COMPETITION FOR SOIL NITRATE AND INVASIVE WEED RESISTANCE OF THREE SHRUB-STEPPE GROWTH FORMS

by

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ABSTRACT

Competition for Soil Nitrate and Invasive Weed Resistance of Three Shrub-Steppe Growth Forms

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Determining mechanisms responsible for weed resistance and invasion success are two issues that have potential in aiding successful land management decisions. The first experiment evaluates the competitive effects of an invasive annual grass downy brome (*Bromus tectorum* L.), an invasive biennial forb dyer's woad (*Isatis tinctoria* L.), and a reclamation shrub prostrate kochia (*Kochia prostrata* [L.] Schrad.) on nitrate acquisition, shoot and root growth, leaf carbon: nitrogen ratio, and leaf N of a perennial grass crested wheatgrass (*Agropyron cristatum* [L.] Gaertner x *A. desertorum* [Fisch. ex Link] Schultes), a native forb western yarrow (*Achillea lanulosa* Nutt.), and a native shrub big sagebrush (*Artemisia tridentata var.wyomingensis* [Beetle & A. Young] Welsh). In addition the growth traits of the six species were compared to understand the differences in nitrate acquisition and nitrogen allocation. The grasses acquired more nitrate than neighbors of different growth forms, western yarrow was equally competitive with the invasive forb and prostrate kochia, and all neighbors acquired more nitrate than big sagebrush. The invasive weeds and prostrate kochia had lower leaf C: N ratio ($P < 0.01$), and greater leaf N concentration ($P < 0.01$), which is correlated with leaf longevity and nutrient use efficiency, indicating differing strategies to persist in semiarid shrub-steppe ecosystems.

A second experiment evaluated the invasion of downy brome and dyer's woad into single- and four-species plots, and a three-growth form plot composed of perennial grasses, perennial broad-leafed forbs, and shrubs. Species density was altered in single-species plots to determine if disturbance increases invasion into each growth form. Seeds of both invasive species were introduced in autumn of 2004 and 2005, and seedling density was quantified in the following two summers. Downy brome invasion was lowest in plots that contained grass species ($P < 0.01$). Invasion of dyer's woad was consistently lowest in the single-species shrub and three-growth form mix plots ($P < 0.01$). Both species had relatively low invasion into the three-growth form mix. Disturbance increased seedling density of both invasive species. This study provides some clues to better inform potential restoration efforts in the Great Basin and sagebrush-steppe ecosystems.

(85 pages)

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CHAPTER 1

INTRODUCTION

Long-term stability of sagebrush-steppe ecosystems are threatened on many fronts, including over-grazing, increased wildfire frequency, and non-native species invasion (Young and Evans 1978; West 1988; Whisenant 1990; Noss et al. 1995; Anderson and Inouye 2001). Even though only a small percent of non-native introductions in the United States lead to invasions that alter ecosystem function, invasive weeds affect human health and the economy (Pimentel et al. 2000). Within plant communities, non-native invasive species alter primary productivity, decomposition, hydrology, nutrient cycling, and natural disturbance regimes (Vitousek 1990).

Plant invasions result from complex interactions between species traits, community traits, and abiotic conditions. However, the relationship between species composition and resistance to weed invasion has not been formally evaluated in many ecosystems. Many studies show a positive correlation between native species diversity and plant community resistance to weed invasion. For example, it has been demonstrated that high species diversity presents a barrier to invasion by more complete resource use of species (Tilman 1994, 1997; Kennedy et al. 2002; Prieur-Richard and Lavorel 2002). Similarly, McGrady-Steed et al. (1997) and Naeem and Wright (2003) demonstrate that the loss of diversity leads to increased weed invasion. In contrast, at larger ecosystem scales, native species diversity has been shown to be positively correlated with a higher richness of non-native species (Stohlgren et al. 2003).

Demystifying the relationship between plant diversity and resistance to weed invasion should focus on the possible mechanisms and the structural and functional attributes of the plant community. Law and Morton (1996) show that certain combinations of species resist invasion better than others of equal diversity and that communities assembled from large species pools are more resistant to invasion than those assembled from small species pools. Similarly, Prieur-Richard and Lavorel (2000) found that a rich assemblage of functionally unique species negatively affect the performance of exotic species.

In semiarid shrub-steppe communities, Anderson and Inouye (2001) found that abundance of non-native species was negatively correlated with plant cover, but not with richness of native species, suggesting that adequate cover of native species can render them more resistant to invasion. Shrub-steppe communities composed of species that occupy different niches, or that are characterized by different growth forms (e.g., grasses, forbs, and shrubs) are predicted to be more resistant to weed invasion (Sheley et al. 1996; Larson et al. 1997; Sheley and Kruger-Mangold 2003). These examples suggest that plant and/or growth form diversity is somewhat related to the vulnerability of plant communities to weed invasion. However, ecosystems that appear intrinsically resistant to invasion may have only been visited by weak invaders (Mack et al. 2000). Thus, the relationship between resident species composition and invasibility should be evaluated using multiple invasive weed species within systems composed of various levels of species and/or growth form diversity.

This project was designed to evaluate whether plant communities constructed with variable species and growth form diversity possess differences in resistance to weed invasion. Seeds of an invasive grass and forb were introduced into constructed plots that were either left intact or disturbed by removing plants from plots to determine how disturbance affects invasion by the two weeds. In addition, I conducted a competition experiment in two field locations to more closely evaluate the competitive interactions between three common big sagebrush-steppe species and an invasive grass and forb species and a reclamation shrub. Relative ability to acquire a ^{15}N tracer in spring as well as the comparative shoot and root growth of the six species were evaluated. Because weed invasion and disturbance provide an overwhelming need to rehabilitate shrub-steppe communities in the Great Basin, this research may provide new insights into the importance of managing landscapes for greater species and growth form diversity and reduce the frequency of disturbance.

LITERATURE REVIEW

Relationships between plant diversity and resistance to weed invasion

The relationship between species diversity and patterns of weed invasion within ecosystems has not been consistently observed across spatial scales. Most small-scale studies (<1ha) support the general hypothesis that species richness acts as a barrier to successful invasion by weed species (Tilman 1986, 1997; Naeem et al. 2000; Gastine et al. 2003; Xu et al. 2004; Lu and Ma 2005). However, in some small scale studies (Foster 2002; Palmer and Maurer 1997; Stohlgren et al. 2002), and most large-scale studies (>1ha), a positive relationship has been found between the desired species diversity and weed diversity (Lonsdale 1999; Stohlgren et al. 1998, 1999, 2001, 2002, 2003), suggesting that species-rich environments are also hot-spots for high weed species richness. However, in a review of large-scale studies, Lundholm and Larson (2004) proposed that there was either no relationship or a negative relationship between site diversity and weed diversity. Lu and Ma (2005) investigating the invasion of croftonweed (*Eupatorium adenophorum* Sprengel.) in southwest China found that at the 25m^2 scale, plant diversity had a negative relationship with invasion success, while at the 400m^2 scale both positive and negative relationships were found.

Reconciling scale-dependency of ecological processes and patterns is a common challenge because it attempts to merge aspects of space, time, and organizational complexity (Levin 1992, 2000). Understanding patterns for species richness and weed richness at these various scales necessitates identifying the factor(s) that predominate at each scale (Wiens 1989), because the factors that control processes at fine scales often differ from those operating at broad scales (Turner et al. 1995). How diversity is defined is also important. For example, Xu et al. (2004) investigating the differences between functional group diversity vs. species diversity, found that the biomass of alligator weed (*Alternathera philoxeroides* [Mart.] Grisb.) was reduced more in plots by functional group diversity.

Small-scale studies may be more appropriate to tease-out the mechanisms responsible for the relationships observed between species richness and invasion success. Most small-scale studies demonstrate that more diverse plots will have less available resources as compared to less diverse plot with similar site conditions. Some of the important resources that have been associated with this response include soil water, soil N, photosynthetically active radiation (PAR), safe sites, and the temporal and spatial variability of these resources (Tilman 1986, 1997; Sphen et al. 2000; Farigione et al. 2003; Gastine et al. 2003; Lu and Ma 2005). In particular, Fargione et al. (2003) identified the availability of soil nitrate, safe sites, and light transmittance as the most important factors in promoting species invasion in small-scale (9 m^2) plots. Larson et al. (1997) determined that the key plant community resources in the Great Basin rangelands to be light, water, soil nutrients, and safe sites.

In most small scale-studies, more complete use of the available resources by the resident species has been the identified as the mechanism responsible for the ability of high-diversity plots to reduce weed invasion (Tilman 1997). Thus, it is not species diversity in and of itself, but the elimination of safe sites and exploitation of resources that resists weed invasion (Tilman 1986). For example, high diversity plots in Gastine et al. (2003) had the lowest soil inorganic nitrogen content and high species diversity resulted in greater competition for available resources. Hooper and Vitousek (1998) suggest that species diversity fosters spatial and temporal site occupation, and highlight the importance of species phenology, rooting depth, root: shoot biomass ratio, plant stature, and leaf C: N content. The effectiveness of small-scale studies to remain mechanistic is also attributed to their ability to avoid site differences in slope, aspect, soil type, and soil water regime. In contrast, larger-scale studies have not sufficiently identified the mechanism responsible for the positive relationship between native species diversity and weed diversity because of the greater heterogeneity of most landscape-scale studies.

Disturbance may also have direct or indirect effects on the success of weed invasion in plots by altering aboveground structure and soil resources. Disturbance may provide an opportunity for weed invasion by producing a pulse in nutrient availability, creating safe-sites for seeds to germinate, creating canopy gaps that increase available light resources, and possibly reducing competition for water and soil nutrients. Integrating the effects of disturbance on soil nutrients, Case (1990) and Davis and Liebman (2001) found that regardless of the level of plant diversity, resource competition intensity controlled invasibility.

Small-scale experiments evaluating the relationship between species richness and invasion success typically utilize constructed communities. Walker (1992) advocates this approach because these experiments provide the potential to incorporate functional groups that occur in the ecosystem being evaluated. For example, constructing communities with species of multiple functional groups (e.g., grasses, forbs, and shrubs) could be an effective way to evaluate whether diversity fosters more complete spatial and temporal resource use and occupation of space (Hooper and Vitousek 1998). In a review article, Prieur-Richard and Lavorel (2000) found that many diversity studies lacked divergence in spatial and temporal resource use, and suggested that future studies should vary functional group diversity while holding species diversity constant. Thus, documenting above and belowground resource status of plots containing varying combinations of species from different functional groups appears to be a reasonable approach to determining a mechanistic understanding of weed invasion.

Plant Invasions in the Great Basin

The economic impacts of invasive rangeland weeds are estimated to be around $2 billion annually (Bovey 1987; Pimentel et al. 2000). Aside from economic losses, invasive plants have the potential to displace native species (Wilcove et al. 1998; Sala et al. 2000) by altering structural and functional ecosystem attributes (Vitousek et al. 1996; Keeley 2000; Ehrenfeld et al. 2001). To proactively stem the spread of invasive weeds, ecologists attempt to understand and identify attributes of problematic species (Lodge 1993; Burke and Grime

1996; Rejmánek and Richardson 1996; Goodwin et al. 1999) and characteristics of the ecosystem, because the success of an invader often strongly depends on complex interactions between the species and its target community (D'Antonio 1993; Thebaud et al. 1996; Radford and Cousens 2000).

Weed invasion and the associated ecological and socioeconomic impacts in the Great Basin have greatly accelerated since pioneer settlement in the 1840s. During this era, pioneers introduced livestock into the Intermountain sagebrush-steppe semi-deserts and salt-desert shrublands to support new human settlements and the growing mining industry. The large-scale vegetation changes induced by unrestricted livestock use were clearly evident by the end of century (West 1983). The main changes induced by heavy grazing included a decline in perennial grasses and other herbaceous plants (i.e., forbs) and an increase in dominance of sagebrush that was less favorable to livestock (Pickford 1932). Heavy livestock grazing not only initiated the destruction of perennial native herbaceous plants, but also had profound impacts on plant litter dynamics and microphytes that help maintain soil aggregate stability and infiltration of precipitation (Blackburn et al. 1992). These disturbances created the ideal backdrop for weed invasion.

Many annual plant species have invaded the Great Basin (Young et al. 1972; Allen and Knight 1984; Brandt and Rickard 1994); however, invasion by the annual grass downy brome (*Bromus tectorum* L.) has dominated the attention of resource managers since the 1930s (Knapp 1993; Young and Allen 1997). The earliest account of downy brome in Utah was made in 1894 (Yensen 1981). Initial dispersal throughout this region was likely associated with crop seeds like wheat and alfalfa (Mack 1986). Downy brome was initially considered to be strictly a weed of cultivated fields and roadsides, and later moved from these areas into overgrazed rangelands (Young and Allen 1997). Downy brome also showed a tight affinity to railroad right-of-ways because they were frequently disturbed by fires started by locomotives (Yensen 1981). Many factors were likely responsible for downy brome invasion following its initial dispersal. Biologically, downy brome has a rapid growth rate, especially at low temperatures. Prolific seed production and seeds that remain viable in the soil for a number of years (Mack and Pyke 1983), allowed it to spread and become a stiff competitor to native perennial species. In addition, its annual life form and high growth rate provides downy brome with the potential to respond rapidly to soil nutrient pulses that often accompany wildfire and soil disturbances (Blank et al. 1994; Monaco et al. 2003a, 2003b).

Invasion of downy brome had profound impacts on the structure and function of shrub-steppe communities in the Great Basin primarily through altering wildfire frequency. Vegetation prior to European settlement was largely comprised of bunchgrasses and shrubs that probably produced infrequent, low temperature fires that did not alter species composition drastically (Daubenmire 1975). However, downy brome invasion drastically changed the intensity and frequency of wildfire throughout the Great Basin. Downy brome is very productive, especially in wet years, and begins to senesce in late spring, when soil moisture becomes limiting. High productivity of downy brome has been estimated to exceed that of native steppe several fold (Rickard 1985). Productivity and fuel production by downy brome facilitates these lands to burn much more frequently than in the past (Whisenant 1990). The downy brome induced fire-cycle makes it extremely difficult to re-establish perennial vegetation back into semi-arid rangelands. Longer-lived perennial grasses and shrubs cannot survive frequent wildfires or sufficiently compete with downy brome (Harris 1967).

In addition to annual weeds, the spread of invasive biennial/perennial forb weeds (Young and Longland 1996; DiTomaso 2000) has drawn the attention of resource managers in the last two decades. While the causes for annual weed invasion were clear, the mechanisms responsible for invasion by deep-rooted, longer-lived forbs like the knapweeds (*Centaurea* and *Acroptilon spp*.), leafy spurge (*Euphorbia esula* L.), and dyer's woad (*Isatis tinctoria*) remain elusive. Some have suggested that these perennial weeds possess novel biological traits to interfere with native vegetation (Callaway and Ridenour 2004) or have escaped specialist herbivores in their introduced ranges (Stastny et al. 2005). Others suggest that the proliferation of these perennial weeds is associated with available resources and empty niches created by disturbances (Sheley et al. 1996) and the loss of native forb species (Pokorny et al. 2004, 2005). The latter interpretation assumes that diverse weed-resistant communities occupy the spatial and temporal niches and pre-empts weed resource use. This interpretation makes sense because disturbance within plant communities generates opportunities for plant invasions by disrupting competitive interactions (Wilson and Tilman 1993) and increasing the availability of limiting resources (Hobbs and Huenneke 1992). A recent theory contends that fluctuating resource availability may be the key factor controlling weed invasion into an environment (Davis et al. 2000). This theory assumes that species are more likely to successfully invade a community if it does not encounter intense competition for available resources from resident species, because competition intensity decreases as unused resources increases.

Determining relative competitive effects in neighborhood designs

Neighborhood designs have been considered an excellent way to evaluate competition as well as helpful in describing a species zone of influence (Tremmel and Bazzaz 1995; Gibson et al. 1999; Casper et al. 2003). In brief, these designs designate a plant or a set of plants as the target(s), while the neighborhood is constructed with variable neighboring species. In its simplest form, the target-neighbor design provides an efficient way of comparing the relative competitive effects of numerous species on a target species. Environmental factors and resources can also be easily manipulated to determine interactions with neighbor identity. Fowler (1990) used a design where plants were placed in disturbed and undisturbed vegetation, planted singly or pairs, and into three vegetation types. Another study by Hall et al. (1999) evaluated the effects of competition between neighbors. They found that antelope bitterbush grew better with bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) than crested wheatgrass (*Agropyron cristatum* var. *cristatum* [L.] Gaertn.) and downy brome. Tremmel and Bazzaz (1995) evaluated the change in species architecture as a response to neighbor effects on resources. These studies illustrate the wealth of information obtained by identifying the effects one species on another.

Target-neighbor designs can also be used to determine relative competitive ability (i.e., nutrient uptake ability) of species by injecting isotopes into the soil between competing pairs and determining uptake into shoots. This approach was used to determine the relative competitive ability in dominant and subordinate pairs of perennial grasses in native grassland (Hendon and Briske 2002). Caldwell et al. (1985) using P^{32} and P^{33} were able to determine the relative competitive effects of two perennial grass species on phosphorous uptake of

Artemisia tridentata ssp. vaseyana (Rydb.) Beetle. Similarly, ^{15}N-labeled NH_4^+ was used to determine the relative NH_4^+ utilization by annual and perennial grasses and two shrub species (Duke and Caldwell 2001). In another study, growth, biomass production, and leaf-N content of the invasive weed downy brome was determined when grown with different perennial neighbors (Yoder and Caldwell 2002). Resource availability within the Great Basin is restricted to ephemeral pulses following snowmelt or precipitation events. Bilbrough and Caldwell (1997) utilizing a ^{15}N tracer highlighted the functional importance of acquiring nutrient in pulses in Great Basin species. Downy brome is capable of germination at low seedbed temperatures as well as use soil water earlier than many of the native species (Harris 1967; Aguirre and Johnson 1991). Using ^{15}N-labeled NH_4^+, Booth et al. (2003) were able to determine that growth suppression of downy brome by the short-lived perennial grass bottlebrush squirreltail (*Elymus elymoidies* [Raf.] Swezey) and suppression of big sagebrush (*Artemisia tridentata* Nutt.) by downy brome was more closely related to soil moisture than acquisition of soil nitrogen. Collectively, these studies are intriguing because they demonstrate relative competitive ability for a nutrient as well as the relative competitive effects of one species on another.

OBJECTIVES

Competition for soil nitrogen between three common sagebrush-steppe species from three growth forms (grass, forb, and shrub) and an invasive grass and forb and a reclamation shrub was evaluated by injecting isotopically labeled nitrate between plant pairs. This experiment tested two specific hypotheses: 1) the invasive grass (downy brome), invasive forb (dyer’s woad), and introduced-exotic reclamation shrub (prostrate kochia) would differentially affect nitrate uptake and shoot and root growth of three representative sagebrush-steppe species, and 2) within a growth form, species with shorter plant- (downy brome and dyer’s woad) and/or leaf-lifespan (prostrate kochia) would be better competitors for nitrate. In addition, we evaluated a *post hoc* comparison to identify traits responsible for species and growth form differences in nitrate acquisition and how these traits may suggest the presence of differing strategies to persist within disturbed semiarid shrub-steppe ecosystems. A second experiment was established to provide insights into the relative ability of the three sagebrush-steppe growth forms to resist invasion of two distinctly different weeds that complicate restoration efforts in disturbed sagebrush-steppe communities. Utilizing plots constructed from three growth forms (grass, forb, shrub) in single- and four-species plots and a mix plot with the three growth forms, I tested the following three hypotheses: 1) a mix of the three morphologically distinct growth forms (grass, forb, and shrub) provides greater weed resistance than single species of individual growth forms, 2) resistance to invasion is greater in plots that contain species of the same growth form as the invader, and 3) disturbance similarly facilitates invasion in single-species grass, forb, and shrub plots.

LITERATURE CITED

Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. *Journal of Range Management* 44:347-354.

Allen, E. B., and D. H. Knight. 1984. The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. *The Southwestern Naturalist* 29:407-421.

Anderson J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs* 71:531-556.

Bilbrough, C. J., and M. M. Caldwell. 1997. Exploitation of springtime ephemeral N pulses by six Great Basin plant species. *Ecology* 78:231-243.

Blackburn, W. H., F. B. Pierson, C. L. Hanson, T. L. Thurow, and A. L. Hansen. 1992. The spatial and temporal influence of vegetation on surface soil factors in semiarid rangelands. *Transactions of the American Society of Agricultural Engineering* 35:479-480.

Blank, R. R., F. Allen, and J. A. Young. 1994. Growth and elemental content of several sagebrush-steppe species in unburned and post-wildfire soil and plant effects on soil attributes. *Plant and Soil* 164:35-41.

Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* 91:36-48.

Bovey R. W. 1987. Weed control problems, approaches, and opportunities in rangeland. *Review of Weed Science* 3:57-91.

Brandt, C. A., and W. H. Rickard. 1994. Alien taxa in the North American shrub-steppe four decades after cessation of livestock grazing and cultivation agriculture. *Biological Conservation* 68:95-105.

Burke M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77:776-790.

Caldwell M. M., D. M. Eissenstat, J. H. Richards, and M. E. Allen. 1985. Competition for phosphorus: differential uptake from dual-isotope-labeled soil interspaces between shrub and grass. *Science* 229:384- 86.

Callaway, R. M., and W. M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2:436-443.

Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. In: Proceedings of the National Academy of Sciences of the United States of America 87:9610-9614.

Casper, B. B., H. J. Schenk, and R. B. Jackson. 2003. Defining a plant's belowground zone of influence. *Ecology* 84:2313-2321.

D'Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology* 74:83-95.

Daubenmire, R. 1975. Plant succession on abandoned fields, and fire influences, in a steppe area in southeastern Washington. *Northwest Science* 49:36-48.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invisibility. *Journal of Ecology* 88:528-534.

Davis, A. S., and M. Liebman 2001. Nitrogen source influences wild mustard growth and competitive effect on sweet corn. *Weed Science* 49:558-566.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Science* 48:255-265.

Duke, S. E., and M. M. Caldwell. 2001. Nitrogen acquisition from different spatial distributions by six great basin species. *Western North American Naturalist* 61:93-102.

Ehrenfeld, J. G., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* 11:1287-1300.

Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *In*: Proceedings of the National Academy of Science USA 100:89-168920.

Foster, B. L., V. H. Smith, T. L. Dickson, and T. Heldebrand. 2002. Invasibility and compositional stability in a grassland community: relationships to diversity and extrinsic factors. *Oikos* 99:300-307.

Fowler, N. L. 1990. The effects of competition and environmental heterogeneity on three coexisting grasses. *Journal of Ecology* 78:389-402.

Gastine, A., J. Roy, and P. W. Leadley. 2003. Plant biomass production and soil nitrogen in mixtures and monocultures of old field Mediterranean annuals. *Acta Oecologia* 24:65-75.

Gibson, D. J., J. Connolly, D. C. Hartnett, and J. D. Weidenhamer. 1999. Designs for greenhouse studies of interactions between plants. *Journal of Ecology* 87:1-16.

Goodwin, B. J., A. J. McCallister, and L. Fahrig. 1999. Predicting invasiveness of plant species based on biological information. *Conservation Biology* 13:422-426.

Hall, D. B., V. J. Anderson, and S. B. Monsen. 1999. Competitive effects of bluebunch wheatgrass, crested wheatgrass, and cheatgrass on antelope bitterbrush seedling emergence and survival. USDA Forest Service, Rocky Mountain Research Station, RMRS-RP-16.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89-111.

Hendon, B. C., and D. D. Briske. 2002. Relative herbivory tolerance and competitive ability in two dominant: subordinate pairs of perennial grasses in a native grassland. *Plant Ecology* 160:43-51.

Hobbs, R., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6:324-337.

Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* 68:121-149.

Keeley, J. E. 2000. Fire and invasive species in mediterranean-climate ecosystems of California. *In*: K.M. Galley TPS [ED.]. Proceedings of the Invasive species workshop: the role of fire in the control and spread of invasive species. Tall Timbers Research Station, Miscellaneous Publication No. 11, San Diego, California, p. 81-94.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636-638.

Knapp, P. A. 1993. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin desert. *Global Environmental Change* 6:37-57.

Law, R., and R. D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* 77:762-775.

Larson, L., M. McInnis, and G. Klemnec. 1997. Rangeland weed invasion. *Rangelands* 19: 30-32.

Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.

Levin, S. A. 2000. Multiple scales and the maintenance of biodiversity. *Ecosystems* 3:498-506.

Lodge, D. M. 1993. Biological invasion: lessons for ecology. *Trends in Ecology and Evolution* 8:133-137.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522-1536.

Lu, Z., and K. Ma. 2005. Scale dependent relationships between native plant diversity and the invasion of croftonweed (*Eupatorium adenophorum*) in southwest China. *Weed Science* 53:600-604.

Lundholm, J. T., and D. W. Larson. 2004. Dominance as an overlooked measure of invader success. *Biological Invasions* 6:505-510.

Mack, R. N., and D. A. Pyke. 1983. The demography of *Bromus tectorum*: variation in time and space. *Journal of Ecology* 71:69-93.

Mack, R. N. 1986. Alien plant invasion into the Intermountain West: A case history. *In*: Mooney, H. A., J. A. Drake [EDS.]. Ecology of biological invasions of North America and Hawaii. Springer, New York. p.191-213.

Mack R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710.

McGrady-Steed, J., P. M. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. *Nature* 390:162-165.

Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003a. Contrasting responses of Intermountain West grasses to soil nitrogen. *Journal of Range Management* 56:282-290.

Monaco, T. A., C. T. Mackown, D. A. Johnson, T. A. Jones, J. M. Norton, J. B. Norton, and M. G Redinbaugh. 2003b. Nitrogen effects on seed germination and seedling growth. *Journal of Range Management* 56:646-653.

Naeem, S., J. M. H. Knops, D. Tilman. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91:97-108.

Naeem, S., J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecological Letters* 6:567-579.

Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28. U.S. Department of the Interior National Biological Service, Washington, D.C.

Palmer, M. W., and T. A. Maurer. 1997. Does diversity beget diversity? A case study of crops and weeds. *Journal of Vegetation Science* 8:235-240.

Pickford, G. D. 1932. The influence of continued heavy grazing and of promiscuous burning on spring-fall ranges in Utah. *Ecology* 13:159-171.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50:53-65.

Pokorny, M. L., R. L. Sheley, T. J. Svejcar, and R. E. Engel. 2004. Plant species diversity in a grassland plant community: Evidence for forbs as a critical management consideration. *Western North American Naturalist* 64:219-230.

Pokorny, M. L., R. L. Sheley, C. A. Zabinski, R. E. Engel, A. J. Svejcar, and J. J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* 13:1-12.

Prieur-Richard, A., and S. Lavorel. 2000. Invasions: the perspective of diverse plant communities. *Austral Ecology* 25:1-7.

Radford, I. J., and R. D. Cousens. 2000. Invasiveness and comparative life-history traits of exotic and indigenous *Senecio* species in Australia. *Oecologia* 125:531-542.

Rejmánek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* 77:1655-1661.

Rickard, W. H. 1985. Shoot production and mineral nutrient assimilation in cheatgrass communities. *Northwest Science* 59:169-179.

Sala, O. E, F. S. Chapin III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M.T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770-1774.

Sheley, R. L., and J. Kruger-Mangold. 2003. Principles for restoring invasive plant-infested rangeland. *Weed Science* 51:260-265.

Sheley, R. L., T. J. Svejcar, and B. D. Maxwell. 1996. A theoretical framework for developing successional weed management strategies on rangeland. *Weed Technology* 10:766-773.

Sphen, E. M., J. Joshi, B. Schmid, M. Diemer, and C. Körner. 2000. Above-ground resource use increases with plant species richness in experimental grassland ecosystems. *Functional Ecology* 14:326-337.

Stastny, M., U. Schaffner, and E. Elle. 2005. Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? *Journal of Ecology* 93:27-37.

Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. A. Villa, and M. Lee. 1998. Riparian zones as havens for exotic plant species in the central grassland. *Plant Ecology* 138:113-125.

Stohlgren, T. J., C. Binkley, G. W. Chong, M. A. Kalkhan, M. Bashkin, and Son Yowhan. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69:25-46.

Stohlgren, T. J., Y. Otsuki, C. A. Villa, M. Lee, and J. Belnap. 2001. Patterns of plant invasions: a case example in native species hotspots and rare habitats. *Biological Invasions* 3:37-50.

Stohlgren, T. J., G. W. Chong, L. D. Schell, K. A. Rimar, Y. Otsuki, M. Lee, M. A. Kalkhan, and C. V. Villa. 2002. Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. *Environmental Management* 29:566-577.

Stohlgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment* 1:11-14.

Thebaud, C., A. C. Finzi, and L. Affre. 1996. Assessing why two introduced *Conyza* differ in their ability to invade Mediterranean old fields. *Ecology* 77:791-804.

Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. *Ecology* 67:555-563.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2-16.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81-92.

Tremmel, D. C. and F. A. Bazzaz. 1995. Plant architecture and allocation in different neighborhoods: implications for competitive success. *Ecology* 76:262-271.

Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. G. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit populations-models in land management. *Ecological Applications* 5:12-16.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57:7-13.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:468-478.

Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6:18-23.

West, N. E. 1983. Western Intermountain sagebrush steppe. *In*: N. E. West [ED.]. Temperate deserts and semi-deserts. Elsevier, Amsterdam. p. 351-374.

West, N. E. 1988. Intermountain deserts, shrub steppes, and woodlands. *In:* M. G. Barbour and W. D. Billings [EDS.]. North American terrestrial vegetation. Cambridge, UK: Cambridge University Press. p. 209-230.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake Rive Plains: Ecological and management implications *In*: E. D. McArthur, E. M. Romney, S. D Smith, and P. T. Tueller [EDS.]. Proceedings of the Symposium On Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management. USDA-FS Intermountain Research Station, Ogden, UT, Gen. Tech. Rep. INT-276. p. 4-10.

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48:607-615.

Wilson, S. D., and D. Tilman. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74:599-611.

Xu, K., W. Ye, H. Cao, X. Deng, Q. Yang, and Y. Zhang. 2004. The role of diversity and functional traits of species in community invasibility. *Botanical Bulletin of the Academy of Sci*ence 45:149-157.

Yensen, D. 1981. The 1900 invasion of alien plants into southern Idaho. *Great Basin Naturalist* 41:176-183.

Yoder, C., and M. Caldwell. 2002. Effects of perennial neighbors and nitrogen pulses on growth and nitrogen uptake by Bromus tectorum. *Plant Ecology* 158:77-84.

Young, J. A. and F. A. Allen. 1997. Cheatgrass and range science: 1930-1950. *Journal of Range Management* 50:530-535.

Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* 31:283-289.

Young, J. A., R. A. Evans, and J. Major. 1972. Alien plants in the Great Basin. *Journal of Range Management* 25:194-201.

Young, J. A. and W. S. Longland. 1996. Impact of alien plants on Great Basin Rangelands. *Weed Technology* 10:384-391.

CHAPTER 2

INVASIVE FORB, ANNUAL GRASS, AND EXOTIC SHRUB COMPETITION WITH THREE SAGEBRUSH-STEPPE GROWTH FORMS: ACQUISITION OF A SPRING ^{15}N TRACER

ABSTRACT

Understanding competition for soil nitrate between common shrub-steppe, potential reclamation species, and common invasive species is necessary to identify mechanisms associated with ecosystem invasion and may assist with developing weed management scenarios. We designed a field experiment to evaluate the differential competitive effects of the invasive annual grass downy brome (*Bromus tectorum* L.), the invasive biennial forb dyer's woad (*Isatis tinctoria* L.), and the reclamation shrub prostrate kochia (*Kochia prostrata* [L.] Schrad.) on nitrate acquisition of the perennial grass crested wheatgrass (*Agropyron cristatum* [L.] Gaertner x *A. desertorum* [Fisch. ex Link] Schultes), the native forb western yarrow (*Achillea lanulosa* Nutt.), and the native shrub big sagebrush (*Artemisia tridentata var.wyomingensis* [Beetle & A. Young] Welsh) at two sites in northern Utah. Individual plants were grown in two-plant neighborhoods and a $K^{15}NO_3$ tracer was injected into the soil between plants and recovered from leaf material within 15 days. We also evaluated neighbor effects on shoot and root growth, leaf carbon: nitrogen ratio, and leaf N concentrations as well as a *post hoc* comparison of the six species to better understand how these traits are associated with differences in nitrate acquisition and nitrogen allocation among the three growth forms. Nitrate acquisition of crested wheatgrass and western yarrow were lower when competing with downy brome than with dyer’s woad and prostrate kochia (*P* < 0.01); however, the three growth forms had similar competitive effects on nitrate acquisition of big sagebrush. Nitrate acquisition ratios between competing neighbors revealed that 1) the grasses always acquired more nitrate than neighbors of a different growth form, 2) western yarrow was equally competitive with an invasive forb and prostrate kochia, and 3) all neighbors acquired more nitrate than big sagebrush. Greater competition for nitrate in the grasses was associated with greater specific root length. The two invasive weeds and prostrate kochia always had lower leaf C: N ratio (*P* < 0.01), and greater leaf N concentration (*P* < 0.01), which have been broadly correlated with leaf longevity, nutrient use efficiency, and indicate differing strategies to persist in the semiarid shrub-steppe ecosystems.

INTRODUCTION

The sagebrush-steppe ecosystem in the Great Basin is threatened by a combination of factors associated with climate change, invasive weeds, and modified disturbance regimes (Young and Evans 1978; West 1988; Whisenant 1990; Noss et al. 1995; Anderson and Inouye 2001). Prior to European settlement, this ecosystem was dominated by big sagebrush (*Artemisia tridentata* [Beetle & A. Young] Welsh) and an understory of perennial bunchgrasses and forbs (West 1988). European settlement resulted in widespread disturbances in the form of overgrazing, sagebrush removal, and timber harvest in the mountain foothills (Brotherson and Brotherson 1981). These disturbances decreased native species dominance and diversity and opened the ecosystem up for weed invasion (Young and Allen 1997). Disturbed sagebrush-steppe ecosystems have been historically dominated by invasive annual species like downy brome (*Bromus tectorum* L.) (Young and Evans 1978;

Buman et al. 1988; Melgoza et al. 1990; Humphrey and Schupp 2004). More recently, attention has been given to invasive forbs that possess complex and efficient strategies for colonization and long-term occupancy (*i.e.,* knapweeds: *Centaurea* and *Acroptilon spp*. L., leafy spurge: *Euphorbia esula* L., rush skeletonweed: *Chondrilla juncea* L., and dyer's woad: *Isatis tinctoria* L.)(Dewey et al. 1991; Young and Longland 1996; DiTomaso 2000; Liao et al. 2000; LeJeune and Seastedt 2001).

The success of downy brome within disturbed sagebrush-steppe is associated with its capacity to exploit short-duration nutrient pulses coupled with greater growth at low seedbed temperature than native perennial species (Harris 1967; Aguirre and Johnson 1991; Duke and Caldwell 2001). The coupling of prolific root production and the ability to rapidly capture soil resources (Svejcar 1990; Bilbrough and Caldwell 1997) also provides a competitive advantage over sagebrush and native perennial grasses in relatively unproductive sagebrush-steppe, where soil nitrate availability coincides with ephemeral pulses following precipitation events (Cui and Caldwell 1997a; Goldberg and Novoplansky 1997). Unlike downy brome, the ability of invasive forbs to spread and dominate within semiarid shrub-steppe ecosystems appears to be less attributed to greater acquisition of particular resources (Herron et al. 2001; Smith and Knapp 2001; Lowe et al. 2002). For example, studies have shown that invasive forbs are not more responsive to nitrogen availability or pulses than the native grasses with which they compete (Blicker et al. 2002; Olson and Blicker 2003), suggesting that they may gain dominance through physiological flexibility to variable environmental conditions and/or greater tolerance to low nutrient conditions (Hill and Germino 2005; Monaco et al. 2005).

A contemporary restoration strategy to reverse the detrimental effects of invasive weeds includes planting exotic transitional species into disturbed big sagebrush-steppe to assist the reestablishment of native herbaceous species (Cox and Anderson 2004). For example, crested wheatgrass (*Agropyron cristatum* [L.] Gaertner) has been planted on thousands of hectares in the United States to stabilize areas after disturbance and prevent invasion by downy brome (Rogler and Lorenz 1983). Crested wheatgrass is generally considered to be a more effective competitor with downy brome than native sagebrush-steppe species because it has shown greater ability to acquire soil-N (Aguirre and Johnson 1991; Bilbrough and Caldwell 1997). Similarly, the introduced exotic perennial shrub prostrate kochia (*Kochia prostrata* [L.] Schrad.) establishes well in downy brome dominated areas and is considered more competitive than big sagebrush because it has high soil water use in the spring and summer and has shorter-lived leaves, which are characteristic of this suffrutescent shrub (Romo and Haferkamp 1988; Monaco et al. 2003b). Prostrate kochia has been used primarily as a fuel break in wildfire prone regions (Harrison et al. 2000; Sullivan and Anderson 2001) and it remains unknown whether it competes strongly for soil nitrate, as has been shown for crested wheatgrass.

Species with different growth forms and/or originating from habitats with differing soil fertility have evolved adaptive strategies of biomass allocation and nutrient storage that influence nutrient uptake capacity (Aerts and Chapin 2000). Leaf lifespan is also an important functional trait that dictates biomass productivity and nutrient acquisition (Reich et al. 1997, 2003). Fast-growing species with short leaf lifespan (invasive weeds and disturbance adapted species) have greater plasticity in biomass allocation that contributes to high rates of nutrient acquisition in nutrient rich habitats (Lambers and Poorter 1992; Grime et al. 1997). In contrast, leaves with longer lifespan (perennial grasses and shrubs) have characteristically lower leaf N concentration, growth rates, and nutrient acquisition as part of their strategy to reduce nutrient losses in nutrient poor habitats (Berendse and Aerts 1987; Reich et al. 1992). Accordingly, the outcome of competition between invasive, introduced-exotic, and native species in sagebrush-steppe ecosystems may be associated with growth form status, patterns of biomass allocation, leaf and/or plant lifespan, and nutrient uptake capacity.

We designed a field experiment with two grasses, forbs, and shrubs that differ broadly in plant and leaf lifespan to characterize the outcome of competition for NO_3^- using a ^{15}N tracer. The long-lived species crested wheatgrass, western yarrow (*Achillea lanulosa* Nutt.), and big sagebrush (*Artemisia tridentata var.wyomingensis* [Beetle & A. Young] Welsh) were each paired with an invasive annual grass (downy brome), an invasive biennial forb (dyer's woad), and an introduced-exotic shrub with short leaf lifespan (prostrate kochia). Nitrate ($K^{15}NO_3$) was injected between plant pairs to evaluate competition (Gibson et al. 1999; Hendon and Briske 2002) and test two specific hypotheses: 1) the invasive grass (downy brome), invasive forb (dyer's woad), and introduced-exotic shrub (prostrate kochia) differentially affect nitrate uptake and shoot and root growth of three representative sagebrush-steppe species, and 2) within a growth form, species with shorter plant- (downy brome and dyer's woad) and/or leaf-lifespan (prostrate kochia) have greater acquisition of the ^{15}N tracer. In addition, we evaluated a *post hoc* comparison to identify traits responsible for species and growth form differences in nitrate acquisition and how these traits may suggest the presence of differing strategies to persist within disturbed semiarid shrub-steppe ecosystems.

MATERIALS AND METHODS

Study Sites and Species

Experiments were conducted in summer 2005 at Millville, UT (41° 39.44'N, 111° 48.88' W, 1402 m) and Hyde Park, UT (41° 48.41' N, 111° 49.21' W). Soil at the Millville site belongs to the Ricks series (coarse-loamy over sandy or sandy-skeletal, mixed, superactive, mesic Calcic Haploxerolls). Soil at the Hyde Park site belongs to the Nibley series (fine, mixed, active, mesic, Aquic Argixerolls). Long-term mean annual precipitation (30-yr) averaged for three local weather stations is 480 mm. Annual precipitation for the 2005 water year was 690 mm. The three weather stations recorded 10 rain events during our study amounting to an average of 80 mm precipitation. Prior to settlement in the mid-1800s, these sites were dominated by typical shrub-steppe species (Hull and Hull 1974). Both study sites were used for corn and alfalfa production for the past 50 years, but these crops were abandoned, plowed, sprayed with glyphosate [N-(phosphonomethyl)glycine] at 2 kg a.i. ha^{-1} in spring 2004, and left fallow until experiments were initiated in 2005. Soil nitrate was measured in April 2005 at both sites by taking 2 cm diameter x 15 cm deep soil cores (n = 6) to obtain soil samples, which were thoroughly mixed and extracted with 2 M KCl within 4 h of collection. The KCl solutions were filtered through pre-leached filter paper and frozen until analyzed colorimetrically with a flow injection autoanalyzer to determine concentrations of NO_2^- plus NO_3^- (Lachet Instruments, Milwaukee, WI.).

Two grasses (downy brome and crested wheatgrass), two forbs (dyer's woad and western yarrow), and two shrubs (prostrate kochia and wyoming big sagebrush) were germinated in 4 cm wide by 21 cm long plastic planting cones filled with a 3:1 mix of sand

and peat moss. Seeds of sagebrush, prostrate kochia (‘Immigrant’), western yarrow (‘Yakima’), and crested wheatgrass (‘CD-II’; *Agropyron cristatum* [L.] Gaertner x *A. desertorum* [Fisch. ex Link] Schultes) were acquired from a commercial seed company. Downy brome and dyer’s woad seeds were collected locally in Cache County, UT. Plants were grown under ambient solar radiation in a glasshouse on Utah State University campus with air temperature set to 70°C and controlled with a thermostat and radiant heaters in January 2005. Seedlings were transplanted into the field in April 2005 with intact root systems when grasses had 5-10 tillers, forbs had approximately five leaves, and shrubs were predominately single-stemmed and under 10 cm in height.

Transplants were arranged using a two-plant competitive pair design. Longer-lived shrub-steppe species (crested wheatgrass, western yarrow, and sagebrush) were each paired with the short-lived species (downy brome, dyer’s woad, and prostrate kochia). Downy brome and prostrate kochia leaves die or predominantly senesce reflecting their annual and suffrutescent nature, respectively. Although dyer’s woad plants are constrained to a shorter lifespan due to being a biennial forb, its basal-rosette leaves could possibly have a longer lifespan than seasonal western yarrow leaves. Species pairs were spaced 15 cm apart and separated from other pairs by 1 m and randomly arranged with 15 replicates at each site. Both sites were periodically weeded to remove incidental annual weeds carried-over from the seed bank.

Plant Response Variables

Competition for a spring nitrate pulse was assessed by injecting $K^{15}NO_3$ (at 99 atom% ^{15}N) midway between six of the 15 replications of each species pair using a spinal needle

(15-cm needle, 5-ml syringe). Injections were made on 3 June at Hyde Park and 16 June at Millville. Injections were designed to elevate the nitrate pool at each site by ~25% based on soil nitrate concentrations measured in April (see above). Mean soil nitrate concentration was two times greater at Millville than at Hyde Park (n = 6; 47.85 vs. 22.01 mg kg^{-1} respectively). We assumed that the volume of soil enriched represented 3 cm diameter x 15 cm length soil column (106 cm^3). Thus, 1.36 and 0.67 mg of $K^{15}NO_3$ were added to 3 ml of water and injected at Millville and Hyde Park, respectively, by slowly evacuating the syringe from a depth of 15 cm to the soil surface. The ^{15}N tracer was recovered from shoots when they were harvested 5 and 11 days after injecting for Millville and Hyde Park, respectively (Harvest 1). Shoots were oven-dried at 65ºC for 48 h, weighed to determine dry shoot mass, then ground to pass a 1 mm screen. Approximately 4.0-4.5 mg of ground shoot samples were placed in tin foil capsules and analyzed for ^{15}N atom% using continuous-flow, direct combustion mass spectrometry on a Europa Scientific ANCA 2020 system (SerCon, Cheshire, England). Mean natural abundance ^{15}N atom% of shoot samples collected from the six species prior to ^{15}N injection (n = 5) was subtracted from post-injection values to determine ^{15}N atom% excess, which was multiplied by shoot mass (g) and shoot nitrogen to calculate ^{15}N atom% excess pool. Ratio of ^{15}N atom% excess pools for target: neighbor species pairs (hereafter referred to ^{15}N pool ratio) were used to quantify relative nitrate acquisition between two species. Ratios greater than 1.0 indicate greater ^{15}N acquisition and allocation into shoot biomass by the target species.

The remaining nine competitive-pair replications remained in the field until aboveground biomass was harvested on July 26th and 27th and processed as above (Harvest 2). The differences between Harvest 2 and 1 provided an unbiased measure of shoot growth over a 40-day period for the six species and accounts for the differences in initial plant size. Shoots from Harvest 2 were dried and ground as described above and leaf carbon: nitrogen ratio, and leaf N were obtained by direct combustion with a LECO CHN–2000 autoanalyzer (LECO Corp., St. Joseph, MI). Following Harvest 2, soil cores (10 cm diameter x 17 cm deep, 1450 cm^3) were taken from the 15-cm interspaces between competitive-pairs where injections were made using a golf cup cutter (H10 Hole Cutter, KSAB Golf Equipment, Västerås, Sweden). Thus, soil cores only include new root growth into the interspace between pairs. Cores were stored at 3°C and gently washed over a 2-mm sieve to collect all root material. Roots were sorted by species, spread-out on transparent acetate sheets, and digital images were taken with a flatbed scanner. Root images were analyzed at 300 dpi for root length and diameter using WinRHIZO Pro version 2005b (Regent Instrument Inc., Quebec, Canada). Roots samples were oven-dried at 6ºC for 48 hours and weighed to determine root dry mass. Specific root length was calculated by dividing root length (m) by root dry mass (g).

Statistical Analysis

The experiment was a completely randomized design replicated at two sites. Nitrate acquisition data were analyzed as a two-way factorial to evaluate the effects of site and neighbor for each of the three long-lived species. The same model was used to analyze all other variables for each of the six species. All variables were also analyzed to determine species differences in traits associated with nitrate uptake and nitrogen allocation (*post hoc* hypothesis). All data were analyzed using GLM procedures (SAS 9.0, SAS Institute Inc., Cary, NC). Transformations were performed for each variable as needed to meet the assumptions of normality as closely as possible. We report the arithmetic least-squared means, which were compared using least significant difference and Duncan's multiple range tests ($\alpha = 0.01$). To determine whether ^{15}N pool ratio of competing neighbors differed from 1.0, we used the Wilcoxon sign rank test ($\alpha = 0.01$) in JMP 5.1.2 (SAS Institute Inc.).

RESULTS

Competition for the ^{15}N Tracer

Downy brome, dyer's woad, and prostrate kochia differentially affected ^{15}N pool ratio of crested wheatgrass and western yarrow. Crested wheatgrass ^{15}N pool ratio was greater when competing with prostrate kochia than with dyer's woad, which was greater than downy brome (Table 2-1, Fig. 2-1). Similarly, western yarrow had greater ^{15}N pool ratios when competing with prostrate kochia and dyer's woad than with downy brome. Big sagebrush ^{15}N pool ratios were similar at Hyde Park, but lower ($P < 0.01$) at Millville when competing with dyers woad and prostrate kochia than with downy brome (interaction means not shown). The outcome of competition for $K^{15}NO_3$ revealed that nitrate acquisition of crested wheatgrass was equal to downy brome, yet greater than dyer's woad and prostrate kochia (Table 2-2). In contrast, nitrate acquisition of western yarrow was lower than downy brome, but equal to dyer's woad and prostrate kochia. Big sagebrush always had lower nitrate acquisition than its neighbors.

Neighbor Effects on Shoot and Root Growth

Shoot and root growth of the representative shrub-steppe species was not differentially affected by the three shorter-lived neighbors (Table 2-3, 2-4). Conversely, the representative shrub-steppe species affected shoot dry mass, root dry mass, root length and specific root length of the shorter-lived species. Prostrate kochia had 67% lower shoot dry mass when grown with crested wheatgrass than with western yarrow and big sagebrush. Dyer's woad had about 61% greater root dry mass when competing with big sagebrush. Root length of dyer's woad was greatest when paired with big sagebrush and lowest when grown with crested wheatgrass. Root length of prostrate kochia was about 59% lower when competing with crested wheatgrass than with western yarrow or big sagebrush. Specific root length of downy brome was 18% greater when competing with big sagebrush than with crested wheatgrass or western yarrow.

Site Effects on Shoot and Root Growth

Site had numerous effects on shoot growth, carbon: nitrogen ratio, leaf N concentration, and root growth (Tables 2-3 and 2-5). Dyer's woad and prostrate kochia's shoot dry mass was (62 and 42%) greater at Hyde Park than at Millville. Leaf carbon: nitrogen ratio was 9, 26, and 21% greater for western yarrow, dyer's woad, and prostrate kochia at Millville than Hyde Park, respectively. Likewise, leaf N concentration was 9, 22, and 21% lower for western yarrow, dyer's woad, and prostrate kochia at Millville than Hyde Park, respectively. Root dry mass of downy brome was 36% greater at Millville than Hyde Park. Prostrate kochia root length at Millville was 46% greater than at Hyde Park. Dyer's woad root diameter was 23% greater at Hyde Park than Millville, while specific root length was 29% lower at Hyde Park than at Millville.

***Post hoc* Species comparisons**

The six species had significantly different shoot dry mass, leaf carbon: nitrogen ratio, leaf nitrogen, root dry mass, root length, root diameter, and specific root length ($F_{5, 624}$, $P<0.001$, analysis not shown). For the forbs and shrubs, species with shorter plant- and/or leaf-longevity had greater shoot dry mass; however, crested wheatgrass had greater shoot dry mass than the annual downy brome (Fig. 2-2). Leaf carbon: nitrogen ratio was always greater for the longer-lived species. In addition, long-lived species always had lower leaf nitrogen concentration than the short-lived species (Fig. 2-2).

Similar to shoot dry mass, root dry mass was greater for the short-lived forb and shrub, but was greater for the long- than the short-lived grass (Fig. 2-3). Grasses had nearly twice the amount of root length and two-times greater specific root length than the forbs and shrubs. Root length was greater for the long-lived grass and forb; however, prostrate kochia had greater length than big sagebrush. Root diameter was similar between the grasses, but greater for the short- than the long-lived forb and shrub species. Specific root length was greater for the short-lived grass. In contrast, the long-lived forb and shrub species had greater specific root length than short-lived species.

DISCUSSION

We hypothesized that 1) two invasive species and an introduced exotic shrub would differentially affect nitrate uptake and shoot and root growth of three longer-lived representative sagebrush-steppe species and that 2) within a growth form, species with shorter plant- and/or leaf-lifespan would be better competitors for the nitrate pulse. Both hypotheses were not rejected because ^{15}N pool ratios of crested wheatgrass and western yarrow were lowest when grown with downy brome and highest when competing with prostrate kochia. In contrast, the invasive species and prostrate kochia had similar effects on ^{15}N pool ratio big sagebrush. The outcome of competition for the ^{15}N tracer between the nine possible competing pairs indicated that the grasses always acquired more nitrate than neighbors of a different growth form, western yarrow was equally competitive with an invasive forb and prostrate kochia, and all neighbors acquired more nitrate than big sagebrush. Although shoot and root growth of the representative shrub-steppe species was not differentially affected by the three shorter-lived neighbors, the *post-hoc* comparison revealed that the six species broadly differed in productivity, biomass allocation, root morphology, and leaf nutritional aspects which provides insights into the differential strategies enabling these species to persist within disturbed semiarid shrub-steppe ecosystems.

Nitrogen absorption rate has been positively correlated with growth rate in annual and perennial grasses (Poorter et al. 1990; Nakamura et al. 2002; Liao et al. 2004). Compared to fast-growing weeds, crested wheatgrass is one of the few perennial bunchgrasses to contest these weeds by having early spring seedling emergence, root growth (Eissenstat and Caldwell 1988; Pyke 1990), and high shoot and root growth rate (Harris and Wilson 1970; Arredondo et al. 1998; Monaco et al. 2003a). Our results showed that nitrate acquisition by crested wheatgrass and downy brome were fairly well matched. Although downy brome has been shown to utilize concentrated patches of ^{15}N-labeled nitrogen to a greater extent than crested wheatgrass or big sagebrush (Duke and Caldwell 2001), downy brome and crested wheatgrass both respond strongly to early and mid-spring N-pulses relative to big sagebrush and the native perennial bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) (Bilbrough and Caldwell 1997; Cui and Caldwell 1997b). In addition, although crested wheatgrass had greater root dry mass than downy brome in our study, overall nitrate acquisition of downy brome was similar to crested wheatgrass at both sites, suggesting that greater specific root length of downy brome increased its acquisition capacity (Eissenstat 1991; Eissenstat and Caldwell 1988). However, when considering the differences in phenology and duration of resource use between downy brome and crested wheatgrass, it is reasonable to assume that perennial grasses make more efficient use of nitrogen than annual grasses as has been shown in Mediterranean grasslands (i.e., Joffre 1990). Efficient use of soil-N may provide a competitive advantage to crested wheatgrass stands by preventing nitrate accumulation under downy brome once it senesces, which may otherwise be used by germinating weed seedlings in autumn (Booth et al. 2003). The similarity of nitrate uptake between downy brome and crested wheatgrass also provides a mechanistic explanation for the ability of crested wheatgrass neighbors to reduce aboveground growth of downy brome more so than big sagebrush neighbors (Yoder and Caldwell 2002) and helps explain its effectiveness to reduce the reestablishment of downy brome within shrub-steppe ecosystems (Klomp and Hull 1972; Whitson and Koch 1998).

Although fluctuating resource availability has been hypothesized as the key factor controlling invasibility (Davis et al. 2000), and high plant diversity is associated with dampening fluctuations and discouraging invasion of non-resident species (Hooper and Vitousek 1998; Pokorny et al. 2005), the role that competition for limiting resources plays in the success of invasive forbs remains unclear. Our observation that dyer’s woad is less competitive for nitrate than downy brome when grown with crested wheatgrass and western yarrow agrees with previous suggestions that the success of an invasive forb (i.e., spotted knapweed) cannot be explained wholly by a greater response to N-pulses (Olson and Blicker

2003). Lower nitrate acquisition of dyer's woad than downy brome in this short-term evaluation also may be reflective of lower N requirement of dyer's woad (Monaco et al. 2005), potential differences in root characteristics or distribution (Peek et al. 2005), or greater uptake ability associated with more extensive root systems in grasses (Niklaus et al. 2001; Craine et al. 2002; Scherer-Lorenzen et al. 2003). Our observation that dyer's woad had the lowest specific root length, which has been positively correlated with nitrogen uptake (Eissenstat 2000), suggests that root morphology and/or distribution differences are important determinants of nitrate acquisition in this biennial weed (Sorgona and Cacco 2002; James et al. 2006). High root length and small root diameter of downy brome and other grasses are associated with high nitrate acquisition of fibrous root systems (Sullivan et al. 2000; Liao et al. 2004).

Low nitrate uptake of prostrate kochia compared to the grasses coupled with its relatively low effects on the nitrate acquisition of crested wheatgrass and western yarrow, suggest that this suffrutescent shrub does not intensely compete for soil nitrate with the fibrous root systems of herbaceous species. However, it does establish well in crested wheatgrass stands (Sullivan and Anderson 2001), and almost entirely suppresses downy brome in former annual dominated communities (McArthur et al. 1990; Monaco et al. 2003b). The ability of prostrate kochia to competitively exclude downy brome is likely associated with rapid use of soil water in early spring while maintaining more favorable water status than big sagebrush (Romo and Haferkamp 1988) and high drought tolerance during the summer season associated with NADP-ME C_4 photosynthesis and Kranz anatomy (Pyankov et al. 2001). These physiological and phenological advantages may also partially explain why annual weeds are scarce within prostate kochia plantings, whereas big sagebrush often forms stable successional states with an abundant annual weed understory on degraded landscapes (West 1988; Laycock 1991; Hemstrom et al. 2002).

Low nitrate acquisition of big sagebrush even though it had greater specific root length (SRL) than all species except the grasses suggests that high SRL alone does not enhance nitrate acquisition in this native long-lived shrub. Unsuccessful competition for nitrate of big sagebrush when competing with three shorter-lived growth forms may have been associated with having significantly lower root mass within the top 15 cm where soil cores were taken. Downy brome roots not only have smaller diameter than big sagebrush (Peek et al. 2005), but these very fine roots often dominate A horizons and diminish in lower soil horizons in sagebrush-steppe (Norton et al. 2004). In addition, if big sagebrush roots were deeper than the 15 cm, the conspicuous taproot systems dyer’s woad and prostrate kochia (Farah et al.1988; Harrison et al. 2000) may have provided the ample opportunity to compete with big sagebrush for nitrate.

Trade-offs are known to exist for traits that reduce nutrient losses and traits that lead to high dry matter productivity (Aerts and Chapin 2000). Significantly lower leaf nitrogen concentration and greater leaf C: N ratio in big sagebrush, western yarrow, and crested wheatgrass than their respective growth form counterparts suggests that the longer-lived species may be using a different adaptive strategy that comprises nutrient conservation at the cost of productivity. Although species with longer leaf lifespan are known to have lower relative growth rate which limits nutrient uptake and productivity these species may benefit under low resource availability because they can maximize biomass per unit of N (Reich et al. 1992; Aerts and Chapin 2000). On the other hand, dyer’s woad and prostrate kochia may achieve greater productivity than their native longer-lived counterparts by utilizing a strategy characterized by producing leaves with high nitrogen concentration to facilitate rapid growth.

CONCLUSIONS

The ability of downy brome to acquire nitrate in pulse events more efficiently than sagebrush-steppe species provides it with significant competitive advantages. Thus, developing management scenarios that reduce soil nitrate availability or reduce downy brome’s ability to acquire soil nitrate are essential to improving shrub-steppe communities. Crested wheatgrass matched or exceed shoot and root productivity of downy brome and reduced soil nitrate acquisition of downy brome and the invasive forb dyer’s woad, suggesting that fibrous root systems with high specific root length are associated with its competitive success against downy brome. Dyer’s woad was less competitive than downy brome for soil nitrate, which confirms previous conclusions that resource competition is not the primary mechanism responsible for its dominance and proliferation. However, because both crested wheatgrass and western yarrow reduced dyer’s woad nitrate uptake, opportunities should be actively explored to identify whether niche-differentiated, weed-resistant plant communities can be created. Our results also provide a clearer picture of the compatibility between prostrate kochia and other shrub-steppe species. While prostrate kochia had the greatest impact on nitrate acquisition of big sagebrush, its overall greater nitrate uptake capacity and comparative root and shoot growth than big sagebrush suggests that additional studies are required to determine the outcome of competition between these two shrubs at the community level and whether prostrate kochia may reduce downy brome within stable associations with big sagebrush.

LITERATURE CITED

Aerts, R., and F. S. Chapin III. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *In:* A. H. Fitter, and D. G. Raffaelli [EDS.]. Advances in Ecological Research. San Diego, CA: Academic Press. 30:1-67.

Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. *Journal of Range Management* 44:347-354.

Anderson J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs* 71:531-556.

Arredondo, J. T., T. A. Jones, and D. A. Johnson. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. *Journal of Range Management* 51:584-589.

Berendse, F., and R. Aerts. 1987. Nitrogen-use-efficiency: a biologically meaningful definition? *Functional Ecology* 1:293-296

Bilbrough, C. J., and M. M. Caldwell. 1997. Exploitation of springtime ephemeral N pulses by six Great Basin plant species. *Ecology* 78:231-243.

Blicker , P. S., B. E. Olson, and R. Engel. 2002. Traits of the invasive *Centaurea maculosa* and two native grasses: effect of N supply. *Plant and Soil* 247:261–269.

Booth, M. S., J. M. Stark, and M. M. Caldwell. 2003. Inorganic N turnover and availability in annual- and perennial-dominated soils in a northern Utah shrub-steppe system. *Biogeochemistry* 66:311-330.

Brotherson, J. D., and W. T Brotherson. 1981. Grazing impacts on the sagebrush communities of central Utah. *Great Basin Naturalist* 41:335-340.

Buman, R. A., S. B. Monsen, and R. H. Abernethy. 1988. Seedling competition between mountain rye, 'Hycrest' crested wheatgrass, and downy brome. *Journal of Range Management* 41:30-34.

Craine, J. M., D. Tilman, D. Wedin, P. Reich, M. Tjoelker, and J. Knops. 2002. Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology* 16: 563–574.

Cox, R. D., and V. J. Anderson. 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *Journal of Range Management* 57:203-210.

Cui, M., and M. M. Caldwell. 1997a. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant and Soil* 191:291-299.

Cui, M., and M. M. Caldwell. 1997b. Growth and nitrogen uptake of *Agropyron desertorum* and *Pseudoroegneria spicata* when exposed to nitrate pulses of different duration. *Australian Journal of Plant Physiology* 24:637-642.

Davis, M. A., and J. P. Grime, K. Thompson. 2000. Fluctuating resources in plant communities: a general threory of invasibility. *Journal of Ecology* 88:528-534.

Dewey, S. A., K. P. Price, and D. Ramsey. 1991. Satellite remote sensing to predict potential distribution of Dyers Woad (*Isatis tinctoria*). *Weed Technology* 5:479-484.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Science* 48:255-265.

Duke, S. E., and M. M. Caldwell. 2001. Nitrogen acquisition from different spatial distributions by six great basin species. *Western North American Naturalist* 61:93-102.

Eissenstat, D. 1991. On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. *New Phytologist* 118:63-68.

Eissenstat, D. 2000. Root structure and function in an ecological context. *New Phytologist* 148:353-354.

Eissenstat, D. M., and M. M. Caldwell. 1988. Seasonal timing of root growth in favorable microsites. *Ecology* 69:870-873.

Farah, K. O., A. F. Tanaka, and N. E. West. 1988. Autecology and population biology of dyers woad (*Isatis tinctoria*). *Weed Science* 36:186-193.

Gibson, D. J., J. Connolly, D. C. Hartnett, and J. D. Weidenhamer. 1999. Designs for greenhouse studies of interactions between plants. *Journal of Ecology* 87:1-16.

Goldberg, D., and A. Novoplansky. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* 85:409-418.

Grime, J. P., K. Thompson, R. Hunt, J. G. Hodgson, J. H. C. Cornelissen, I. H. Rorison, G. A. F. Hendry, T. W. Ashenden, A. P. Askew, S. R. Band, R. E. Booth, C. C. Bossard, B. D. Campbell, J. E. L. Cooper, A. W. Davison, P. L. Gupta, W. Hall, D. W. Hand, M. A. Hannah, S. H. Hillier, D. J. Hodkinson, A. Jalili, Z. Liu, J. M. L. Mackey, N. Matthews, M. A. Mowforth, A. M. Neal, R. J. Reader, K. Reiling, W. Ross-Fraser, R. E. Spencer, F. Sutton, D. E. Tasker, P. C. Thorpe, and J. Whitehouse. 1997. Integrated screening validates primary axes of specialization in plants. *Oikos* 79:259-281.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89-111.

Harris, G. A., and A. M. Wilson. 1970. Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Ecology* 51:530-534.

Harrison, R. D., N. J. Chatterton, B. L. Waldron, B. W. Davenport, A. J. Palazzo, W. H. Horton, and K. H. Asay. 2000. Forage kochia - Its compatibility and potential aggressiveness on Intermountain rangelands. Utah Agricultural Experiment Station Research Report 162. Logan, UT: Utah State University. p. 66.

Hemstrom, M. A., M. J. Wisdom, W. J. Hann, M. M. Rowland, B. C. Wales, and R. A. Gravenmier. 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the interior Columbia Basin, U.S.A. *Conservation Biology* 16:1243-1255.

Hendon, B. C., and D. D. Briske. 2002. Relative herbivory tolerance and competitive ability in two dominant subordinate pairs of perennial grasses in a native grassland. *Plant Ecology* 160:43-51.

Herron, G. J., R. L. Sheley, B. D. Maxwell, and J. S. Jacobsen. 2001. Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. *Restoration Ecology* 9:326-331.

Hill, J. P., and M. J. Germino. 2005. Coordinated variation in ecophysiological properties among life stages and tissue types in an invasive perennial forb of semiarid shrub steppe. *Canadian Journal of Botany* 83:1488-1495.

Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* 68:121-149.

Hull Jr., A. C., and M. K. Hull. 1974. Presettlement vegetation of Cache Valley, Utah and Idaho. *Journal of Range Management* 27:27-29.

Humphrey, D., and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405-422.

James, J. J., and J. H. Richards. 2006. Plant nitrogen capture in pulse-driven systems: interactions between root responses and soil processes. *Journal of Ecology* 94:765-777.

Joffre, R. 1990. Plant and soil nitrogen dynamics in Mediterranean grasslands: a comparison of annual and perennial grasses. *Oecologia* 85: 142–149.

Klomp, G. J., and A. C. Hull Jr. 1972. Methods for seeding three perennial wheatgrasses on cheatgrass ranges in southern Idaho. *Journal of Range Management* 25:266-268.

Lambers, H., and H. Poorter. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *In*: M. Begon and A. H. Fitter [EDS.], Advances in Ecological Research, vol. 23. Academic Press, London. p. 187-261.

Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:427-433.

LeJeune, K. D., and T. R. Seastedt. 2001. *Centaurea* species: the forb that won the west. *Conservation Biology* 15:1568-1574.

Liao, J. D., S. B. Monsen, V. J. Anderson, and N. L. Shaw. 2000. Seed biology of rush skeletonweed in sagebrush steppe. *Journal of Range Management* 53:544-549.

Liao, M., I. R. P. Fillery, and J. A. Palta. 2004. Early vigorous growth is a major factor influencing nitrogen uptake in wheat. *Functional Plant Biology* 31:121-129.

Lowe, P. N., W. K. Lauenroth, and I. C. Burke. 2002. Effects of nitrogen availability on growth of native grasses exotic weeds. *Journal of Range Management* 55:94-98.

McArthur E. D., A. C. Blauer, and R. Stevens. 1990. Forage kochia competition with cheatgrass in central Utah. *In:* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller [COMPS.], Proc. Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 5-7 April 1989; Las Vegas, NV. Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Research Station. GTR-276. p. 56-65.

Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (Cheatgrass) and two native species. *Oecologia* 83:7-13.

Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003a. Contrasting responses of Intermountain West grasses to soil nitrogen. *Journal of Range Management* 56:282-290.

Monaco, T. A., B. L. Waldron, R. L. Newhall, and W. H. Horton. 2003b. Re-establishing perennial vegetation in cheatgrass monocultures. *Rangelands* 25:26-29.

Monaco, T. A., D. A. Johnson, and J. E. Creech. 2005. Morphological and physiological responses of the invasive weed *Isatis tinctoria* to contrasting light, soil-nitrogen and water. *Weed Research* 45:460-466.

Nakamura, T., J. J. Adu-Gyamfi, A. Yamamoto, S. Ishikawa, H. Nakano, and O. Ito. 2002. Varietal differences in root growth as related to nitrogen uptake by sorghum plants in low-nitrogen environment. *Plant and Soil* 245:17–24.

Niklaus, P. A., E. Kandeler, P. W. Leadley, B. Schmid, D. Tscherko, and C. Korner. 2001. A link between plant diversity, elevated CO_2 and soil nitrate. *Oecologia* 127:540-548.

Norton, J. B., T. A. Monaco, J. M. Norton, D. A. Johnson, and T. A. Jones. 2004. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. *Journal of Arid Environments* 57:445-466.

Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. National Biological Service Biological Report 28. U.S. Department of the Interior, Washington, D.C. p. 58.

Olson, B. E., and P. S. Blicker. 2003. Response of the invasive *Centaurea maculosa* and two native grasses to N-pulses. *Plant and Soil* 254:457-467.

Peek, M. S., A. J. Leffler, C. Y. Ivans, R. J. Ryel, and M. M. Caldwell. 2005. Fine root distribution and persistence under field conditions of three co-occurring Great Basin species of different life form. *New Phytologist* 165:171-180.

Pokorny, M. L., R. L. Sheley, C. A Zabinski, R. E. Engel, T. J. Svejcar, and J. J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* 13:448-459.

Poorter, H., H. Remkes, and H. Lambers. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiology* 94:621-627.

Pyankov, V. I., E. G. Artyusheva, G. E. Edwards, C. C. Black Jr., and P. S. Soltis. 2001. Phylogenetic analysis of tribe Salsoleae (Chenopodiaceae) based on ribosomal ITS sequences: implications for the evolution of photosynthetic types. *American Journal of Botany* 88:1189-1198.

Pyke, D. A. 1990. Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. *Oecologia* 82:537-543.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological. Monographs* 62:365–392.

Reich P. B, M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* 94:13730-13734.

Reich P. B, I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* 164:S143-S164.

Rogler, G. A., and R. Lorenz. 1983. Crested wheatgrass--early history in the United States. *Journal of Range Management* 36:91-93.

Romo, J. T., and M. R. Haferkampt. 1988. Comparative water relation in *Artemisia tridentata* Nutt. *subsp. wyomingensis* and *Kochia prostrata* L. Schrad. *Journal of Arid Environments* 15:53-64.

Sherer-Lorenzen, M., C. Palmborg, A. Prinz, and E. D. Schulze. 2003. The role of plant diversity and composition for nitrate leaching in grasslands. *Ecology* 84:1539-1552.

Smith, M. D., and A. K. Knapp. 2001. Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. *International Journal of Plant Science* 162:785-792.

Sorgona, A., and G. Cacco. 2002. Linking the physiological parameters of nitrate uptake with root morphology and topology in wheat (*Triticum durum*) and citrus (*Citrus volkameriana*) rootstock. *Canadian Journal of Botany* 80:494-503.

Sullivan, A., and V. Anderson. 2001. Effects of disturbance on *Kochia prostrata* spread in native and exotic Great Basin communities. Ecological Society of America 86th Annual Meeting 5-10 August 2001; Madison, WI. Washington, D.C.: Ecological Society of America. Abstract 62.

Sullivan, W. M., Z. Jiang, and R. J. Hull. 2000. Root morphology and it s relationship with nitrate uptake in Kentucky bluegrass. *Crop Science* 40:765-772.

Svejcar, T. 1990. Root length, leaf area, and biomass of crested wheatgrass and cheatgrass seedlings. *Journal of Range Management* 43:446-448.

West, N. E. 1988. Intermountain deserts, shrub steppes, and woodlands. *In:* M.G. Barbour and W.D. Billings [EDS.]. North American terrestrial vegetation. Cambridge, UK: Cambridge University Press. p. 209-230.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho’s Snake Rive Plains: Ecological and management implications *In*: E. D., McArthur, E. M. Romney, S. D Smith, and P. T. Tueller [EDS.]. Proceedings of the Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management. USDA-FS Intermountain Research Station, Ogden, UT, Gen. Tech. Rep. INT-276. p. 4-10.

Whitson, T. D., and D. W. Koch. 1998. Control of downy brome (*Bromus tectorum*) with herbicides and perennial grass competition. *Weed Technology* 12:391-396.

Yoder, C., and M. M. Caldwell. 2002. Effects of perennial neighbors and nitrogen pulses on growth and nitrogen uptake by *Bromus tectorum*. *Plant Ecology* 158:77-84.

Young, J. A., and F. L. Allen. 1997. Cheatgrass and range science: 1930-1950. *Journal of Range Management* 50:530-535.

Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* 31:283-289.

Young, J. A., and W. S. Longland. 1996. Impact of alien plants on Great Basin Rangelands. *Weed Technology* 10:384-391.

Table 2-1. Analysis of variance evaluating the effects of site and neighbor on ^{15}N pool ratio of three representative sagebrush-steppe species. Significance is denoted with ** (*P* < 0.01), *** (*P* < 0.001), and NS (*P* > 0.01).

	df	Crested wheatgrass	Western yarrow	Big sagebrush
Site (S)	1	NS	NS	**
Neighbor (N)	2	***	***	NS
S x N	2	NS	NS	**

Table 2-2. Outcome of competition for nitrate ($K^{15}NO_3$) between three representative sagebrush-steppe species (crested wheatgrass, western yarrow and big sagebrush), two invasive species (downy brome and dyer's woad), and prostrate kochia. Three outcomes were possible based on ^{15}N pool ratio of competing plants in Figure 1: equal acquisition (=, $P > 0.01$), representative sagebrush-steppe species acquiring more ^{15}N (+, $P < 0.01$), and sagebrush-steppe species acquiring less ^{15}N (-, $P < 0.01$).

	Downy Brome	Dyer's woad	Prostrate kochia
Crested wheatgrass	=	+	+
Western yarrow	-	=	=
Big sagebrush	-	-	-

Table 2-3. Analysis of variance evaluating the effects of site and neighbor on shoot dry mass, leaf carbon: nitrogen ratio, leaf nitrogen, root dry mass, root length, root diameter, and specific root length of two grasses (crested wheatgrass and downy brome), two forbs (western yarrow and dyer's woad), and two shrubs (big sagebrush and prostrate kochia). Significance is denoted with ** (*P* < 0.01), *** (*P* < 0.001), and NS (*P* > 0.01). Dashes indicate responses that were not analyzed because of unreliable sampling.

Species	Effect	df	Shoot dry mass	Carbon: nitrogen ratio	Leaf nitrogen	Root dry mass	Root length	Root diameter	Specific root length
Crested wheatgrass	Site (S)	1	NS	NS	NS	NS	NS	NS	NS
	Neighbor (N)	2	NS	NS	NS	NS	NS	NS	NS
	S x N	2	NS	NS	NS	NS	NS	NS	NS
Downy brome	Site (S)	1	NS	NS	NS	**	**	NS	NS
	Neighbor (N)	2	NS	NS	NS	NS	NS	NS	**
	S x N	2	NS	NS	NS	NS	NS	NS	NS
Western yarrow	Site (S)	1	NS	***	***	NS	NS	NS	NS
	Neighbor (N)	2	NS	NS	NS	NS	NS	NS	NS
	S x N	2	NS	NS	NS	NS	NS	NS	NS
Dyer's woad	Site (S)	1	***	***	***	NS	NS	***	***
	Neighbor (N)	2	NS	NS	NS	**	**	NS	NS
	S x N	2	NS	NS	NS	NS	NS	NS	NS
Big sagebrush	Site (S)	1	NS	NS	NS	NS	NS	NS	NS
	Neighbor (N)	2	NS	NS	NS	NS	NS	NS	NS
	S x N	2	NS	NS	NS	NS	NS	NS	NS
Prostrate kochia	Site (S)	1	***	***	***	NS	***	NS	NS
	Neighbor (N)	2	**	NS	NS	NS	***	-	-
	S x N	2	NS	NS	NS	NS	NS	-	-

Table 2-4. Mean (n = 36) and SE for shoot dry mass, leaf carbon: nitrogen ratio, leaf nitrogen concentration, root dry mass, root length, root diameter, and specific root length of six species when competing with three different neighbors. Means within a species and variable followed by different lowercase letters are different ($P < 0.01$). Dashes indicate responses that were not analyzed because of unreliable sampling.

Species	Neighbors	Shoot dry mass (g)	Carbon: nitrogen ratio	Leaf nitrogen (mg g^{-1})	Root dry mass (g)	Root length (m soil core^{-1})	Root diameter (mm)	Specific root length (m g^{-1})
Crested wheatgrass	Downy brome	23.25 (2.64)	14.01 (0.4)	31.90 (0.82)	0.31 (0.04)	7.56 (0.70)	0.88 (0.05)	26.46 (2.00)
	Dyer’s woad	21.80 (2.77)	14.29 (0.34)	30.74 (0.82)	0.37 (0.04)	7.72 (0.65)	0.86 (0.05)	26.27 (1.87)
	Prostrate kochia	25.41 (2.77)	15.18 (0.32)	29.29 (0.78)	0.34 (0.04)	7.62 (0.64)	0.78 (0.5)	27.90 (1.84)
Downy brome	Crested wheatgrass	13.84 (1.67)	11.87 (0.16)	33.28 (0.74)	0.14 (0.03)	4.98 (0.83)	0.80 (0.07)	38.21 (2.64) b
	Western yarrow	16.07 (1.62)	11.65 (0.15)	33.25 (0.71)	0.18 (0.02)	5.96 (0.68)	0.85 (0.5)	37.95 (2.14) b
	Big sagebrush	18.59 (1.62)	11.22 (0.16)	34.63 (0.73)	0.14 (0.02)	5.97 (0.69)	0.89 (0.05)	46.48 (2.18) a
Western yarrow	Downy brome	20.11 (2.48)	14.90 (0.34)	28.44 (0.64)	0.22 (0.05)	1.96 (0.29)	0.93 (0.04)	11.73 (1.19)
	Dyer’s woad	18.50 (2.76)	14.93 (0.34)	27.45 (0.63)	0.24 (0.04)	2.50 (0.28)	0.85 (0.04)	13.47 (1.17)
	Prostrate kochia	24.71 (2.79)	15.13 (0.34)	27.30 (0.64)	0.26 (0.05)	2.75 (0.33)	0.94 (0.05)	13.53 (1.36)
Dyer’s woad	Crested wheatgrass	49.40 (4.75)	10.04 (0.26)	38.35 (1.17)	1.75 (0.31) b	0.94 (0.14) b	2.64 (0.12)	0.86 (0.12)
	Western yarrow	63.50 (4.68)	9.93 (0.25)	38.36 (1.16)	1.69 (0.32) b	1.30 (0.15) ab	2.45 (0.12)	1.11 (0.12)
	Big sagebrush	61.27 (4.95)	10.09 (0.25)	37.30 (1.15)	2.76 (0.32) a	1.50 (0.15) a	2.67 (0.13)	0.74 (0.12)
Big sagebrush	Downy brome	7.09 (1.12)	19.72 (0.67)	22.40 (0.74)	0.04 (0.05)	0.58 (0.25)	0.92 (0.05)	15.29 (7.58)
	Dyer’s woad	5.08 (1.18)	20.71 (0.58)	20.74 (0.66)	0.14 (0.03)	1.44 (0.17)	0.81 (0.03)	22.21 (5.14)
	Prostrate kochia	7.54 (1.10)	20.21 (0.66)	21.48 (0.75)	0.12 (0.06)	1.60 (0.32)	0.77 (0.06)	7.18 (8.87)
Prostrate kochia	Crested wheatgrass	55.25 (7.10) b	13.77 (0.32)	29.30 (0.78)	0.29 (0.11)	0.90 (0.29) b	-	-
	Western yarrow	85.86 (7.54) a	13.89 (0.32)	28.24 (0.78)	0.46 (0.11)	2.35 (0.28) a	-	-
	Big sagebrush	79.85 (7.11) a	13.73 (0.35)	28.80 (0.84)	0.28 (0.09)	2.09 (0.23) a	-	-

Table 2-5. Mean (n = 54) and SE for shoot dry mass, leaf carbon: nitrogen ratio, leaf nitrogen concentration, root dry mass, root length, root diameter, and specific root length of six species when grown at two sites in northern Utah. Means within a species and variable followed by different lowercase letters are different ($P < 0.01$).

Species	Site	Shoot dry mass (g)	Carbon: nitrogen ratio	Leaf nitrogen (mg g^{-1})	Root dry mass (g)	Root length (m soil core^{-1})	Root diameter (mm)	Specific root length (m g^{-1})
Crested	Millville	21.72 (2.26)	14.72 (0.26)	29.80 (0.63)	0.38 (0.03)	8.27 (0.54)	0.90 (0.04)	24.82 (1.55)
wheatgrass	Hyde Park	25.25 (2.19)	14.27 (0.28)	31.52 (0.68)	0.30 (0.03)	7.05 (0.54)	0.79 (0.04)	28.93 (1.56)
Downy	Millville	15.71 (1.32)	11.56 (0.12)	34.26 (0.57)	0.19 (0.02) a	6.90 (0.62) a	0.91(0.05)	39.28 (2.00)
brome	Hyde Park	16.62 (1.35)	11.60 (0.12)	33.18 (0.62)	0.12 (0.02) b	4.41 (0.59) b	0.79 (0.05)	41.78 (2.08)
Western	Millville	15.39 (2.53)	15.70 (0.27) a	26.41 (0.54) b	0.21 (0.03)	2.50 (0.25)	0.92 (0.03)	13.59 (1.02)
yarrow	Hyde Park	23.43 (2.41)	14.32 (0.29) b	29.06 (0.54) a	0.27 (0.03)	2.30 (0.24)	0.90 (0.03)	12.23 (1.01)
Dyer’s	Millville	31.24 (3.71) b	11.50 (0.19) a	33.38 (0.88) b	1.69 (0.24)	1.37 (0.11)	2.25 (0.09) b	1.07 (0.10) a
woad	Hyde Park	84.88 (4.10) a	8.54 (0.22) b	42.63 (1.01) a	2.52 (0.27)	1.12 (0.12)	2.93 (0.11) a	0.77 (0.11) b
Big	Millville	5.52 (0.95)	20.91 (0.49)	20.66 (0.54)	0.09 (0.04)	1.22 (0.21)	0.82 (0.04)	15.98 (6.26)
sagebrush	Hyde Park	7.62 (0.89)	19.79 (0.56)	22.428 (0.62)	0.11 (0.04)	1.19 (0.21)	0.84 (0.04)	33.81 (5.75)
Prostrate	Millville	53.68 (4.23) b	15.42 (0.25) a	2.54 (0.06) b	0.47 (0.08)	2.31 (0.21) a	1.09 (0.05)	9.95 (1.50)
kochia	Hyde Park	92.30 (4.18) a	12.17 (0.29) b	3.22 (0.07) a	0.22 (0.09)	1.25 (0.23) b	1.09 (0.06)	10.73 (1.65)

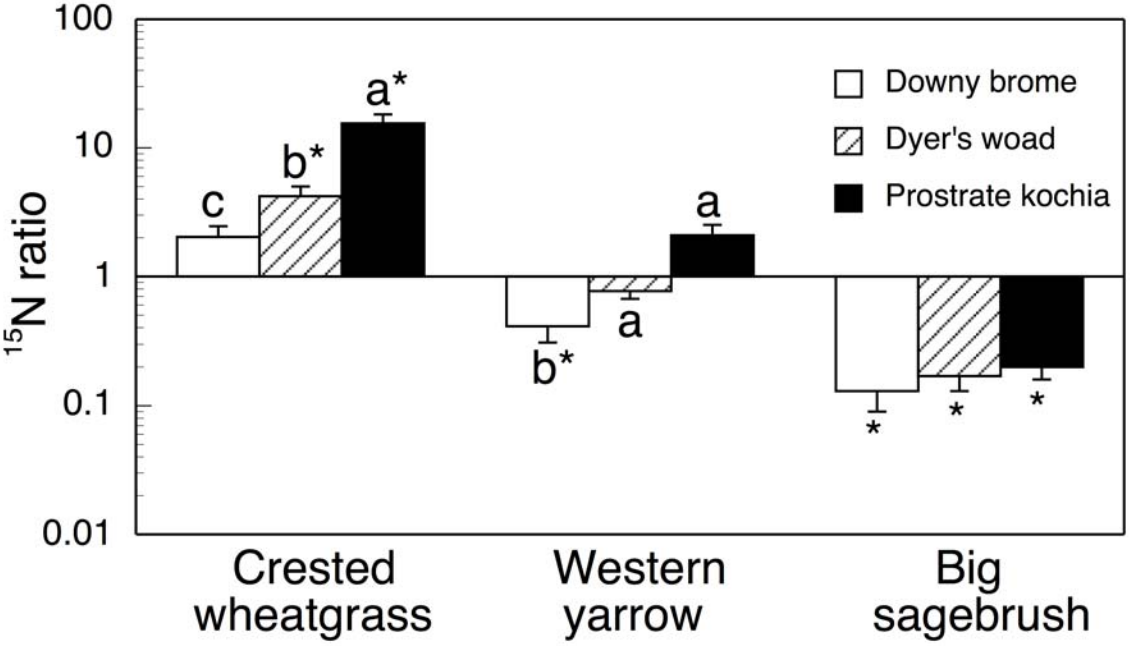

Figure 2-1. Mean (n = 24) and SE for log ^{15}N pool ratio of (crested wheatgrass, western yarrow, and big sagebrush) when competing with three neighbors (downy brome, dyer's woad, and prostrate kochia). Different lowercase letters indicate when neighbors differentially affect ^{15}N acquisition of the representative shrub-steppe species ($P < 0.01$). Asterisks denotes when ^{15}N pool ratios are significantly different than 1.0 ($P < 0.01$).

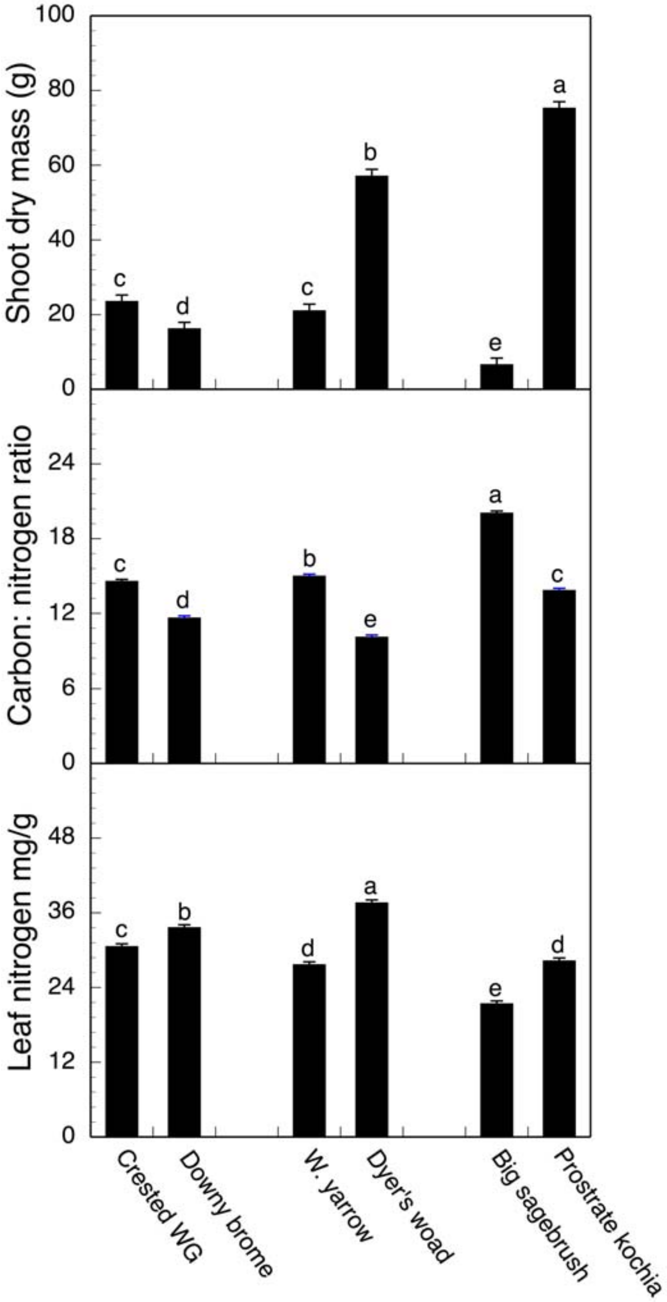

Figure 2-2. Mean (n=108) and SE for shoot dry mass, leaf carbon: nitrogen ratio, and leaf nitrogen concentration of two grasses (crested wheatgrass and downy brome), two forbs (western yarrow and dyer's woad), and two shrubs (big sagebrush and prostrate kochia). Means followed by different lowercase letters are significantly different at $P < 0.0001$.

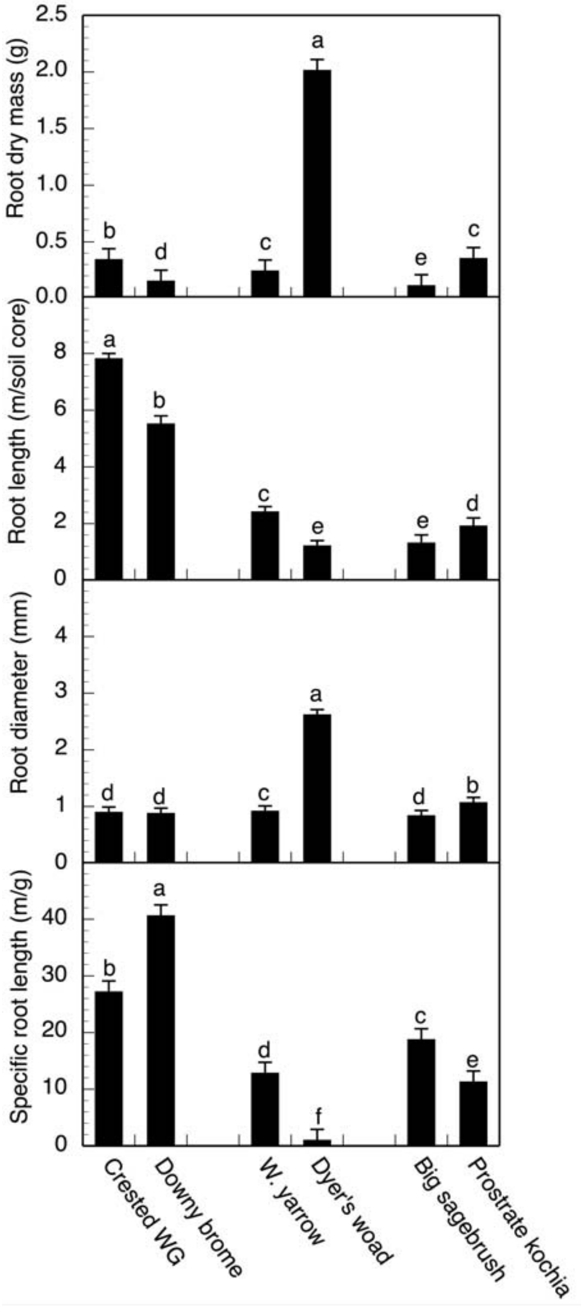

Figure 2-3. Mean (n = 108) and SE for root dry mass, root length, root diameter, and specific root length of two grasses (crested wheatgrass and downy brome), two forbs (western yarrow and dyer’s woad), and two shrubs (big sagebrush and prostrate kochia). Means followed by different lowercase letters are significantly different at $P < 0.0001$.

CHAPTER 3

INVASIVE WEED RESISTANCE OF THREE SHRUB-STEPPE GROWTH FORMS

ABSTRACT

Invasion of downy brome (*Bromus tectorum* L.) and dyer's woad (*Isatis tinctoria* L.) was evaluated in single- and four-species plots composed of the following three growth forms: perennial grasses, perennial broad-leafed dicot forbs, and shrubs, as well as a mixed growth form plot composed of one species from each growth form. Species density was altered by removing four individuals in single-species plots to determine if disturbance similarly increases invasion into each growth form. Seeds of both invasive species were introduced in autumn of 2004 and 2005, and seedling density was quantified in the following two summers. We sought to identify differences in invasion success and how these may be influenced by growth forms and disturbance. Downy brome invasion into the three growth form mix and the single-species grass plot was significantly lower than the single-species forb and shrub plots ($P < 0.01$). Similarly, downy brome invasion was lower in the four-species grass plots than the four-species forb and shrub plots in 2005 and the four-species forb plot in 2006. Invasion of dyer's woad into the three growth form mix was only significantly lower than single-species grass and forb plots in 2005 and single-species forb plots in 2006 ($P < 0.01$). Dyer's woad invasion was lower in both single- and four-species forb plots than comparable grass plots in 2005 ($P < 0.01$); however, its invasion was greatest in single-species forb plots and similar between four-species grass and forb plots in 2006. Disturbance consistently increased seedling density of both invasive species regardless of growth form composition of plots. Low invasion of downy brome in the three growth form and grass plots suggests that greater diversity and similarity in resource use, respectively, are important factors for resisting invasion of downy brome. The low invasion of both species into the three growth form mix gives more evidence for the importance of establishing more diversity in restoration plantings to reduce the impacts of invasive species.

INTRODUCTION

Big sagebrush communities (*Artemisia tridentata* Nutt.) in the Great Basin have been degraded by the synergistic consequences of overgrazing, annual weed invasion, and subsequent changes in wildfire frequency, intensity, and scale (Young and Evans 1978; West 1988; Whisenant 1990). These disturbances have caused major reductions in native species abundance and richness, which are recognized as fundamental ecosystem components (Stewart and Hull 1949; Passey and Hugie 1963; Harris 1967; Vale 1975; Harniss and Wright 1982; Mack and Thompson 1982; West 1983; Allen and Knight 1984; Young and Allen 1997; Clark et al. 1998). In addition, many disturbance regimes maintain the dominance of invasive annual species in the absence of native species (Sher and Hyatt 1999). While reestablishing less flammable perennial vegetation to repair ecosystems functions and minimize flammable weed dominance is the overarching goal of restoration efforts, it remains unclear which species, or combinations of species, most effectively resist weed invasion.

In particular, some studies suggest that the establishment of high species diversity is most effective based on the positive correlations between native species richness and plant community resistance to weed invasion (Tilman 1997; Levine and D'Antonio 1999; Naeem et al. 2000; Gastine et al. 2003; Xu et al. 2004; Lu and Ma 2005). The underlying mechanism for greater weed resistance is that high diversity fosters greater spatial and temporal niche occupation and competition for available resources with invading species (Hooper and Vitousek 1998; Spehn et al. 2000; Fargione et al. 2003; Fargione and Tilman 2005). On the other hand, low species diversity has been linked to the deterioration of ecosystem processes and greater community invasibility because low diversity creates a situation where niches may be vacant, or underutilized (McGrady-Steed et al. 1997; Mack et al. 2000; Naeem and Wright 2003). Thus, restoring species diversity in big sagebrush communities may be an effective measure to dampen fluctuating resources (Hobbs and Huenneke 1992; Lozon and MacIssac 1997), which theoretically functions as the primary mechanism determining invasibility (Davis et al. 2000). Evidence exists that reducing resource availability has negative effects on invasive annual grasses (Young et al. 1998; Beckstead and Augspurger 2004; Corbin and D'Antonio 2004), but it is unknown whether species diversity can similarly promote weed resistance.

Other studies suggest that under equal diversity, certain combinations of functionally unique species resist invasion better than others (Law and Morton 1996; Prieur-Richard and Lavorel 2000; Xu et al. 2004). Functional group or growth form diversity may provide greater weed resistance than species richness because it insures the presence of species that function similarly to potential invaders (Hooper and Vitousek 1998; Brown 2004). On the contrary, increasing species richness may only add species with redundant ecological functions (Walker 1992). Restoring functional group diversity is a particularly appealing approach for big sagebrush communities because it emphasizes reestablishing different structural growth forms that may help resists invasion of various types of weeds. In the past, rangeland managers recognized that reseeding big sagebrush communities with perennial forage grasses alone could stabilize soil, reduce wildfires, and discourage annual weeds (Whitson and Koch 1998). However, widespread invasion by deep-rooted, long-lived forbs like the knapweeds (*Centaurea* and *Acroptilon spp*.), leafy spurge (*Euphorbia esula* L.), and short-lived forbs like dyer's woad (*Isatis tinctoria* L.) warrant the comparison of distinct growth forms and mixtures to determine whether they resist weed invasion equally or greater than perennial grasses alone. Recent studies in Rocky mountain grasslands suggest that multiple functional groups, particularly broad-leafed forbs, promote weed resistance (Pokorny et al. 2004, 2005; Sheley and Carpinelli 2005). Similar studies comparing the effectiveness of different functional groups to resist invasion of multiple weed types have not been conducted with species commonly reseeded in degraded big sagebrush communities.

A contemporary restoration strategy to reverse the detrimental effects of invasive weeds includes planting exotic species into disturbed big sagebrush-steppe to assist the reestablishment of native herbaceous species (Cox and Anderson 2004). For example, crested wheatgrass (*Agropyron cristatum* [L.] Gaertner) has been planted on thousands of hectares in the United States to stabilize areas after disturbance and prevent invasion by downy brome (Rogler and Lorenz 1983). Crested wheatgrass is generally considered to be a more effective competitor with downy brome than native sagebrush-steppe species because it has shown greater ability to acquire soil-N (Aguirre and Johnson 1991; Bilbrough and Caldwell 1997). However, the Great Basin Restoration Initiative seeks to preserve a wider range of ecological function through structural and plant community diversity and gives priority to use of native species (Pellant et al. 2004).

Thus, I designed a field study utilizing both native and exotic species that are common and desirable restoration species, readily available, and represent the three dominant sagebrush-steppe growth forms (perennial grasses, broad-leafed dicot forbs, and shrubs) to evaluate the response of weed invasion to species and growth form diversity, and disturbance. Resistance to weed invasion was evaluated with single- and four-species plots of each growth form as well as a plot composed of one species from the three growth forms. Seed of the invasive annual grass downy brome and the invasive forb dyer's woad was introduced into experimental plots for two consecutive years and resistance to invasion was determined by quantifying seedling density in the following summers. We also reduced plant density within single-species plots of the three growth forms to simulate an acute disturbance event. I anticipate that this research may provide insights into the relative ability of three shrub-steppe growth forms to resist invasion of two distinctly different weeds that complicate restoration efforts in disturbed sagebrush-steppe communities.

I tested the following three hypotheses:

1) a mix of the three morphologically distinct growth forms (grass, forb, and shrub) provides greater weed resistance than single species of individual growth forms.
2) resistance to invasion is greater in plots that contain species of the same growth form as the invader.
3) disturbance similarly facilitates invasion in single-species grass, forb, and

shrub plots.

MATERIALS AND METHODS

Study Site

The experiment was conducted at Millville, UT (41° 39.44’N, 111° 48.88’ W, 1402 m). Soil is a Ricks gravelly loam series (coarse-loamy over sandy or sandy-skeletal, mixed, superactive, mesic Calcic Haploxerolls). The site was used for corn and alfalfa production in the past, and fallowed from fall 2002 to spring 2003. Prior to settlement in the 1850s, this area was dominated by typical big sagebrush-steppe species (Hull and Hull 1974). The 30-yr average annual precipitation is 457 mm. Annual precipitation for the 2005 and 2006 water year was 690, and 535 mm, respectively. Plots (1.5 m x 1.5 m) were established in May 2003 from transplants reared in a greenhouse and consisted of 24 plants in a 5 x 5 square arrangement equally spaced (30 cm apart) with the center plant missing to accommodate experimental measurements and 1 m aisles separating plots. The following seven plot-types were randomly located and replicated 30 times: single- and four-species grass, forb, or shrub plots and a mixed growths form plot composed of one species from each of the three growth form. The three single-species plots were either disturbed or left intact. The disturbance treatment consisted of removing four plants from the center of 15 plots mid November 2004 to acutely disturb plots, create safe sites to potentially increase above and below-ground resources, and facilitate invasion by the two invasive species. The plots were constructed with common sagebrush-steppe species and non-native species widely used for re-vegetation within of sagebrush-steppe communities. Single-species grass, forb, and shrub plots were constructed with crested wheatgrass (*Agropyron cristatum* [L.] Gaertner *x A desertorum* [Fisch. Ex Link] Schultes), western yarrow (*Achillea lanulosa* [Nutt.] Piper), or big sagebrush (*Artemisia tridentata var*.*wyomingensis* [Beetle & A. Young] Welsh), respectively. Four-species plots contained six randomly located individuals of: crested wheatgrass, Sandberg's bluegrass (*Poa secunda* Presl.), big squirreltail (*Elymus multisetus* [J.G. Smith] M.E. Jones), and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) for grass plots; western yarrow, small burnett (*Sanguisorba minor* Scop.), Munro's globe mallow (*Sphaeralcea munroana* [Dougl.] Spach in Gray), and Utah sweetvetch (*Hedysarum boreale* Nutt.) for forb plots; and big sagebrush, antelope bitterbrush (*Purshia tridentata* [Pursh] DC.), prostrate kochia (*Kochia prostrata* [L.] Schrader), and rubber rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britt.) for shrub plots. The mixed growth form plot contained eight randomly arranged individuals of crested wheatgrass, western yarrow, and big sagebrush.

Weed Invasion

The experimental plots were seeded with the invasive annual grass downy brome (*Bromus tectorum* L.) and the invasive forb dyer's woad (*Isatis tinctoria* L.) in mid November of 2004 and late October 2005. A total of 400 seeds of both species were combined and broadcasted over the central 1 m^2 of 15 replications the intact and disturbed single-species plots, four-species plots, and three growth form mix plots. In the laboratory, a germination test determined the pure live seed content to be 87 and 43% in 2004, and 91 and 28% in 2005 for downy brome and dyer's woad, respectively. Prior to seeding the invasive weed seed, the central 1 m^2 area of each plot was lightly scarified with a small garden rake to a depth of ~1 cm, to decrease movement of seed outside the plots. Weed invasion by both species was determined by removing and quantifying emerged seedlings from the plots in July 2005 and late June 2006.

Statistical Analysis

The experiment was a completely randomized design. All variables were analyzed as a two-way factorial to evaluate the main effects and interactions between growth form (grass, forb, shrub) and treatment (intact and disturbed) in the single-species plots only (Model1). Model 2 analyzed the main effects of growth form in the four-species plots. Model 3 analyzed differences between the single-species plots and the three growth form mix. All data were analyzed with analysis of variance using GLM procedures (SAS 9.0, SAS Institute Inc., Cary, NC) with $\alpha = 0.01$. Transformations were performed for each variable as needed to meet the assumptions of normality as closely as possible. We report the arithmetic least-squared means, which were compared with the least significant difference ($LSD_{0.01}$) mean separation test (main-effect means) and the Duncan's multiple range test (interaction means).

RESULTS

Seedling Density of Seeded Invasive Species

Downy brome seedling density in the three growth form mix and the single-species grass plot were similar and significantly lower than the single-species forb and shrub plots in both years (Table 3-1; Fig. 3-1). Downy brome density was also lower in the four-species grass plots than the four-species forb and shrub plots in 2005 and the four-species forb plot in 2006. Forb and shrub plots had similar downy brome density in 2005, but density was greater in forb plots than shrub single-species plots in 2006. Disturbance similarly increased downy brome invasion across single-species growth form plots by 39% in both 2005 and 2006 (Table 3-2).

Dyer's woad seedling density in the three growth form mix was only lower than the single-species grass and forb plots in 2005 and single-species forb plots in 2006 (Table 3-1; Fig. 3-2). Dyer's woad seedling density was also lower in both single- and four-species forb plots than comparable grass plots in 2005 ($P < 0.01$); however density was greatest in single-species forb plots and similar between four-species grass and forb plots in 2006. The disturbance treatment equally increased dyer's woad seedling density within the single-species growth forms plots by 66 and 52% (Table 3-2).

DISCUSSION

I conducted this study to address three hypotheses. First, I sought to determine whether a mix of three morphologically distinct growth forms provides greater weed resistance than single species of individual growth forms. Based on the results of this study, this hypothesis was rejected because the three growth form mix plots failed to have invasive seedling density significantly lower than the lowest single-species plot. I also tested whether resistance to invasion would be reduced when plots contained species of the same growth form as the invader. I failed to reject this hypothesis for downy brome because plots that contained grasses had the lowest invasion by the annual grass downy brome. However, hypothesis two was rejected for dyer's woad because invasion was highest or not significantly lower in forb plots than grass or shrub plots. My third hypothesis tested whether disturbance similarly facilitates invasion in the single-species grass, forb, and shrub plots. This hypothesis was not rejected because the disturbance treatment similarly increased weed invasion in all single-species growth form plots.

The possible mechanism leading to the rejection of hypothesis one could be that the three growth form plot less effectively occupyed the niche needed for invasive species compared to single growth form plots. If the density of each species had been increased with addition of growth forms, the outcome of my experimental results might have better supported this hypothesis. For example, each intact experimental plot consisted of 24 individuals. The single-species grass plots had 24 crested wheatgrass plants while the three growth form mix had only eight individuals of each growth form and potentially reducing the ability of each species to effectively occupy their respective niche compared to when grown alone at maximum density. While this hypothesis was rejected these plots did provide among the greatest weed resistance to both invasive species.

The failure to reject hypothesis two for the invasive annual grass species showcases how the presence of grasses, regardless of diversity can best restrict invasion. The grasses in this study are all cool season grasses, which have rapid growth in early spring, early reproductive maturity, and low growth potential in late summer (Frank et al. 1996; Arredondo et al. 1998). High redundancy in phenology among the grasses may be the primary reason why downy brome invasion followed a similar pattern in both single- and four-species plots. Similar weed resistance between the single- and four-species grass plots and the three species growth form mix in 2005 could be the result of the overriding competitive effect (i.e., a sampling effect) of crested wheatgrass grass present in these assemblages (Farigone and Tilman 2005). The similarity among all plots that contain grass species could be due to the presence of crested wheatgrass, which has proven to be a good competitor with downy brome. In addition, lower downy brome invasion in grass plots than plots of only forbs and shrubs provides strong evidence that grasses are an integral component of weed resistance within sagebrush-steppe ecosystems. Rich historical evidence of the coincidence of widespread invasion by alien species and the loss of perennial grasses within big sagebrush communities supports this claim (Mack 1981). On the other hand the failure of forb plots to present significantly greater resistance to invasion of dyer's woad except for when four forbs are present could be due to the characteristics of the species included in the single- versus four-species plots. In contrast to the strongly conserved growth form of grasses, forbs are known to have much higher variability in growth form and phenology (Blicker et al. 2002; LeJeune et al. 2006). The single-species forb plots consisted of the drought-tolerant, rhizomatous herb western yarrow. Poor invasion resistance of this species may be associated with low use of soil water and nitrate. On the other hand, the inclusion of additional forbs, from three different plant families into the four-species forb plots (Utah sweetvetch, Leguminoseae; small burnet, Rosaseae; and globemallow, Malvaceae) likely provided a much broader opportunity to interfere with the growth potential of the invasive forb. Coincidentally, the importance of forb diversity to weed resistance has recently been demonstrated in field studies (Pokorny et al. 2004).

The fact that disturbance equally increased invasion of both species in grass, forb and shrub plots, confirms the importance that this phenomenon may have in altering species interactions. Many studies show a positive relationship between disturbance events and increases in available resources or safe sites for weed invasion (Sher and Hyatt 1999; Davis et al. 2000; Sheley and Krueger-Mangold 2003; Beckstead and Augspurger 2004). Thus, the failure to reject the third hypothesis provides additional justification to reduce the recurrence of disturbance events in the sagebrush-steppe in order to reduce the impacts of invasive species.

These three hypotheses are most important when considering their implications on land management and restoration of degraded sagebrush-steppe ecosystems. They provide insight into the ability and relative importance of including a diversity of growth forms and species when pursuing revegetation as well as the need to dampening the effects of disturbance. While, the former management paradigm to effectively control invasion of annual grasses by planting crested wheatgrass may also be effective against invasive forbs, this might not effectively address wider management goals (i.e., watershed improvement, increased forage value for livestock, and wildlife habitat). This study was able to demonstrate that the combination of crested wheatgrass with other grasses and species from two other growth forms provides comparable weed resistance to plots of crested wheatgrass alone, which may better match goals that include establishing native grasses for wildlife habitat improvement and restoration. These results agree with previous studies that have simultaneously seeding crested wheatgrass with desirable native species to effectively providing quick site stabilization coupled with weed resistance (Waldron et al. 2005). This study also gives clues that using a greater suite of forb species in restoration mixes has potential to more effectively reduce dyer’s woad invasion than a planting of a single forb. Ultimately, using a mixture of growth forms that mimic the natural structural variation of intact sagebrush-steppe could potentially reduce the impact of a greater suite of invasive species.

LITERATURE CITED

Allen, E. B., and D. H. Knight. 1984. The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. *The Southwestern Naturalist* 29:407-421.

Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. *Journal of Range Management* 44:347-354.

Arredondo, J. T., T. A. Jones, and D. A. Johnson. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. *Journal of Range Management* 51:584-589.

Beckstead, J., and C. K. Augspurger. 2004. An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages. *Biological Invasions* 6:417-432.

Bilbrough, C. J., and M. M. Caldwell. 1997. Exploitation of springtime ephemeral N pulses by six Great Basin plant species. *Ecology* 78:231-243.

Blicker, P. S., B. E. Olson, and R. Engel. 2002. Traits of the invasive *Centaurea maculosa* and two native grasses: effect of N supply. *Plant and Soil* 247:261–269.

Brown, T. J., B. L. Hall, and A. L. Westerling. 2004. The impact of twenty-first century climate change on wildland fire danger in the western United States: An application perspective. *Climatic Change* 62:365-388

Clark, P. E., W. C. Krueger, L. D. Bryant, and D. R. Thomas. 1998. Spring defoliation effects on bluebunch wheatgrass: II. Basal area. *Journal of Range Management* 51:526-530.

Corbin, J. D., and C. M. D'Antonio 2004. Can carbon addition increase competitiveness of native grasses? A case study from California. *Restoration Ecology* 12:36-43.

Cox, R. D., and V. J. Anderson. 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *Journal of Range Management* 57:203-210.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invisibility. *Journal of Ecology* 88:528-534.

Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceeding of the National Academy of Science USA 100:8916-8920.

Fargione, J. E., and D. Tilman. 2005. Diversity decreases invasion via both sampling and complementarity effects. *Ecological Letters* 8:604-611.

Frank, A. B., S. Bittman, and D. A. Johnson. 1996. Water relations of cool-season grasses. *In:* L. E. Moser, D. R. Buxton, M. D. Casler [EDS.]. Cool-season forage grasses, American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, WI. p. 127-164.

Gastine, A., J. Roy, and P. W. Leadley. 2003. Plant biomass production and soil nitrogen in mixtures and monocultures of old field Mediterranean annuals. *Acta Oecologia* 24:65-75.

Harniss, R. O., and H. A. Wright. 1982. Summer grazing of sagebrush-grass range by sheep. *Journal of Range Management* 35:13-17.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89-111.

Hobbs, R., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6:324-337.

Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* 68:121-149.

Hull Jr., A. C., and M. K. Hull. 1974. Presettlement vegetation of Cache Valley, Utah and Idaho. *Journal of Range Management* 27: 27-29.

Law, R., and R. D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* 77:762-775.

LeJeune, K. D., K. N. Suding, and T. R. Seastedt. 2006. Nutrient availability does not explain invasion and dominance of a mixed grass prairie by the exotic forb *Centaurea diffusa* Lam. *Applied Soil Ecology* 32:98-110.

Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15-26.

Lozon, J. D., and H. J. MacIsaac. 1997. Biological invasions: are they dependent on disturbance? *Environmental Reviews* 5:131–144.

Lu, Z., and K. Ma. 2005. Scale dependent relationships between native plant diversity and the invasion of croftonweed (*Eupatorium adenophorum*) in southwest China. *Weed Science* 53:600-604.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* 7:145-165

Mack. R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hooved animals. *American Naturalist* 119:757-773

Mack R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710.

McGrady-Steed, J., P. M. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. *Nature* 390:162-165.

Naeem, S., J. M. H. Knops, and D. Tilman. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91:97-108.

Naeem, S., and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecological Letters* 6:567-579.

Passey, H. G., and V. K. Hugie. 1963. Sagebrush on relict ranges in the Snake River Plains and Northern Great Basin. *Journal of Range Management* 15:273-278.

Pellant, M., B. Abby, and S. Karl. 2004. Restoring the great basin desert, U.S.A.: integrating science, management, and people. *Environmental Monitoring and Assessment* 99:169-179.

Pokorny, M. L., R. L. Sheley, T. J. Svejcar, and R. E. Engel. 2004. Plant species diversity in a grassland plant community: evidence for forbs as a critical management consideration. *Western North American Naturalist* 64:219-230.

Pokorny, M. L., R. L. Sheley, C. A. Zabinski, R. E. Engel, A. J. Svejcar, and J. J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* 13:1-12.

Prieur-Richard, A., and S. Lavorel. 2000. Invasions: the perspective of diverse plant communities. *Austral Ecology* 25:1-7.

Rogler, G. A., and R. Lorenz. 1983. Crested wheatgrass--early history in the United States. *Journal of Range Management* 36:91-93.

Sheley, R. L., and M. F. Carpinelli. 2005. Creating weed-resistant plant communities using niche-differentiated nonnative species. *Rangeland Ecology and Management* 58:480-488.

Sheley, R. J., and J. Kruger-Mangold. 2003. Principles for restoring invasive plant-infested rangeland. *Weed Science* 51:260-265.

Sher, A. A., and L. A. Hyatt. 1999. The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. *Biological Invasions* 1:107-114.

Sphen, E. M., J. Joshi, B. Schmid, M. Diemer, and C. Körner. 2000. Above-ground resource use increases with plant species richness in experimental grassland ecosystems. *Functional Ecology* 14:326-337.

Stewart, G., and A. C. Hull, Jr. 1949. Cheatgrass (*Bromus tectorum* L.) An ecological intruder in southern Idaho. *Ecology* 30:58-74.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81-92.

Vale, T. R. 1975. Presettlement vegetation in the sagebrush-grass area of the Intermountain West. *Journal of Range Management* 28:32-36.

Waldron, B. L., T. A. Monaco, K. B. Jensen, R. D. Harrison, A. J. Palazzo, and J. D. Kulbeth. 2005. Coexistence of native and introduced perennial grasses following simultaneous seeding. *Agronomy Journal* 97:990-996

Walker, B .H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6:18-23.

West, N. E. 1983. Western Intermountain sagebrush steppe. *In*: N. E West, [ED.]. Temperate deserts and semi-deserts. Elsevier, Amsterdam. p. 351-374.

West, N. E. 1988. Intermountain deserts, shrub steppes, and woodlands. *In*: North American terrestrial vegetation. M. G. Barbour, W.D. Billings [EDS.]. Cambridge, Cambridge University Press. p. 209-230.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: Ecological and management implications *In*: E. D. McArthur, E. M. Romney, S. D Smith, and P. T. Tueller [EDS.], Proc. Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. USDA-FS Intermountain Research Station, Ogden, UT, Gen. Tech. Rep. INT-276. p. 4-10.

Whitson, T. D., and D. W. Koch. 1998. Control of downy brome (*Bromus tectorum*) with herbicides and perennial grass competition. *Weed Technology* 12:391-396.

Xu, K., W. Ye, H. Cao, X. Deng, Q. Yang, and Y. Zhang. 2004. The role of diversity and functional traits of species in community invasibility. *Botanical Bulletin of the Academy of Science* 45:149-157.

Young, J. A., and F. A. Allen. 1997. Cheatgrass and range science: 1930-1950. *Journal of Range Management* 50:530-535.

Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* 31:283-289.

Young, J. A., J. D Trent, R. R. Blank, and D. E. Palmquist. 1998. Nitrogen interactions with medusahead (*Taeniatherum caput-medusae* spp. *asperum*) seedbanks. *Weed Science* 46:191-195.

Table 3-1. Three analysis of variance models to evaluate the effects of a disturbance treatment (single-species plots) (Model 1), growth form (four-species plots) (Model 2), and growth form (single-species and three growth form mix) (Model 3) on invasive weed seedling density. Significance is demonstrated with ** ($P < 0.01$), *** ($P < 0.001$) and NS ($P > 0.01$).

Seedling density			Downy Brome		Dyer's woad	
		df	2005	2006	2005	2006
Model 1	Growth Form (G)	2	***	***	***	***
	Treatment (T)	1	***	***	***	**
	G x T	2	NS	NS	NS	NS
Model 2	Growth Form (G)	2	***	***	***	***
Model 3	Growth Form (G)	3	***	***	***	***

Table 3-2. Mean (n =15) seedling density of two invasive weeds within intact and disturbed plots in summer 2005 and 2006. Values in parentheses are 1 SE of the mean, and asterisks indicate significant differences between treatments within an invasive weed (*P* < 0.01).

Species		Seedling density	
	Treatment	2005	2006
Downy brome	Intact	28.67 (3.56) *	139.31 (17.35) *
	Disturbance	47.31 (3.56)	229.60 (28.22)
Dyer’s woad	Intact	17.29 (2.95) *	11.08 (2.14) *
	Disturbance	50.51 (2.95)	23.16 (2.14)

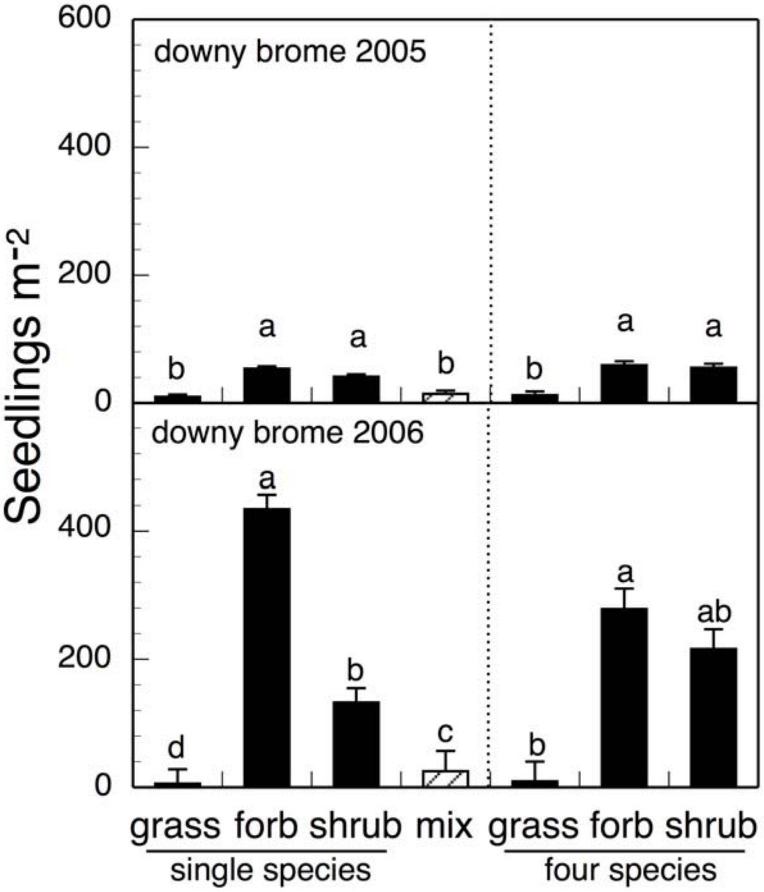

Figure 3-1. Mean seedling density of the invasive annual grass (downy brome) in (2005 and 2006). Means (n = 30) within single-species and (n=15) three growth form mix plots followed by the same lower case letter are not significantly different. Means (n = 15) within four-species plots followed by the same upper case letter are not significant different. Error bars indicate 1 standard error.

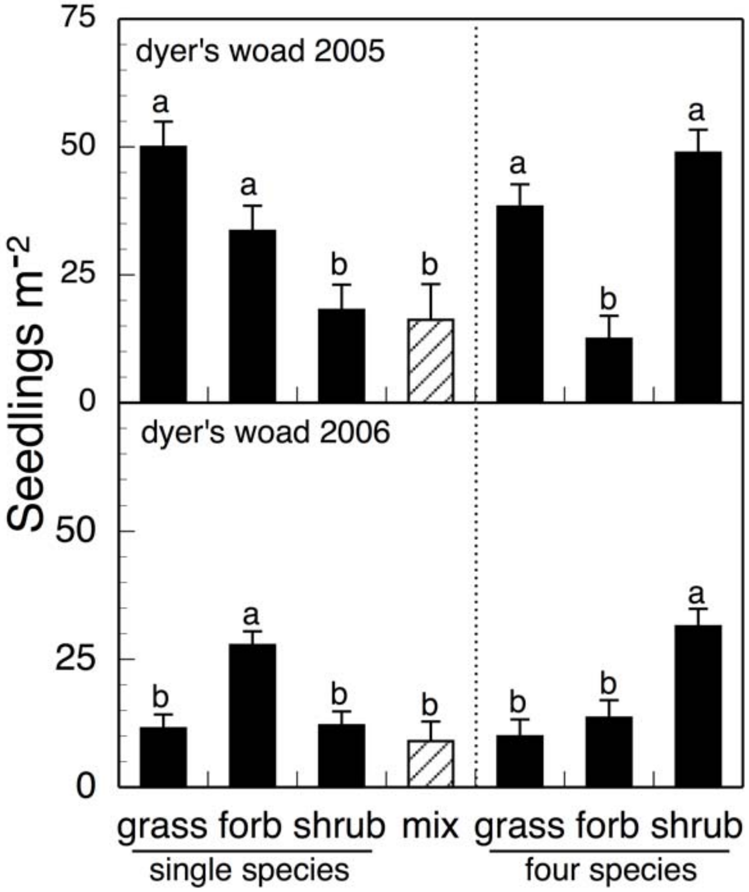

Figure 3-2. Mean seedling density of the invasive biennial forb (dyer's woad) in (2005 and 2006). Means (n = 30) within single-species and (n=15) three growth form mix plots followed by the same lower case letter are not significantly different. Means (n = 15) within four-species plots followed by the same upper case letter are not significant different. Error bars indicate 1 standard error.

CHAPTER 4

CONCLUSION

Because restoration efforts in the Great Basin sagebrush-steppe must incorporate some aspect of weed management, I conducted this study to address questions relevant to this issue. Focus was directed toward gaining a better understanding of how two invasive species (the annual grass downy brome, and the biennial forb dyer's woad), a potential restoration species (the introduced exotic shrub prostrate kochia) and common sagebrush species interact. Taking this focused approach, I developed two experiments based on previous restoration paradigms and the characteristics of the invasive species.

Experiment one was designed to determine the relative differences and effects between species with short-life and/or leaf longevity on the acquisition of a ^{15}N tracer of three longer-lived species. This question is important because the success of downy brome is associated with its capacity to exploit short-duration nutrient pulses coupled with greater growth at low seedbed temperature than native perennial species (Harris 1967; Aguirre and Johnson 1991; Duke and Caldwell 2001). It was also important to understand whether the success of dyer's woad invasion as well as the if the ability of crested wheatgrass and prostrate kochia to establish in downy brome stands and suppress downy brome seedlings are also associated with soil nitrogen acquisition. Comparing differences in shoot and root growth as well as carbon: nitrogen ratio, and leaf N concentration could help identify traits responsible for the differences in nitrate acquisition and the presence of traits that confer persistence within disturbed semiarid shrub-steppe ecosystems. From this experiment, I was able to determine that crested wheatgrass's ability to suppress downy brome is most likely associated with similar soil nitrate acquisition. Prostrate kochia did not have higher acquisition than its neighbors suggesting that nitrate acquisition is not likely the mechanism prostrate kochia uses to persist in downy brome stands. Previous research suggests that the use of soil water in early spring and drought tolerance of prostrate kochia are more likely the key mechanisms responsible for its persistence and establishment in downy brome dominated stands (Romo and Haferkamp 1988). Similarly, it is apparent that, as previous research suggests, dyer's woad does not acquire soil nitrate to a greater degree than its neighbors (Monaco et al. 2005). The high growth rate of both dyer's woad and prostrate kochia compared to their growth form counterpart, shows that both species have an advantage in establishing within disturbed sagebrush-steppe.

The second experiment focused on the ability of different species compositions to suppress invasion of downy brome and dyer's better than other combinations of species and the role of disturbance in mediating invasion. The contemporary management paradigm to reverse the detrimental effects of invasive weeds includes planting exotic transitional species into disturbed big sagebrush-steppe to assist the reestablishment of native herbaceous species (Cox and Anderson 2004). For example, crested wheatgrass (*Agropyron cristatum* [L.] Gaertner) has been planted on thousands of hectares in the United States to stabilize areas after disturbance and prevent invasion by downy brome (Rogler and Lorenz 1983). Crested wheatgrass is generally considered to be a more effective competitor with downy brome than native sagebrush-steppe species because it has shown greater ability to acquire soil-N (Aguirre and Johnson 1991; Bilbrough and Caldwell 1997). While our results support this relationship they also suggest that the invasion of downy brome is similarly reduced in higher diversity (four-species plots) with the addition of native grasses. Conversely, dyer's woad invasion was more consistently reduced by the inclusion of a wide range of grass and forb species as well as growth forms than crested wheatgrass alone.

It is evident that disturbance plays and important role in increasing the success of invasion of both invasive species. These results coincide with the intent of the Great Basin Restoration Initiative (GBRI) that seeks to restore plant and structural diversity in an effort to build communities, which provide a wider suite of ecosystem services (i.e. watershed stability, weed resistance, disturbance resilience, increased wildlife habitat, etc.) (Pellant et al. 2004). Additionally, the GBRI seeks to accomplish this goal through scientific research that incorporates both economics and ecology. My research evaluating species that are readily available, moderately priced, and represent the general structural components of intact sagebrush-steppe assemblages help address this initiative.

The implications of both studies can be summarized into several suggestions for land management practices. Previous studies have concentrated on reducing the availability of soil nitrogen as a strategy to reduce the invasion and dominance of downy brome (i.e., Paschke et al. 2000). However, the increasing invasion of exotic forb species does not appear to be tightly coupled to levels of soil nitrogen. A management strategy that narrowly focuses on reducing soil nitrogen could potentially leave a system vulnerable to dominance by exotic forb species. While this study does not confirm that forb invasion is not mediated in some way by resources, it is evident that dyer's woad emergence is not tightly coupled with soil nitrate alone. The increased invasion of both species in response to the disturbance treatment highlights the importance of dampening the effects of disturbance and maintaining species that are resilient to disturbance. While my experiments were not designed to test long-term resilience to disturbance, the role of species and growth form diversity on invasion was evaluated. The incorporation of a wider range of growth forms as well as greater diversity of species within the grass and forb growth forms represent historic structural variation that may potentially increase invasion resistance to a wider suite of invasive species. This study hopefully provides some clues to better inform potential restoration efforts in the Great Basin and sagebrush-steppe ecosystems.

LITERATURE CITED

Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. *Journal of Range Management* 44:347-354.

Bilbrough, C. J., and M. M. Caldwell. 1997. Exploitation of springtime ephemeral N pulses by six Great Basin plant species. *Ecology* 78:231-243.

Cox, R. D., and V. J. Anderson. 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *Journal of Range Management* 57:203-210.

Duke, S. E., and M. M. Caldwell. 2001. Nitrogen acquisition from different spatial distributions by six great basin species. *Western North American Naturalist* 61:93-102.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89-111.

Monaco, T. A., D. A. Johnson, and J. E. Creech. 2005. Morphological and physiological responses of the invasive weed *Isatis tinctoria* to contrasting light, soil-nitrogen and water. *Weed Research* 45:460-466.

Paschke, M. W., T. McLendon, and E. F. Redente. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* 3:144-158.

Pellant, M., B. Abby, and S. Karl. 2004. Restoring the great basin desert, U.S.A.: integrating science, management, and people. *Environmental Monitoring and Assessment* 99:169-179.

Rogler, G. A., and R. Lorenz. 1983. Crested wheatgrass--early history in the United States. *Journal of Range Management* 36:91-93.

Romo, J. T., and M. R. Haferkampt. 1988. Comparitive water relation in *Artemisia tridentata* Nutt. *subsp. Wyomingensis* and *Kochia prostrata* L. Schrad. *Journal of Arid Environments* 15:53-64.