td>
<td>0.25</td>
<td>0.01</td>
<td>0.22</td>
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<td>0.01</td>
<td>0.16</td>
<td>13.35</td>
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<td>0.01</td>
<td>0.16</td>
<td>14.86</td>
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<tr>
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<td>37.31</td>
<td>0.01</td>
<td>0.01</td>
<td>0.16</td>
<td>28.20</td>
</tr>
</tbody>
</table>

Site 1  | 1997 | Site 2  | 1997 | Site 2  | 1998 |

Source | df | Density (Plants m$^{-2}$) | Cover (Percent) | Density (Plants m$^{-2}$) | Cover (Percent) | Biomass (Grams m$^{-2}$) |
| N      | 1  | 15.54                     | 0.03            | 4.16                       |                |
| Rye    | 1  | 13.35                     | 0.01            | 3.42                       |
| Squirreltail | 1  | 14.86                     | 0.01            | 3.85                       |
| Wheatgrass | 1  | 28.20                     | 0.04            | 5.78                       |

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Appendix B

RESPONSE SURFACES FOR THE PREDICTION OF BLUEBUNCH WHEATGRASS BIOMASS
Figure 8. Response surface using bluebunch wheatgrass and spotted knapweed density to predict bluebunch wheatgrass biomass - control treatment.

\[ W_{bb} = 0.37(1 + 0.225(N_{bb} + 0.17N_{sk}))^{-0.627} \]
Figure 9. Response surface using bluebunch wheatgrass and spotted knapweed density to predict bluebunch wheatgrass biomass - annual rye treatment.

\[ W_{bb} = 0.02(1 + 0.225(N_{bb} + 9.9N_{sk}))^{-1} \]
APPENDIX C
RESPONSE SURFACES FOR THE PREDICTION OF SPOTTED Knapweed Biomass
Figure 10. Response surface using bluebunch wheatgrass and spotted knapweed density to predict spotted knapweed biomass - control treatment.

\[
Wsk = 0.106(1+0.225(Nsk+0.3758*Nbb))^{-0.58}
\]
Figure 11. Response surface using bluebunch wheatgrass and spotted knapweed density to predict spotted knapweed biomass - bottlebrush squirreltail treatment.

\[ W_{sk} = 0.132(1 + 0.225(N_{sk} + 0.5947 \times N_{bb}))^{0.571} \]
Figure 12. Response surface using bluebunch wheatgrass and spotted knapweed density to predict spotted knapweed biomass - annual rye treatment.

\[ W_{sk} = 0.0057(1 + 0.225(N_{sk} + 0.02N_{bb}))^{0.137} \]
Figure 13. Response surface using bluebunch wheatgrass and spotted knapweed density to predict spotted knapweed biomass - nitrogen treatment.

\[ W_{sk} = 0.0738(1 + 0.225(N_{sk} + 0.231N_{bb}))^{2.65} \]
Figure 14. Response surface using bluebunch wheatgrass and spotted knapweed density to predict spotted knapweed biomass - phosphorus treatment.

\[ W_{sk} = 0.195 (1 + 0.225 (N_{sk} + 0.5368 \times N_{bb}))^{-1.304} \]