



Designing Weed-Resistant Plant Communities by Maximizing Niche Occupation and Resource Capture
by MICHAEL F CARPINELLI

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

To develop an ecological basis for designing weed-resistant plant communities, I tested the hypothesis that susceptibility to weed invasion is determined by temporal and spatial resource availability and by the ability of weeds to capture those resources. In two competition experiments, three desirable species with differing spatial and temporal growth patterns (crested wheatgrass, intermediate wheatgrass, and alfalfa), and one weed (spotted knapweed) were used to determine the potential for minimizing weed invasion by maximizing niche occupation and resource capture. I tested this potential in two types of plant communities: well-established, uninfested plant communities (invasion) and newly establishing plant communities following revegetation of a previously weed-infested site (revegetation). In these experiments, desirable species richness varied, while the total number of desirable plants was held constant.

Comparative growth of isolated individuals was used to test the hypothesis that a species' growth characteristics, when grown in isolation, may be useful in predicting its relative growth in mixtures. These results were variable and did not aid in interpreting results from the competition experiments. In the invasion experiment, seedlings of the desirable species were planted in spring 1995. Spotted knapweed was sown in fall 1996, simulating invasion of a well-established plant community. Sampling occurred in fall 1997 and fall 1998. Spotted knapweed recruitment was positively related to soil water content and negatively related to desirable species richness. These results suggest that soil water plays a role in spotted knapweed germination and establishment, and that by maximizing niche occupation, soil water may be preempted from invading weeds.

In the revegetation experiment, all species were sown simultaneously in spring 1996. This simulated revegetation of a site containing spotted knapweed seeds in the seed bank because of prior infestation. Sampling occurred in fall 1996 and fall 1997. Spotted knapweed recruitment was not related to desirable species richness in either year. In 1997, spotted knapweed dominated the desirable species. These results suggest that efforts to revegetate weed-infested rangeland must address weed reestablishment from seeds or propagules in the soil. Only then can other strategies, such as maximizing niche occupation by desirable species, be expected to provide long-term success.

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Michael Francis Carpinelli

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ABSTRACT

To develop an ecological basis for designing weed-resistant plant communities, I tested the hypothesis that susceptibility to weed invasion is determined by temporal and spatial resource availability and by the ability of weeds to capture those resources. In two competition experiments, three desirable species with differing spatial and temporal growth patterns (crested wheatgrass, intermediate wheatgrass, and alfalfa), and one weed (spotted knapweed) were used to determine the potential for minimizing weed invasion by maximizing niche occupation and resource capture. I tested this potential in two types of plant communities: well-established, uninfested plant communities (invasion) and newly establishing plant communities following revegetation of a previously weed-infested site (revegetation). In these experiments, desirable species richness varied, while the total number of desirable plants was held constant.

Comparative growth of isolated individuals was used to test the hypothesis that a species' growth characteristics, when grown in isolation, may be useful in predicting its relative growth in mixtures. These results were variable and did not aid in interpreting results from the competition experiments.

In the invasion experiment, seedlings of the desirable species were planted in spring 1995. Spotted knapweed was sown in fall 1996, simulating invasion of a well-established plant community. Sampling occurred in fall 1997 and fall 1998. Spotted knapweed recruitment was positively related to soil water content and negatively related to desirable species richness. These results suggest that soil water plays a role in spotted knapweed germination and establishment, and that by maximizing niche occupation, soil water may be preempted from invading weeds.

In the revegetation experiment, all species were sown simultaneously in spring 1996. This simulated revegetation of a site containing spotted knapweed seeds in the seed bank because of prior infestation. Sampling occurred in fall 1996 and fall 1997. Spotted knapweed recruitment was not related to desirable species richness in either year. In 1997, spotted knapweed dominated the desirable species. These results suggest that efforts to revegetate weed-infested rangeland must address weed reestablishment from seeds or propagules in the soil. Only then can other strategies, such as maximizing niche occupation by desirable species, be expected to provide long-term success.

INTRODUCTION AND LITERATURE REVIEW

The loss of native perennial vegetation from North American rangeland has been accompanied by invasions of aggressive alien weeds. Grassland ecosystems of the West, once dominated by native perennial bunchgrasses, now contain extensive areas dominated by exotic undesirable species (Roché and Talbott 1986). Invasive weedy species have been associated with reduced biodiversity (Tyser and Key 1988, Belcher and Wilson 1989, Kedzie-Webb 2000), reduced wildlife and livestock forage production (Bucher 1984, Spoon et al. 1983), and altered integrity and function of the ecosystem (Hooper and Vitousek 1997, Vinton and Burke 1995). Not all successful invasions alter large-scale ecosystem properties (Simberloff 1981, Baker 1986); however, where an individual species is capable of altering processes such as productivity, soil development, hydrology, or nutrient cycling, that species may affect ecosystem function (Vitousek 1990, Baker 1986, Mack 1986).

The purpose of this chapter is to review the principles and mechanisms involved in the invasion of plant communities by undesirable plant species and show how this information may be used to reduce the potential impact of these invasive species. I discuss (1) species diversity indices, (2) the relationship between invasibility and species richness of plant communities, (3) the niche concept, (4) current rangeland weed management and rangeland revegetation, (5) relevant research that may contribute to future revegetation strategies, (6) a model system for studying the potential to use the niche concept to design weed-resistant plant communities, (7) the quantification of growth, interference, and niche

differentiation, and (8) how the niche concept may be used to design weed-resistant plant communities, including the objectives and hypotheses of this study.

Diversity Indices

Ecologists use species diversity indices to describe the heterogeneity of a community. Diversity has two components: (1) species richness (the number of species) and (2) evenness (the relative abundances of each species). Diversity indices combine these two measures mathematically into a single numerical expression. For example, the Shannon function uses natural logarithms (\ln) to estimate diversity (H') as

$$H' = \sum (p_i \ln p_i)$$

where \sum is the summation symbol and p_i is the proportion of species i in the community (Shannon and Weaver 1949). While these indices most often are based on density, the functional importance of a species in a community may be more appropriately estimated using biomass or productivity (Hurlbert 1971, Lyons 1981). Though species richness and diversity are related, these terms are not interchangeable. Both, however, are used in the ecological literature to describe community heterogeneity.

Invasibility and Species Richness

Elton (1958) proposed that species-rich plant communities are less susceptible to invasion than are species-poor ones. Although this belief has achieved paradigm status among ecologists, it has not always been borne out by empirical evidence (Law and Morton 1996). In a biome-scale investigation, Lonsdale (1999) found invasibility was

positively correlated with native plant species richness. Stohlgren et al. (1999) also found such a relationship at landscape and biome scales. From these two studies, it appears that species richness was probably a surrogate for habitat diversity. That is, as scale increased, so did the number of different habitats. As expected, exotic species richness increased with increasing habitat diversity. However, at the 1-m² scale, Stohlgren et al. (1999) found invasibility of four prairie types in the Central Grasslands to be negatively related to native plant species richness. In that same study, exotic species richness was negatively correlated with native species cover and positively correlated with soil total % N at the 1000-m² scale. In the early stages of a long-term experiment investigating plant community invasibility, Burke and Grime (1996) found that a plant community was most invulnerable if it was disturbed and eutrophic (nitrogen fertilized). However, Tilman (1997) found community invasibility to be negatively correlated with extractable soil nitrogen and initial species richness. While the relationship between invasibility and soil N is unclear, existing evidence indicates a negative relationship between invasibility and species richness at the community level.

The Niche Concept

The niche concept has been used to describe the relationship between an organism and its environment. This includes the "habitat" aspect (Grinnell 1917) emphasizing the environmental requirements of a species. Later, Hutchinson (1957) described the fundamental niche as a multidimensional "hyper-volume." The hyper-volume represents the conditions where an organism's expected absolute fitness is at least zero, a conceptual

space whose axes include all of the environmental variables affecting that species.

Hutchinson (1957) believed this completely defined the ecological properties of that species. In contrast, Elton (1927) and MacArthur and Levins (1967) used the niche concept to describe the effect a species has on its environment based primarily on its trophic level, specifically, short-term impacts of species on resource use. Despite their differences, these niche concepts are consistent with Gause's (1934) competitive exclusion principle. This principle states that where two species overlap sufficiently in niche, the weaker competitor will be eliminated.

To completely define a species' niche, all environmental variables that affect, and are affected by, a species would have to be measured. While it may be impossible to define a species' niche, the niche is a useful concept in assessing potential spatial and temporal niche overlap among species (Vandermeer 1972, Begon et al. 1996). In practice, monitoring a manageable number of environmental variables thought to be most important to a particular group of species may aid in increasing our understanding of the relationships among those species.

The niche concept may help elucidate the relationship between invasibility and species richness. As initial species richness increases, so does the likelihood of niche occupation and the preemption of resources available to a potential invader. Since revegetation is a community-level process, maximizing species richness may be one tool to reduce invasibility.

Current Rangeland Weed Management

To a large extent, weed management strategies are technology- or tool-based and rarely meet long-term land management objectives. In many cases, land managers rely on repeated herbicide applications to control weeds, or wait for the future promise of biological controls. Sole reliance on conventional herbicides provides only short-term control of weeds. Picloram, the most widely used rangeland herbicide, applied at 0.28 to 0.56 kg/ha, provides control of many broadleaf plants for 2 to 5 years (Davis 1990). However, most weeds reinvade because repeated applications are necessary for long-term control, and repeated applications are often omitted because of their expense (Griffith 1999). At this time, biocontrol of most nonindigenous plants is ineffective in reducing weed populations (Wilson and McCaffrey 1999). The nature and magnitude of the invasive plant problem suggest that the establishment of natural enemies alone offers no guarantee of successful biocontrol in the future (Cuda et al. 1989). Grazing management offers some potential for managing a few invasive species, but little is known about sustainable grazing strategies for most weeds (Olson 1999). It is becoming increasingly clear that effective weed management must focus on developing and maintaining desired plant communities rather than simply controlling weeds (Sheley et al. 1996).

Revegetation of weed-dominated rangeland that has focused on establishment of grass monocultures and the use of broadleaf herbicides has produced variable and unpredictable results (Hubbard 1975, Berube and Myers 1982, Huston et al. 1984, Larson and McInnis 1989). The goal of establishing persistent, biologically diverse plant

communities has often been sacrificed to accommodate the short-term goals of plant establishment and soil stabilization (Call and Roundy 1991). Existing revegetation technology often fails to address spatial and temporal diversity within the community. Some monocultures, such as crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult.] that are tolerant of resource limitations and, therefore, highly competitive in semiarid habitats, have remained fairly stable and resisted invasion for decades (Pyke and Archer 1991). In most cases monocultures have not provided resistance to reinvasion (Hull and Klomp 1966, Nichols et al. 1993).

In addition to weed-resistance, another goal of many land managers is consistent forage production. Often the most productive species when resources are plentiful may be the least persistent under limiting conditions. At the community level, year-to-year productivity may be higher and less variable in species-rich communities than in species-poor communities as predicted by May (1973) and shown by Tilman (1996). In the future, our objective must be to establish and maintain diverse plant communities that resist reinvasion and meet other land-use objectives (Sheley et al. 1996).

It has been suggested that long-term, sustainable weed management must focus on establishing desirable species with plant traits and population strategies that promote continuous resource capture and enhance niche occupation (Larson et al. 1994, Chapin et al. 1992, Chapin et al. 1998, Sheley et al. 1996). Plant communities that lack the structure (i.e. niche occupation) necessary to capture available resources may be functioning below their productive capacity and have an increased risk of weed invasion (Larson et al. 1994). Borman et al. (1991) found that established perennial grasses that initiate growth early and

maintain some growth through the winter can limit reinvasion by alien weeds.

Furthermore, establishment of desirable species having contrasting above- and below-ground growth patterns may minimize interspecific competition, maximize community structure, and enhance resource capture (Pyke and Archer 1991, Tilman 1986).

Relevant Research

Austin (1982) and Grace (1988) showed that plant performance in monocultures can often be used to predict plant performance in mixtures. Brown (1998) used growth analysis of individual species grown in low-density monocultures *a priori* to predict relative productivity and resource use of mixtures. Brown (1998) found that variability in species traits such as root distributions, phenologies, and final plant size was higher among functional groups than within functional groups (annual vs. perennial, grass vs. forb, shallow-rooted vs. deep-rooted, etc.). Communities with varying degrees of niche occupation, based on the number of functional groups represented, were established in the field. Community productivity and water use increased as community niche occupation increased. In a field study by Symstad (2000), invasibility by native species and functional group diversity were negatively related. Neither Brown (1998) nor Symstad (2000) quantified niche occupation by member species using relative competitive abilities of member species (Spitters 1983); rather, they assumed community niche occupation was positively related to functional group diversity.

Jacobs and Sheley (1997) studied the effect of defoliation of Idaho fescue (*Festuca idahoensis* Elmer) on water use and the subsequent performance of spotted knapweed.

Defoliation of Idaho fescue growing in mixtures with spotted knapweed increased soil water content, resulting in an increase in spotted knapweed emergence and growth.

Perhaps growth analysis of desirable species may be used *a priori* to predict community resistance to weed invasion based on patterns of resource use by desirable species.

A Model System

This study quantified the interference among one weed and three desirable species. The weed species chosen for this study was spotted knapweed (*Centaurea maculosa* Lam.), a deeply taprooted Eurasian perennial. This species was selected because of its ecological significance and wide distribution. With the potential of spotted knapweed to alter forage production, it has the potential to affect community function (Spoon et al. 1983, Tyser and Key 1989). The three desirable species chosen for this study were crested wheatgrass [*Agropyron cristatum* (L.) Gaertn., var. Hycrest], intermediate wheatgrass [*Elytrigia intermedia* (Host) Nevski, var. Rush], and alfalfa (*Medicago sativa* L., var. Arrow). These four species evolved in the Old World under centuries of heavy pressure from humans. The likelihood that these species are niche-differentiated is higher than that of spotted knapweed and three desirable species that evolved in North America under different environmental pressures (Mack 1986). Since the goal of this study was to examine the effects of niche occupation on invasibility, I chose these three desirable species to increase niche occupation by increasing desirable species richness. Crested wheatgrass, intermediate wheatgrass, and alfalfa are commonly used in revegetation in the

West. There is also experimental evidence that they are niche-differentiated based on their root distributions and phenologies (Holzworth and Lacey 1991).

Plant Materials

Spotted knapweed

Spotted knapweed is native to the grassland steppe of central Europe, and east to central Russia, Caucasia, and western Siberia (Rees et al. 1996, Sheley et al. 1999). In Europe, spotted knapweed is most aggressive in the forest steppe on Typic Argiborolls, but can form dense stands in more moist areas on well-drained soils including gravel, and in drier sites where summer precipitation is supplemented by runoff. It does not compete well with vigorously growing grass in moist areas. Lacey et al. (1995) reported that spotted knapweed has been observed at elevations ranging from 578 to over 3040 m and in precipitation zones ranging from 200 to 2000 mm annually.

Spotted knapweed was introduced to North America from Eurasia as a contaminant in alfalfa (Muller et al. 1988, Roché and Talbott 1986). Spotted knapweed was also apparently introduced through discarded soil used as ship ballast (Roché and Talbott 1986). Spotted knapweed was first recorded in Victoria, British Columbia, in 1883 (Groh 1944) and spread further in domestic alfalfa seeds and hay before it was recognized as a serious problem (Roché and Talbott 1986).

I have documented the geographic spread of spotted knapweed in the western United States up to 1980 using herbarium records compiled by Forcella and Harvey (1980), and current distribution through interviews with weed authorities in the region. In the United

States, spotted knapweed was limited to the San Juan Islands, Washington, until 1920. It had spread to 20 counties in the Pacific Northwest by 1960 and to 48 counties by 1980. Between 1980 and the present, the range of spotted knapweed rapidly increased to include 326 counties in the western United States, including every county in Washington, Idaho, Montana, and Wyoming. It spread at a rate of 27% per year since 1920 (Chicoine et al. 1985) and by 1989 had infested over 2 million hectares of rangeland throughout the western United States (Lacey 1989). Although spotted knapweed spreads most rapidly on disturbed areas, even rangeland in excellent condition is susceptible to invasion (Morris and Bedunah 1984).

In general, knapweed (*Centaurea* spp.) individuals possess many traits that make them superior to native grasses in capturing resources. Intense competitiveness (Powell 1990, Kennett et al. 1992, Sheley and Larson 1994b), rapid growth rates (Sheley et al. 1993), large seed output and longevity (Schirman 1981, Davis 1990, Sheley and Larson 1994b), and extended growing periods (Sheley and Larson 1994b) all contribute to the successful domination of rangeland by knapweeds.

Population characteristics may explain the monotypic domination of grasslands by knapweeds. Most knapweeds have mechanisms that control seed development and release, providing continuous seed rain (Callihan et al. 1989, Davis 1990). Moreover, knapweeds exhibit germination polymorphism that distributes seed germination over time (Nolan and Upadhyaya 1988). Life history models of knapweeds suggest a conspecific hierarchy of size classes result from continuous seedling emergence (Sheley and Larson

1994b). The hierarchy of size classes within the population maximizes resource capture and community structure (Sheley and Larson 1995).

Spotted knapweed is a member of the Asteraceae family. A short-lived perennial, it typically forms a basal rosette its first year and flowers in subsequent years. Basal rosette leaves are borne on short pedicels and grow up to 200 mm long and 50 mm wide. Rosettes are deeply divided, once or twice, into lobes on both sides of the center vein. Lobes are oblong with the broadest part above the middle. Flowering stems are erect, 2 to 12 dm tall, and branched above the middle. Stem leaves are alternate, sessile, and have few lobes; or are linear and entire, and are reduced toward the stem apex. The uppermost leaves are small and simple. Flowerheads are ovate to oblong, 6 mm wide and 12 mm long, and are solitary or borne in clusters of two or three at the branch ends. Involucral bracts are foliaceous, ovate, yellow-green to brown below. Margins have a soft spine-like fringe with the center spine shorter than the lateral spines. Spotted knapweed is so named because of the obvious black margin on the bract tips. Its flowers are purple to pink, rarely white, with 25 to 35 flowers per head. Spotted knapweed blooms from June to October. The flowerheads usually remain on the plant. The achenes are 2.5 to 3.5 mm long, oval, brown to black, with pale longitudinal lines. Seeds bear a persistent pappus of simple bristles that are 1 to 2 mm long.

Crested wheatgrass

Crested wheatgrass is a vigorous perennial bunchgrass with an extensive root system. Native to Russia, it is well-suited to the Northern Great Plains, the central and northern

intermountain region, the subhumid regions of the Pacific Northwest, and higher elevations in the Southwest. It grows at elevations as low as 975 m in the northern Rockies to elevations as high as 2750 m in the Southwest. It does best on deep, neutral to slightly alkaline, well-drained soils, but does well on heavier textured soils. It prefers 200 to 400 mm of annual precipitation, tolerates drought very well, is fairly tolerant of salinity, and is moderately tolerant of flooding or high watertable. It establishes well from seed and performs well on nutrient-poor sites. It is capable of early spring growth, preceding native grasses in the Great Plains. Crested wheatgrass also provides good fall grazing if precipitation is adequate (Wheeler and Hill 1957, Munshower 1991).

Crested wheatgrass stands 3.5 to 7 dm tall. Its culms are erect and range from having the pith hollow to filled. Its blades are flat, pubescent to glabrous above, 20 to 170 mm long, 1.5 to 7 mm wide, with auricles and ligules 0.1 to 1 mm long. The spikes of crested wheatgrass are dense, 20 to 80 mm long, with closely overlapping spikelets that are several times longer than the internodes and strongly divergent. There are 3 to 6 flowers per spikelet with glumes 2 to 6 mm long. The awns, if present, are up to 3.5 mm long. The lemmas are awnless or with awns up to 5 mm long, and the lowest lemma is 4 to 8 mm long. The anthers are 2.4 to 4 mm long. Crested wheatgrass flowers from June to August (McGregor and Barkley 1986).

'Hycrest,' a cultivar of hybrid crested wheatgrass, was used in this study. It is a cross of *Agropyron desertorum* (Fisch. ex Link) Schult. and *A. cristatum* (L.) Gaertn., and it tends to be more robust than its parental species (Asay et al. 1985).

Intermediate wheatgrass

Intermediate wheatgrass, a moderately deeply rooted, cool-season, sod-forming grass, emerges slightly later than crested wheatgrass. Native to Russia, in North America it is best-adapted to the eastern Great Plains and western Midwest, but also does well in the Intermountain Region. In the Rocky Mountains, it grows at elevations as low as 1550 m in the north to elevations as high as 2200 m in the south. It does best on slightly acidic to slightly alkaline, well-drained soils, but does well on sandy loam to clay loam textures. It requires at least 400 mm of annual precipitation, tolerates both drought and flooding or high watertable, is quite tolerant of salinity, and requires fairly fertile sites. Its main virtues are its ease of establishment and high production (Wheeler and Hill 1957, Munshower 1991).

Intermediate wheatgrass stands 6 to 12 dm tall. Its culms are erect and solid. Its blades are stiff, involute to flat, with numerous narrow ridges above, glabrous to scabrous (rarely pilose), 50 to 280 mm long, and 2 to 8 mm wide. The sheaths are glabrous to scabrous and often ciliate-margined. The ligules are 0.2 to 1 mm long, and the auricles are usually pronounced. The spikes of intermediate wheatgrass are fairly open, 130 to 220 mm long, with spikelets that are 4- to 7-flowered. The glumes are blunt-tipped, glabrous to pubescent. The first and second glumes are 5 to 8 mm long and 6 to 9 mm long, respectively. The lemmas are usually blunt, but are sometimes acute or mucronate, especially the upper ones. The lowest glume is 8 to 11 mm long. The lemmas and glumes are awnless. The anthers are 2.5 to 5 mm long. Flowering occurs from June to September (McGregor and Barkley 1986).

The variety 'Rush' was used in this study. It was developed through selection and direct increase from field plots. 'Rush' is noted for its high seedling emergence and drought tolerance. It is an excellent forage producer on sites with at least 30 cm of average annual precipitation (USDA-Natural Resources Conservation Service 1994).

Alfalfa

Alfalfa may be the only forage crop cultivated before recorded history. It most likely originated in southwestern Asia, probably in Iran (Bolton 1962, Ivanov 1988). It is a very deeply taprooted forb with an extended growing period, capable of utilizing groundwater in semiarid environments. The maximum rooting depth of alfalfa exceeds 6 m (Weaver 1926, Taylor and Terrell 1982). It is common throughout North America, requiring at least 400 mm of annual precipitation. In the Rocky Mountains, it grows into the subalpine zone. It does well on all deep soils, preferring slightly acidic to slightly alkaline sandy loams to loams. It requires at least 400 mm of annual precipitation, is intolerant of a watertable within 1.5 m of the soil surface, and is moderately tolerant of drought and salinity (Munshower 1991). Water-soluble compounds from the aboveground portions of alfalfa are autotoxic and allelopathic, primarily affecting germination, although allelopathic effects tend to be greater than autotoxic effects (Hegde and Miller 1990).

Alfalfa is a perennial herb with a knobby or shortly branching crown. Its multiple stems are glabrous to finely hairy, erect to decumbent, and 3 to 6 dm tall. Its leaves are alternate and pinnately trifoliate. The petioles of principal leaves are 10 to 50 mm long. The stipules are lanceolate, slightly toothed, 5 to 20 mm long, and united at the base with

the petiole. The racemose inflorescences are subglobose to short-cylindric, 5- to 40-flowered. The flowers are 5 to 11 mm long and are usually purple, but are occasionally yellowish-green or brownish, yellow, or rarely white. The pods are several-seeded, glabrous to sparsely hairy, usually spiraled 1 to 3 turns or nearly straight or falcate. Flowering occurs from May through September (McGregor and Barkley 1986).

The alfalfa variety 'Arrow' used in this study is highly resistant to *Phytophthora* root rot, bacterial wilt, and *Fusarium* wilt. Its genetic origin includes the varieties Endure, Apollo II, Trident, WL-318, Anchor, Answer, Apollo, and Saranac AR (Certified Alfalfa Seed Council 1992).

Growth Analysis of Isolated Individuals

To be successful designing weed-resistant plant communities, we must understand the phenology and growth of the weed of concern and of the potential desirable species used in revegetation. Growth analysis of isolated individuals describes the phenology, root distribution, and growth rate of plants (Radford 1967, Evans 1972, Grime and Hunt 1975, Erickson 1976, Hunt 1978, Hunt 1982, Hunt 1988). In this study, growth analysis was performed on isolated individuals of spotted knapweed, crested wheatgrass, intermediate wheatgrass, and alfalfa to characterize the inherent growth potential of each species. This characterization may be used, in part, to explain differences in the outcomes of interactions among these species (Radosevich and Rousch 1990).

One objective of the growth analysis experiments in this study was to quantify the growth rate and root distribution of these four species during different stages of growth.

Another objective was to determine the potential to use growth analysis of isolated individuals to predict the interference and resource use among one weed and three desirable species. One of the growth analysis experiments was conducted to study the early stages of establishment and growth in a controlled environment. Two additional growth analysis experiments were conducted to study the growth of these species in a field environment during their second and third growing seasons.

Quantification of Interspecific Interference and Niche Differentiation

Several experimental designs attempt to quantify interspecific interference. Although they were initially developed to assess the effect of weeds on crops, they can be used to quantify interference among any species. Each design has its own unique assumptions, analysis, and conclusions.

Additive design

In this design, the "crop" species is grown at a constant background density and a "weed" species is introduced at a range of densities (Donald 1951). This design confounds effects of total density and species proportion.

The Index of Competition (IC) is used to estimate the crop loss caused by weeds when the population density of the weed and the expected weed-free crop yield are known (Cousens 1991). In the regression model, $B_c = a_c - bN_w^{1/2}$, B_c is the crop biomass produced per unit area, a_c is the maximum weed-free crop biomass, b is the regression coefficient of B_c on the square root of the population density of the weed species, N_w .

The Index of Competition is defined by the formula $IC = b/a_c$. The predicted yield loss is then calculated as $L_c = a_c \cdot IC \cdot N_w$, where L_c is the crop biomass loss caused by the presence of the weed.

Substitutive design

The Replacement Series (de Wit 1960) design maintains constant total density while the proportions of each species vary from 0 to 100% (monoculture). This design avoids the confounding effects of an additive design; however, in a multiple replacement series, an assumption must be made that the influence of a particular species is independent of its proportion in the community. Velagala et al. (1997) have shown that the competitive relationship between intermediate wheatgrass and spotted knapweed was density-dependent.

Addition series design

Also called an additive series, this design systematically varies the density and proportion of each species. Usually two species are used, but it has also included a constant background density of a third species, or even a fourth species in a "plaid" design (Radosevich 1988). Spitters (1983) expanded the reciprocal yield law equation to model yield-density responses of two-species systems:

$$w_x^{-1} = \beta_{0x} + \beta_{xx}N_x + \beta_{xz}N_z$$

where w_x is the mean biomass per plant, N_x and N_z are the neighbor densities of species x and z , respectively, and β_{0x} , β_{xx} , and β_{xz} are regression coefficients. The regression coefficients are interpreted as: $1/\beta_{0x}$ = the yield or biomass of an isolated plant, β_{xx} is the

intraspecific competition coefficient, and β_{xz} is the interspecific competition coefficient.

Assuming that competitive effects are additive, the model can be expanded to include more species:

$$w_x^{-1} = \beta_{0x} + \beta_{xx}N_x + \beta_{xz}N_z + \dots + \beta_{xi}N_i$$

These models are fit with multiple linear regression and the parameter values are used to interpret interference relationships and calculate niche differentiation between species. For example, in a two-species system where

$$w_x^{-1} = \beta_{0x} + \beta_{xx}N_x + \beta_{xz}N_z \text{ and } w_z^{-1} = \beta_{0z} + \beta_{zz}N_z + \beta_{zx}N_x$$

The relative competitive ability (RC_x) of each species is

$$RC_x = \beta_{xx}/\beta_{xz} \text{ and } RC_z = \beta_{zz}/\beta_{zx}$$

RC_x is 1/3 if 1 plant of species x and 3 plants of species z have an equal influence on the average weight per plant of species x (Spitters 1983). Niche differentiation (ND) can also be calculated from the relative competitive abilities of each species:

$$ND = (\beta_{xx}/\beta_{xz})/(\beta_{zx}/\beta_{zz}) = RC_x \cdot RC_z = (\beta_{xx}/\beta_{xz}) \cdot (\beta_{zz}/\beta_{zx})$$

Niche differentiation increases as ND departs from unity; that is, species x and z are decreasingly limited by the same resources (Spitters 1983). This interpretation assumes that both species have equal resource utilization efficiency. Other assumptions include:

- (1) the relationship between density and biomass is rectangularly hyperbolic,
- (2) the effects of interference on the reciprocal of plant biomass of each species are additive,

- (3) the effects of interference are independent of the total population density and of species proportions, and
- (4) the site is homogenous.

The overall goal of this study was to determine the potential for designing a weed-resistant community by maximizing structure and resource capture. The first supporting objective was to determine the potential for manipulating species richness and diversity to facilitate the establishment of a structurally diverse community. I tested the hypothesis that as species richness and diversity increase (niche differentiated species), community structure increases. Community structure was measured as total aboveground biomass.

The second supporting objective was to determine the potential for using knowledge of species' growth rates and root distributions to design plant communities with a high degree of structure and, thus, resource capture. I tested the hypothesis that plants shown to differ when grown in isolation will also differ when grown in mixtures.

The third supporting objective was to determine the potential to predict weed establishment and invasion based on soil water use by desirable species. I tested the hypothesis that as soil water content decreases, weed establishment and invasion decrease.

Sustainable weed management requires understanding complex ecosystem processes that influence the invasion of weeds into plant communities. In this study, I hypothesized that susceptibility to weed invasion and dominance is determined by the temporal and spatial availability of resources within the community and the ability of a particular weed species to capture those resources (Whittaker 1975, Larson et al. 1994, Sheley and Larson 1994a). Sheley and Larson (1995) proposed that maximizing community structure and

resource capture limits weed invasion through resource preemption. However, the theory is largely untested, especially with nonindigenous species. I propose to enhance resource preemption by increasing species richness and diversity. Species richness and diversity affect community structure and resource capture, and hence resource preemption, in the following ways: community structure increases as species richness and diversity increase, as long as member species differ in niche (Whittaker 1975); and as species richness and diversity increase, niche occupation and resource capture increase (Tilman 1986).

Included in this study was a generalized model that attempts to predict plant community dynamics based strictly on intra- and interspecific interference and niche partitioning. The model was used to predict the long-term dynamics of plant communities of crested wheatgrass, intermediate wheatgrass, alfalfa, and spotted knapweed in varying proportions and under different conditions. The model was parameterized using demographic data and competition coefficients from a multiple replacement series experiment (Carpinelli et al. Submitted). The simulations started by assigning an initial seed bank size for each species, setting species demographic and interaction parameters, and selecting the number of generations to run the simulation.

The specific objectives were to:

- (1) Quantify the effects of species richness and diversity on soil water use.

Null hypothesis: Species richness and diversity do not affect soil water use.

Alternative hypothesis: As species richness and diversity increase, soil water use increases.

Rationale: The different root distributions and seasons of growth of crested wheatgrass, intermediate wheatgrass, and alfalfa will allow for more continual water uptake, both temporally and spatially, as species richness and diversity increase.

- (2) Determine the effect of desirable species richness and diversity on the degree of interference between spotted knapweed and three desirable species.

Null hypothesis: Desirable species richness and diversity do not affect spotted knapweed recruitment and biomass production.

Alternative hypothesis: As desirable species richness and diversity increase, spotted knapweed recruitment and biomass production decrease.

Rationale: As increased desirable species richness and diversity increase soil water depletion, less water will be available for the germination, establishment, and growth of spotted knapweed.

- (3) Determine the potential to use growth analysis of isolated individuals to predict interference and resource use among one weed and three desirable species.

Hypothesis: Relative growth rate of isolated individuals does not predict resource use and interference in mixtures.

Alternative hypothesis: Relative growth rate predicts resource use and interference in mixtures.

Rationale: Species shown to differ in relative growth rate when grown in isolation will differ when grown in mixtures.

- (4) Determine possible long-term community dynamics by incorporating data from a multiple replacement series experiment into a predictive model. This hypothesis-generating tool will elucidate key processes and mechanisms involved in weed invasion and revegetation of weed-infested rangeland.

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CHAPTER 2

COMPARATIVE GROWTH AMONG INTERMEDIATE WHEATGRASS, CRESTED WHEATGRASS, ALFALFA, AND SPOTTED KNAPWEED

Introduction

Loss of native perennial vegetation on North American rangelands has been accompanied by invasions of aggressive non-indigenous weeds. Grassland ecosystems of the West, once dominated by native perennial bunchgrasses, now contain extensive areas dominated by exotic undesirable species (Roché and Talbott 1986). Invasive weedy species have been associated with reduced biodiversity (Tyser and Key 1988, Belcher and Wilson 1989, Kedzie-Webb 2000), reduced wildlife and livestock forage production (Bucher 1984, Spoon et al. 1983), and altered functioning of the ecosystem (Hooper and Vitousek 1997, Vinton and Burke 1995).

Revegetation of weed-dominated rangeland that has focused on establishment of grass monocultures and the use of broadleaf herbicides has produced variable and unpredictable results (Hubbard 1975, Berube and Myers 1982, Huston et al. 1984, Larson and McInnis 1989). The goal of establishing persistent, biologically diverse plant communities has often been sacrificed to accommodate the short-term goals of plant establishment and soil stabilization (Call and Roundy 1991). Existing revegetation technology often fails to address spatial and temporal diversity within the community.

It has been suggested that long-term, sustainable weed management must focus on establishing desirable species with plant traits and population strategies that promote continuous resource capture and enhance niche occupation (Larson et al. 1994, Chapin 1992, Sheley et al. 1996). Plant communities that lack the niche occupation necessary to capture available resources may be functioning below their productive capacity and have an increased risk of weed invasion (Larson et al. 1994, Tilman 1997). Establishment of desirable species having contrasting above- and below-ground growth patterns may minimize interspecific competition, maximize community structure, and enhance resource capture (Pyke and Archer 1991, Tilman 1986). Sheley and Larson (1995) proposed that maximizing community structure and resource capture limits weed invasion through resource preemption. However, the theory is largely untested, especially with nonindigenous desirable species.

During the establishment phase of revegetation, the relative timing of emergence and growth rates of species may be an important determinant of community dynamics (Ross and Harper 1972, Harper 1977, Radosevich and Holt 1984). Rehabilitation of yellow starthistle (*Centaurea solstitialis* L.) dominated rangeland has been attempted by revegetating with desirable grasses. These attempts typically fail because of resource preemption by annual weeds which germinate sooner and have a higher initial growth rate than the desirable grasses (Borman et al. 1991). In an experiment by Harris (1967), the winter annual, cheatgrass (*Bromus tectorum* L.), preempted resources from fall-sown bluebunch wheatgrass [*Agropyron spicatum* (Pursh) Scribn. & Smith]. Both species germinated in the fall, but cheatgrass had faster winter root growth than did bluebunch

wheatgrass, thus allowing it to gain control of the site before bluebunch wheatgrass established. Borman et al. (1991) found that established perennial grasses that initiate growth early and maintain some growth through the winter can limit reinvasion by alien weeds.

During the early stages of secondary succession (e.g. revegetation), availability of light, water, and nutrients may be particularly high relative to the demand by a sparse community of establishing plants. In this case, resource preemption may be more important than competition in determining community dynamics (Goldberg 1990). Those plants with the highest growth rates have the highest likelihood of establishing to the exclusion of plants with slower growth rates (Harper 1977). Since establishment is the most critical phase of revegetation, knowledge of the initial growth rate of a species may be the best predictor of the short-term outcome of a revegetation effort (James 1992).

Growth analysis of plants grown in isolation has been used to describe their growth rate, phenology, and resource allocation (Radford 1967, Evans 1972, Grime and Hunt 1975, Erickson 1976, Hunt 1978, Hunt 1982, Hunt 1988). Growth analysis of isolated individuals may have the potential to predict the outcome of a revegetation effort by providing information about relative growth rates of species involved. Where weed seed is present in the seed bank of a site recently sown with desirable species, the relative growth rates of the weed and the desirable species may determine community composition, at least for that period of time when resource preemption is more important than competition.

The objective of this experiment was to quantify the growth rate of three desirable species commonly used in revegetation of weed-infested rangeland and one common rangeland weed species.

Null hypothesis: The relative growth rates of the four species are similar.

Alternative hypothesis: Alfalfa and spotted knapweed (small-seeded dicots) have higher growth rates than intermediate wheatgrass and crested wheatgrass (large-seeded monocots).

Rationale: In studies by Grime and Hunt (1975) and Hunt and Cornelissen (1997), relative growth rate was negatively related to seed size and unrelated to whether species were monocots or dicots.

Materials and Methods

Plant materials

The three desirable species used in this study were crested wheatgrass [*Agropyron cristatum* (L.) Gaertn., var. Hycrest], intermediate wheatgrass [*Elytrigia intermedia* (Host) Nevski, var. Rush], and alfalfa (*Medicago sativa* L., var. Arrow). Crested wheatgrass is a shallowly rooted, early emerging, cool-season bunchgrass. Intermediate wheatgrass, a moderately deeply rooted, cool season, sod-forming grass, emerges later than crested wheatgrass. Alfalfa is a deeply taprooted broadleaf with an extended growing period. These three perennials are commonly used in revegetation in the West. They were chosen because of their potential to maximize niche occupation when used together in a revegetation seed mix (Holzworth and Lacey 1991). The invasive weed species

chosen for this experiment was spotted knapweed (*Centaurea maculosa* Lam.), a deeply taprooted Eurasian perennial forb. This species was chosen because of its ecological significance and wide distribution.

Experimental design

Isolated plants of spotted knapweed, crested wheatgrass, intermediate wheatgrass, and alfalfa were arranged in a randomized-complete-block design. Each of four blocks contained 20 plants (4 species x 5 harvest dates). Plants were grown in pots in an environmental chamber (12°C, 12-h daylength, 500 $\mu\text{E m}^{-2} \text{s}^{-1}$ visible radiation measured at pot height). The pots (100 mm diameter x 1 m length polyvinyl chloride tubes) were split vertically and taped back together to facilitate post-harvest root removal. The pots were filled with sterilized Farland silt loam (fine-silty, mixed Typic Argiboroll; A horizon), water-saturated, and allowed to drain to pot capacity. Ten seeds of a given species were evenly spaced on the soil surface of each pot and covered lightly with soil (<2 mm). The surface was lightly misted with water once daily and covered with clear plastic until emergence (7 days), after which no further watering occurred. Pots were thinned to a single individual per pot (10 days).

Sampling

Seed weight of each species was determined by taking the mean of four subsamples of 100 seeds. First plant harvest occurred 14 days after emergence (DAE). Harvests continued on 14-day intervals until final harvest (70 DAE). Soil was manually rinsed from roots and maximum rooting depth was measured. Root systems were extracted from each

pot, separated from shoots, divided into upper (0 cm - 33 cm), middle (33 cm - 67 cm), and lower (67 cm -100 cm) depth increments, washed, and measured for root length using a root length scanner (Comair Corp., Melbourne, Australia). Leaf area was measured using a LICOR-3100 with conveyor belt (LI-COR, Inc., Lincoln, NE). All plant material (root and shoots) was dried (48 h, 60°C) and weighed.

Data analysis

A regression analysis was used to estimate the instantaneous relative growth rate (RGR) and instantaneous unit leaf rate (ULR) calculated over the 70-day period (Hunt 1982). Slopes were compared using the extra sums of squares procedure ($P \leq 0.05$, Ratkowski 1983). Analysis of variance (PROC GLM, SAS Institute Inc. 1991) was used to test for absolute differences among species in total weight, shoot weight, root weight, leaf area, leaf area ratio, and maximum rooting depth. Mean separations were made using LSD comparisons ($P \leq 0.05$).

Results

Growth rates

Relative growth rates of intermediate and crested wheatgrasses were similar to each other, and approximately twice that of alfalfa and spotted knapweed, which were similar to each other (Figure 1). Unit leaf rates of the four species were similar (Figure 2).

