Biological Invasions (2006) 8:1343–1354
DOI 10.1007/s10530-005-0709-z

Can R*s predict invasion in semi-arid grasslands?

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Received 13 January 2005; accepted in revised form 11 July 2005

Key words: *Agropyron spicatum*, *Centaurea maculosa*, *Helianthus annuus*, nitrogen, plant competition, R* theory, spotted knapweed, succession

Abstract

We estimated R*s and tested the applicability of R* theory on nonindigenous plant invasions in semi-arid rangeland. R* is the concentration of a resource that a species requires to survive in a habitat. R* theory predicts that a species with a lower R* for the most limiting resource will competitively displace a species with a higher R* under equilibrium conditions. In a greenhouse, annual sunflower (*Helianthus annuus* L.), bluebunch wheatgrass (*Agropyron spicatum* Pursh), and spotted knapweed (*Centaurea maculosa* Lam.) were grown in monoculture and 2- and 3-species mixtures for three growth periods in an attempt to reduce soil NO_3-N concentrations below each species' R*. At the end of each growth period, aboveground biomass by species and soil plant available nitrogen were sampled. Decreasing biomass coupled with decreasing soil plant available nitrogen was used to quantify R*s for the three species. R*s for annual sunflower, bluebunch wheatgrass, and spotted knapweed were estimated to be 0.6 ± 0.16 ppm NO_3^-, less than 0.05 ppm NO_3^-, and 0.6 ± 0.13 ppm NO_3^-, respectively. Estimated R*s did not predict the outcome of competition among species. To successfully predict plant community dynamics on semi-arid rangeland with and without the presence of a nonindigenous invasive species, a more comprehensive model that includes mechanisms in addition to competition may have to be considered. We speculate that R* theory may prove most useful for predicting the outcome of competition within functional groups.

Introduction

Competition for essential resources, such as nutrients and light, is an important process structuring plant communities. Competition has been used to create models for explaining and predicting plant community dynamics (Grime 1979; Vance 1984; Huston and DeAngelis 1994). During the last several decades, plant community dynamics have increasingly involved nonindigenous invasive species. Since the 1950s when Elton (1958) introduced the term "ecological resistance", ecologists and land managers have been keenly interested in managing for plant communities that resist invasion by undesirable species. The concept of "ecological resistance" implies that competition for essential plant resources is greater in diverse plant communities compared to communities with fewer species because resident species are using available resources more completely (Elton 1958; Levine and D'Antonio 1999).

Certain species or functional groups are more successful than others at suppressing a given nonindigenous invader, therefore species composition and richness interact to influence community invasibility (Dukes 2002). Invasibility is also affected by resource supply rates (Crawley et al. 1999). Identifying the species that have the highest potential to resist invasion by a given nonindigenous invader under a given resource supply rate would further our management, and restoration when necessary, of invasion-resistant plant communities. One model of resource competition and plant community dynamics that holds promise for these applications is R* (read "R star") theory (Tilman 1981, 1982, 1984, 1988).

R* theory postulates that the outcome of competition can be predicted by a species' R*. R* is the concentration of a resource that a species requires to survive in a habitat. Any resource concentration higher than R* leads to the growth in size of an individual or population; any value lower than R* leads to loss in size of an individual or population (Figure 1). R* theory predicts that a species with a lower R* will competitively displace a species with a higher R* under equilibrium conditions (Tilman 1982, 1988). R*s for selected species have been determined by growing them in monoculture (Tilman and Wedin 1991a, b). When the population reaches equilibrium, the soil is analyzed for the limiting resource, usually plant available soil nitrogen (N) concentration. The resulting soil resource concentration is considered the species' R* for the plant resource of interest.

According to R* theory, late seral species have lower R*s for N than early seral species because they dominate as secondary succession progresses and N availability decreases (Tilman 1986; Tilman and Wedin 1991b). Tilman and Wedin (1991b) found that the outcome of succession was predicted by the relative ability of species to persist under low concentrations of plant available N. Monocultures of the late seral grasses little bluestem (*Schizachyrium scoparium* Nash) and big bluestem (*Andropogon gerardii* Vitman) had lower soil concentrations of nitrate (NO_3^-) (i.e. lower R*s) than the early seral grasses bentgrass (*Agrostis scabra* Willd.) and quackgrass (*Agropyron repens* L.) and displaced them in pairwise competition experiments (Tilman and Wedin 1991b).

Manipulation of N availability may affect plant community dynamics. For example, additions of N inhibited succession from the invasive, annual cheatgrass (*Bromus tectorum* L.) to indigenous native perennial species in sagebrush steppe of northwestern Colorado (McLendon

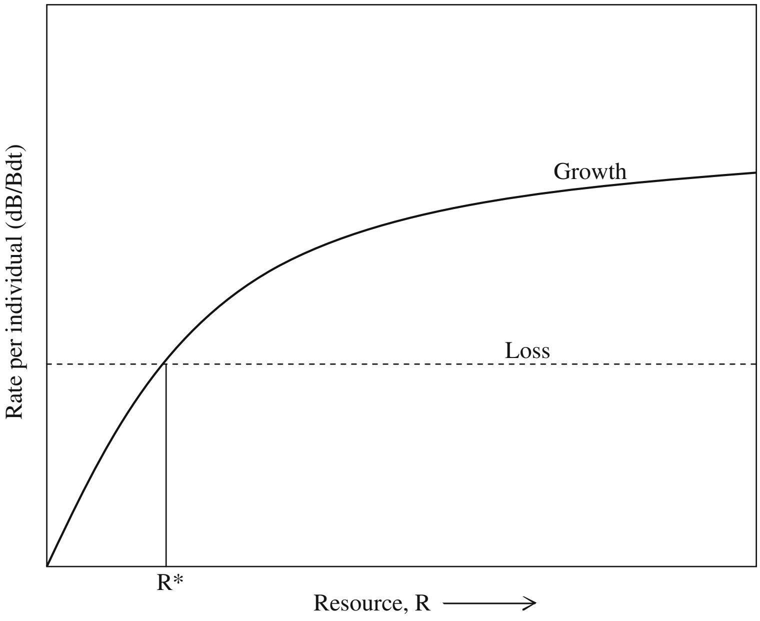

Figure 1. Graphical representation of R* for any given species for any given essential resource. Adapted from Tilman (1982).

and Redente 1991). Increasing N availability may favor invasive, rapid-growing, high N-demanding species like *Centaurea* species (LeJeune and Seastedt 2001). Therefore, the rate of invasion by some nonindigenous species may increase as global N availability increases from human inputs (Vitousek et al. 1997). Once established, nonindigenous species may perpetuate high N availability through positive feedback mechanisms such as less C allocation to belowground structure, reduced C storage in soil, reduced root and litter ratios of C to N, and increased N mineralization and leaching (LeJeune and Seastedt 2001).

Quantifying R*s for some of the most troublesome invaders may help to explain their insidious nature, identify plant communities susceptible to invasion based on resource supply rates and the R*s of dominant species or functional groups, and select species appropriate for revegetation efforts that focus on creating invasion-resistant plant communities. R* theory was developed in a model system using freshwater algae (Tilman 1981). The application of R* theory to terrestrial vascular plants has been most aggressively tested in old-field succession on an N-poor sand plain in Minnesota (Tilman 1984; Tilman and Wedin 1991a, b; Wilson and Tilman 1991). Applicability and usefulness of R* theory in semi-arid rangeland is untested as well as its application for predicting invasion patterns and outcomes of management of nonindigenous plants.

In our companion study, N increased aboveground plant biomass of the dominant functional group more than any other resource addition in an Idaho fescue (*Festuca idahoensis* Elmer)/bluebunch wheatgrass (*Agropyron spicatum* Pursh) plant association (Krueger-Mangold et al. 2004). Therefore, the first objective of this research was to quantify the R* for N for the nonindigenous invader spotted knapweed (*Centaurea maculosa* Lam.) and two indigenous species, annual sunflower (*Helianthus annuus* L.) and bluebunch wheatgrass. We hypothesized that the R* of the early seral species, annual sunflower the R* of the nonindigenous invader, spotted knapweed the R* of the late seral species, bluebunch wheatgrass. Spotted knapweed colonizes disturbed areas and grows rapidly during the first few years, which is characteristic of an early seral species (Watson and Renney 1974). At the same time, spotted knapweed invades and persists on semi-arid grasslands that are dominated by native, late seral species, suggesting that it may be similar to a late seral species (Chicoine et al. 1985). The second objective was to predict the outcome of competition among the three species based on their estimated R*s. We hypothesized that as N availability decreased, the biomass of a species with a higher R* would decrease below that of its monoculture biomass when grown in polyculture with a species that had a lower R*.

Methods

Model system

Spotted knapweed was chosen as a representative nonindigenous invasive species. It is a deeply rooted, perennial forb native to Eurasia, which historically has spread rapidly throughout the northwestern United States and Canada. In the 1960s, spotted knapweed was documented in 20 counties in the Pacific Northwest and by 1980 it had spread to 48 counties. By 1999 it was found in 326 counties in the Northwest, including every county in Washington, Idaho, Montana, and Wyoming (Sheley et al. 1999). Members of the *Centaurea* genus probably represent the most widespread and serious threat to semi-arid rangeland in the Northwest, occupying disturbed sites while also invading relatively undisturbed perennial native plant communities (DiTomaso 2000). Annual sunflower and bluebunch wheatgrass were chosen as representatives of early and late seral indigenous species, respectively. All species occur in the Idaho fescue/bluebunch wheatgrass plant association (Mueggler and Stewart 1980). This plant association occurs at elevations of 1400–2300 m, on northerly exposures at the lower elevations and on southerly exposures at higher elevations. Precipitation averages 35–50 cm, primarily in the form of snow. Soils are typically mollisols. The plant community is dominated by annual and perennial forbs and perennial cespitose and rhizomatous grasses. The amount of soil surface covered by rock ranges from 0 to 40%, whereas the amount of bare soil ranges from 0 to 25% (Mueggler and Stewart 1980). Semi-arid grasslands are characterized by low availability of nutrients, especially N (Charley 1977).

Procedures

Field soil from the surface (0–15 cm) was collected from Montana State University Redbluff Research Ranch about 2 km east of Norris, Montana (45°35′ N, 111°39′ W). Soil was characterized as a fine-loamy, mixed, frigid Calcidic Argiustoll. Field soil was mixed in the ratio 3:1 with sterilized sand to dilute N concentration and aid in infiltration and permeability during watering. The amended soil was placed into 15 cm × 15 cm × 38 cm pots. Annual sunflower, bluebunch wheatgrass, and spotted knapweed were seeded into pots in the greenhouse in monoculture and two- and three-species mixtures beginning April 2002 (Table 1). Seeds were covered with 2 mm of soil and misted daily until emergence. Upon emergence, plants were randomly thinned to six plants per pot and watered lightly every other day. The monocultures contained six plants of one species; the two-species mixtures contained three plants of each species; and the three-species mixtures contained two plants of each species. After thinning, pots were watered to capacity weekly with 1240 ml water followed by 300 ml of a dilute N-free modified Hoagland's solution, thus beginning the first growth period. The Hoagland's solution was used to prevent nutrients other than N from becoming limiting. Additionally, one pot in each replication contained all three species and was watered with a dilute modified Hoagland's solution containing N. One pot in each replication was plant-free and received N-free Hoagland's solution to provide a control for observing soil N dynamics in the absence of any vegetation. Growth periods (GP) averaged about ten weeks and ran from 06/07/02 through 08/14/02 (GP1), 11/13/02 through 02/14/03 (GP2), and 05/29/03 through 07/30/03 (GP3). Each monoculture and species mixture was replicated six times. Pots were placed in a greenhouse in a randomized complete block design. To prevent light from becoming a limiting resource, photoperiod in the greenhouse was extended to 16 h per day using 1000 watt metal halide lamps. Temperatures were maintained at 22 °C (day) and 18 °C (night).

Table 1. Treatment codes and descriptions of species combinations.

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

Between GPs, the pots were placed in a vernalization chamber (4 °C, 10 h photoperiod per day) for about 90 days. Annual sunflower seeds were germinated in flats filled with sand while the pots were in the vernalization chamber and transplanted to their original pots at the beginning of each GP. Bluebunch wheatgrass and spotted knapweed were allowed to resprout from their crowns. Thus, we were comparing progressively more mature bluebunch wheatgrass and spotted knapweed plants to annual sunflower that was at the same age over each GP.

By growing the plants for three GPs, we attempted to deplete plant available soil N (nitrate-N and ammonium-N) to a level where growth would decrease, thus arriving upon species' R*s. Although most plants can use both nitrate-N (NO_3-N) and ammonium-N (NH_4-N) in soil solution (Barber 1995), previous tests of R* theory found the best estimator of R* for N was soil NO_3-N concentration (Tilman and Wedin 1991b; Wedin and Tilman 1993; D. Wedin, personal communication). Under conditions of limited nutrient supply, plants allocate less biomass to aboveground biomass in order to survive (Lambers et al. 1998); and aboveground biomass (hereafter referred to as biomass) has been used as a proxy for fitness (Tilman 1984; Tilman and Wedin 1991b; Wedin and Tilman 1993). We interpreted a decrease in biomass as a decrease in fitness and an indication that plant available soil N concentration was approaching the R* for a species. R*s were estimated to occur within the 95% confidence interval around the mean NO_3-

N concentration at the end of the GP when a species' biomass decreased below that of its biomass in the previous GP.

Sampling

Biomass was harvested by species from each pot when aboveground biomass appeared to reach a maximum, thus marking the end of each GP. Biomass was dried (48 h, 60 °C) and weighed. Soil was sampled at the end of every GP by compositing three randomly collected cores (1.2×18 cm) from each pot. Belowground biomass was not sampled in order to preserve root mass between successive GPs.

Soil samples were air-dried and crushed to pass a 2-mm sieve prior to chemical analyses. Soil concentrations of NO_3-N and NH_4-N were determined from 1 M KCl extracts of soils (5 g soil:50 ml extractant). Aliquots of filtered extracts were analyzed using Cd reduction and salicylate colorimetric methods, respectively (Mulvaney 1996).

Statistical analysis

Analysis of variance (ANOVA) (SAS Institute Inc. 1990) was used to determine the effects of treatment (monoculture, 2- and 3-species mixtures, Table 1) and GP on an individual biomass per plant and soil NO_3-N, NH_4-N and total plant available N concentrations. We used a split-plot in time model, a type of repeated measures analysis, with replication and treatment as the whole plots and GP as the sub-plot (Neter et al. 1996). Whole-plot effects were tested using replication × treatment as the error term and split-plot effects were tested using the residual as the error term. Mean separations for significant (P 0.05) main effects and interactions were achieved using Fisher's protected least significant difference ($LSD_{\alpha = 0.05}$) comparisons (Peterson 1985). In addition to ANOVA, each species' mean biomass per plant in the monoculture treatment was compared between GPs with *t*-tests (SAS Institute, Inc. 1990). In cases where data failed to meet the assumptions of normality and equality of variances based on diagnostic plots, they were square-root or log10 transformed.

Results

Plant biomass

T-tests for monocultures

The biomass of annual sunflower grown in monoculture decreased by about 80% from GP1 to GP2, and remained the same between GP2 and GP3 (Figure 2). Bluebunch wheatgrass' mean biomass did not change from GP1 to GP2, but decreased by about 50% from GP2 to GP3 (Figure 2). The biomass of spotted knapweed decreased by about 30% from GP1 to GP2 and remained the same between GP2 and GP3 (Figure 2).

Analysis of variance

The main effects of GP and treatment affected the biomass of annual sunflower (Table 2). The biomass of annual sunflower across treatments decreased from 9.52 g $plant^{-1}$ during GP1 to 0.70 g $plant^{-1}$ during GP2, but then increased to 4.12 g $plant^{-1}$ during GP3. The A treatment resulted in the highest annual sunflower biomass, although it did not differ from the AB and All treatments (Table 3). The lowest annual sunflower biomass was found in the AS, All, and All + N treatments. Treatment affected spotted knapweed biomass. Spotted knapweed biomass was lower in monoculture than in all other planting treatments, which were similar (Table 3).

Treatment and GP interacted to affect bluebunch wheatgrass biomass (Table 2). Bluebunch wheatgrass biomass was highest in the monoculture during GP1 (Table 4). Biomass decreased from GP1 to GP3 in the monoculture, but that trend was not consistent in the other treatments. When grown with annual sunflower, bluebunch wheatgrass biomass did not change compared to the bluebunch monoculture during GP2 and GP3. In general, bluebunch wheatgrass biomass decreased when grown with spotted knapweed (BS, All, and All + N treatments).

Soil NO_3-N, NH_4-N, and total plant available N concentration

Growth period and treatment interacted to affect soil NO_3-N, NH_4-N, and total plant available N (Table 5). The concentration of NO_3-N for

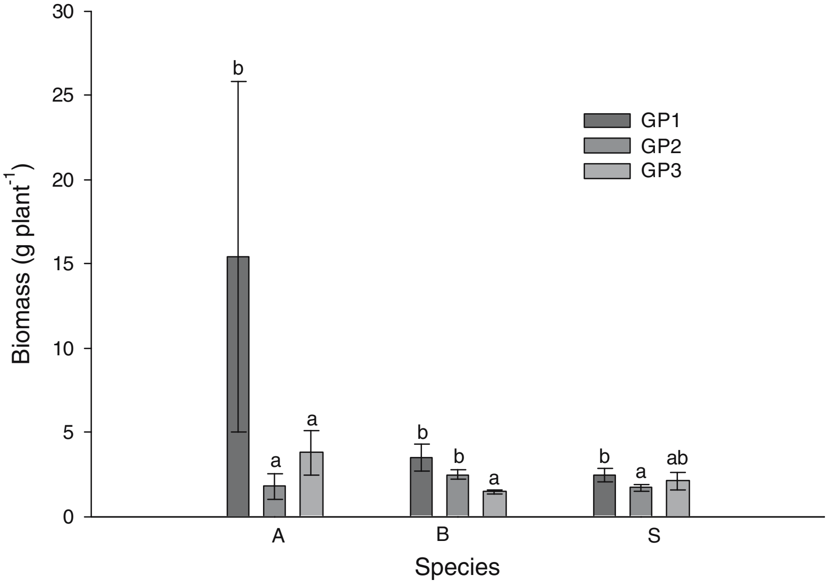

Figure 2. Effect of growth period on mean aboveground biomass per plant of annual sunflower (A), bluebunch wheatgrass (B), and spotted knapweed (S) when grown in monoculture (log10 transformation). Actual means are presented. Different letters separate means that are significantly different within a species based on *P*-values (*P* 0.05) and confidence intervals of transformed means. Error bars represent 1 Std. Dev. GP1, GP2, and GP3 represent growth periods one, two, and three, respectively.

Table 2. *P*-values from ANOVA for main effects and interaction on species biomass (square root transformation). GP equals growth period.

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

Table 3. Effect of treatment on annual sunflower (*F* = 5.06, *P* = 0.0056) and spotted knapweed (*F* = 4.62, *P* = 0.0083) biomass per plant (square root transformation).

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

Actual means are presented. Different letters separate means that are significantly different within species.

Table 4. Effect of treatment by growth period (GP) interaction on bluebunch wheatgrass biomass (square root transformation) (*F* = 3.98, *P* = 0.0015).

Treatment	GP	Biomass (g plant^{-1})
B	1	3.50 g
	2	2.49 f
	3	1.49 d
AB	1	2.58 ef
	2	2.85 f
	3	1.89 d
BS	1	0.88 c
	2	0.23 a
	3	0.34 ab
All	1	0.51 bc
	2	0.37 ab
	3	0.61 bc
All + N	1	1.51 d
	2	0.91 c
	3	0.55 bc

Actual means are presented. Different letters separate means that are significantly different within a column.

monocultures that resulted in decreased biomass from one GP to the next were 0.6–1.5 ppm NO_3-N for annual sunflower and spotted knapweed and 0.05 ppm NO_3-N for bluebunch wheatgrass. The lowest concentration of NO_3-N was found

Table 5. *P*-values from ANOVA for main effects and interaction on soil NO_3^-, NH_4^+, and total plant available N concentration. GP equals growth period.

Source	df	NO_3-N	NH_4-N	Total plant available N
Rep	5	0.53	<0.01	0.02
Treatment	8	<0.01	<0.01	<0.01
GP	2	<0.01	<0.01	<0.01
Treatment × GP	16	<0.01	<0.01	<0.01

after GP3 across all treatments except the spotted knapweed monoculture (Table 6). The concentration of NO_3-N in the majority of the treatments during GP3 was below the detection limit (0.05 ppm), therefore the mean was arbitrarily set at 0.03 ppm. After three GPs, the mean for the S treatment was 0.38 ppm NO_3-N, while that for the A and B treatments was 0.03 ppm.

Table 6. ffect of treatment by growth period (GP) interaction on soil NO_3-N ($F=3.99$, $P<0.0001$), NH_4-N ($F=15.78$, $P<0.0001$), and total plant available N ($F=7.53$, $p<0.0001$) (log10 transformation).

Treatment	GP	NO_3-N (ppm)	NH_4-N (ppm)	Total plant available N (ppm)
A	1	1.00 cd	1.61 b	2.62 cd
	2	0.60 cd	3.37 f	3.97 efg
	3	0.03 a	0.72 a	0.74 a
B	1	1.58 h	3.33 ef	4.92 gh
	2	0.55 c	2.68 cdef	3.23 def
	3	0.03 a	1.01 a	1.04 ab
S	1	1.45 cdefgh	2.28 bc	3.73 def
	2	0.60 cd	3.58 def	4.18 efg
	3	0.38 b	0.97 a	1.35 b
AB	1	1.32 gh	2.83 cdef	4.15 efg
	2	0.55 c	2.43 cdef	2.98 de
	3	0.03 a	0.82 a	0.84 a
AS	1	0.90 cedfgh	2.57 cdef	3.47 efg
	2	0.68 cdefg	2.22 bcd	2.90 de
	3	0.03 a	0.73 a	0.76 a
BS	1	1.07 cdefgh	2.78 cdef	3.85 efg
	2	0.65 cdef	3.88 f	4.53 fg
	3	0.03 a	0.88 a	0.90 ab
All	1	1.32 fgh	2.68 cdef	4.00 efg
	2	0.50 c	2.33 bcde	2.83 cde
	3	0.03 a	0.77 a	0.80 a
All + N	1	1.32 efgh	2.98 cdef	4.30 fg
	2	0.57 cde	2.17 bcd	2.74 de
	3	0.03 a	0.81 a	0.83 a
No plants	1	4.38 i	2.33 bcde	6.72 h
	2	5.83 i	26.31 g	32.15 i
	3	1.25 defgh	0.89 a	2.13 c

Actual means are presented. Different letters separate means that are significantly different within N species.

Trends similar to those of NO_3-N were exhibited by NH_4-N and total plant available N as well. The lowest NH_4-N concentrations occurred in all treatments during GP3, ranging from about 0.7 to 1 ppm NH_4-N, while those for total plant available N ranged from 0.74 to 4.92 ppm N (Table 6). Soil NH_4-N and total plant available N were lowest after three growth periods. Although the All + N treatment was watered with a dilute Hoagland's solution containing N, it resulted in NO_3-N, NH_4-N, and total plant available N concentrations similar to the other treatments (Table 6).

*Estimation of R*s*

Coupling results from biomass of species in monoculture over three GPs with soil NO_3-N concentrations led to estimated R*s for the three species (Figure 3). The estimated R* for annual sunflower occurred as biomass decreased between GP1 and GP2 when soil NO_3-N concentration was 0.6 ± 0.16 ppm. Spotted knapweed's estimated R* occurred when its monoculture biomass decreased from GP1 and GP2 and remained similar during GP3; corresponding soil NO_3-N concentrations were 0.60 ± 0.13 ppm for GP2 and 0.38 ± 0.50 ppm for GP3, so the estimated R* for spotted knapweed is 0.47 and 0.73 ppm NO_3-N. The estimated R* for bluebunch wheatgrass occurred at the end of GP3 when NO_3-N concentration was 0.05 ppm (95% confidence interval $\asymp 0$).

Discussion

*Response of species in monoculture (estimation of R*s)*

The objective of this study was to test the applicability of R* theory on semi-arid rangeland and for management of a nonindigenous invader by quantifying and comparing the R* for annual sunflower, bluebunch wheatgrass, and spotted knapweed. R*s for N have been quantified by growing species in monoculture until population growth equals zero, then analyzing the soil for

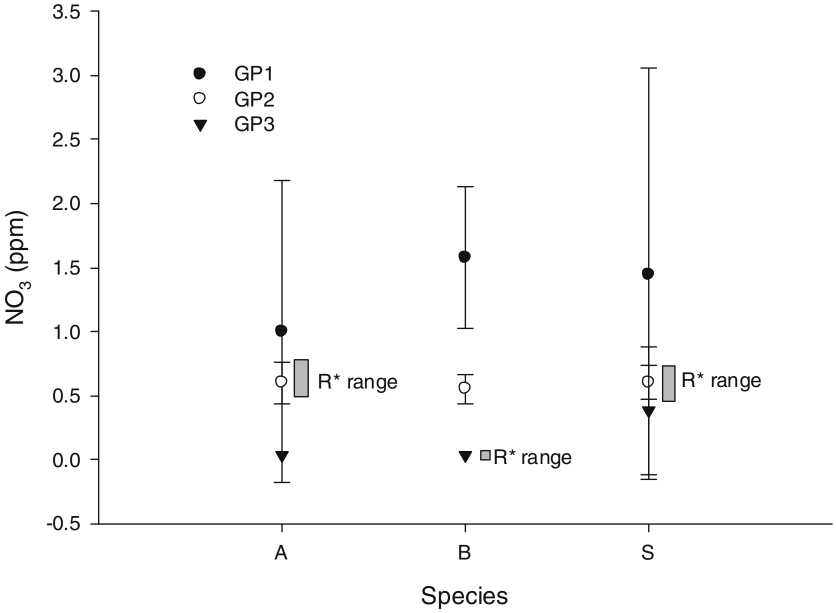

Figure 3. Mean NO_3-N concentrations for monocultures of annual sunflower (A), bluebunch wheatgrass (B), and spotted knapweed (S). Error bars represent 95% confidence intervals around the mean. The shaded regions labeled "R* range" represent where R*s are estimated to occur for each species based on decreasing monoculture mean biomass and soil NO_3-N concentrations. GP1, GP2, and GP3 represent growth periods one, two, and three, respectively.

plant available N content (Tilman and Wedin 1991a, b; Wedin and Tilman 1993). In another study, R*s based on soil NO_3-N concentration successfully predicted the outcome of competition between two species in all six cases tested (Wedin and Tilman 1993). Because we used biomass as a proxy for fitness, decreasing biomass from one GP to the next indicated that plant available soil N was approaching the R* of a species when grown in monoculture (Tilman 1984; Tilman and Wedin 1991b; Wedin and Tilman 1993).

Based upon their traits, we had hypothesized that the R* of annual sunflower the R* of spotted knapweed the R* of bluebunch wheatgrass. Our results suggest that we can accept this hypothesis, with the caveat that the R* of annual sunflower is not higher than, but equal to the R* of spotted knapweed. This is consistent with the observed ruderal behavior of spotted knapweed, and many other invasive plants, whose establishment and expansion are associated with increased resource availability following disturbance (Lozon and MacIsaac 1997). Our estimated R* of bluebunch wheatgrass is similar to estimated R*s of other late seral grasses. Tilman and Wedin (1991b) and Wedin and Tilman (1993) found R*s for late seral grasses were below 0.05 ppm NO_3-N. An extremely low R* is consistent with the late seral nature of bluebunch wheatgrass and its ability to persist under N-limiting conditions.

The growth patterns differed among species and were not always consistent with estimated R*s. The biomass of annual sunflower and bluebunch wheatgrass monocultures responded as their R*s predicted, but the biomass of spotted knapweed monocultures was not predicted by its R*. Annual sunflower produced a large amount of biomass when plant available soil N was highest, typical of a ruderal species. The rapid growth rate of ruderal species, like annual sunflower, is associated with rapid exploitation of readily available resources (Crawley 1997). Bluebunch wheatgrass did not produce nearly as much biomass per plant at the beginning of the study, but maintained its biomass for a longer duration of the study. Late seral perennials, like bluebunch wheatgrass, typically do not have rapid growth rates, but can store carbohydrate and nutrients in below ground tissue that helps to maintain above ground biomass as plant available N decreases (Lambers et al. 1998).

Spotted knapweed biomass was relatively low compared to annual sunflower, and more similar to that of bluebunch wheatgrass. Although R* is not a proxy for absolute productivity, we expected spotted knapweed to produce quantities of biomass more similar to that of annual sunflower based on estimated R*s. The spotted knapweed monoculture did not reduce soil NO_3-N as low as the other monocultures by the end of the study. These results suggest that spotted knapweed may adjust its biomass and N-use efficiency to a threshold soil N concentration that is different than its estimated R*. This may be reflected by spotted knapweed's ability to invade and persist in relatively undisturbed plant communities dominated by native, late successional grass (Chicoine et al. 1985; Blicker et al. 2002), and suggests that R* theory may not predict succession when nonindigenous, invasive plants are involved.

R* is a component of the resource ratio hypothesis (Tilman 1988). The resource ratio hypothesis postulates that plants face an unavoidable trade-off between the ability to compete for above versus belowground resources: in order to obtain a higher portion of belowground resources, plants must allocate more biomass to root tissue at the expense of allocation of biomass to shoot structures, and vice versa (Tilman 1988). Although previous investigations into the capacity of species' R*s to predict the outcome of competition have focused on above ground biomass (Tilman and Wedin 1991a, b; Wedin and Tilman 1993), other studies have suggested that the ability to compete for essential resources is not just a function of biomass allocation, but also of morphological characteristics like specific leaf area, specific root length, leaf arrangement, and rooting structure (Olff et al. 1990; Aerts et al. 1991). We speculate that measuring below ground biomass, root:shoot ratios, specific leaf area, specific root length, reproductive output (i.e. seeds or ramets) may have provided additional insight into mechanisms by which spotted knapweed is capable of maintaining its biomass even though soil NO_3-N fell below its estimated R*.

Response of species in mixtures

R* theory predicts that a population with a lower R* will competitively displace a population with a higher R* (Tilman 1982; 1988). We hypothesized that estimated R*s from monocultures could successfully predict the outcome of competition in two- and three-species mixtures. Our estimated R*s did not predict the outcome of competition. The biomass of annual sunflower, whose estimated R* was an order of magnitude higher than bluebunch wheatgrass, did not decrease when grown with bluebunch wheatgrass. Annual forbs and perennial grasses have very different life histories and growth forms and are generally considered members of different functional groups (Symstad 2000; Dukes 2002). Their response to decreasing resource availability and its subsequent effects on population survival may be so different from one another because of their specific life histories and growth forms, that simply observing biomass response cannot adequately predict the outcome of competitive interactions. For example, Aerts et al. (1991) compared biomass allocation patterns and competitive ability among two evergreen dwarf shrubs and a perennial grass in fertilized and unfertilized conditions. While the biomass of all three species increased when fertilized, they found that the greater competitive ability of the grass relative to the shrubs was partly attributed to its ability to alter the spatial arrangement of its leaf layers. To our knowledge, other studies where R*s have predicted the outcome of competition used species in a similar functional group, perennial grasses, that respond comparably to low resource availability (Tilman and Wedin 1991a, b; Wedin and Tilman 1993). Based on our results, we speculate that R* theory may prove most useful for predicting the outcome of competition within a functional group.

Furthermore, we were not able to predict the outcome of competition when spotted knapweed was present based on estimated R*s. Because we concluded that spotted knapweed's R* for N is equal to annual sunflower's and higher than that of bluebunch wheatgrass, we would have predicted spotted knapweed biomass to remain the same or decrease below that of the monoculture when grown with annual sunflower or bluebunch wheatgrass, respectively. Conversely, spotted knapweed biomass increased when grown with either of the other species. Similar to our results, Blicker et al. (2002) found that spotted knapweed biomass was greater when grown with bluebunch wheatgrass than with itself or with western wheatgrass (*Agropyron smithii* Rybd.), another late seral species native to semi-arid rangeland. These results suggest that competition for N may not be the most influential process occurring. Other complex plant–plant interactions, in addition to competition for N, may permit spotted knapweed to outperform bluebunch wheatgrass under low N conditions even though we estimated its R* for NO_3-N to be higher.

Some evidence suggests that competitive relationships between native *Centaurea* species may be mediated through mycorrhizae. In one study, spotted knapweed biomass was 66% greater when grown with Idaho fescue in the presence of arbuscular mycorrhizal (AM) fungi than when AM fungi were absent, possibly due to C transfer through fungal linkages between species (Marler et al. 1999). Zabinski et al. (2002) later showed that spotted knapweed may be able to exploit mycorrhizal hyphae more effectively than native species, especially grasses, thus allowing luxury consumption of phosphorus (P). Plants growing under nutrient poor soils tend to allocate relatively more to roots (Tilman 1988). Nutrient availability should also control allocation to AM structures because AM symbioses are integral to most root systems (Johnson et al. 2003). Because spotted knapweed may be able to exploit AM hyphae more effectively than native grasses, then it may reap larger benefits from the symbioses as soil nutrient availability decreases. If so, then spotted knapweed's success may be partly attributable to AM fungi, and an estimated R* for N may not possess as much predictive power.

Other studies have suggested that *Centaurea* species may exude allelopathic chemicals that may facilitate invasion of indigenous plant communities. Ridenour and Callaway (2001) found that spotted knapweed decreased root elongation rates of Idaho fescue by 50% when grown together. This effect was removed when activated C was added to ameliorate chemical effects. Similarly, diffuse knapweed (*Centaurea diffusa* Lam.) had a much stronger negative effect on North American grasses, including bluebunch wheatgrass, than it had on Eurasian grasses, and the effect was removed in the presence of activated C (Callaway and Aschehoug 2000). Plants growing in resource-limited conditions often exhibit higher tissue concentrations of secondary compounds, including allelochemicals, compared to plants growing under less stressful conditions (Tang et al. 1995). It has been proposed that allelopathic effects may be more pronounced in environments with low resource availability (Tang et al. 1995). We should consider the possibility that resource and non-resource mechanisms, such as allelopathy, work simultaneously with their degree of importance varying from one ecological context to the next (Hierro and Callaway 2003).

Blicker et al. (2002) contend that a combination of factors, including competitive ability, release from natural enemies and grazers, mycorrhizal associations, and allelopathy, probably account for spotted knapweed's success. Based on our results and the results of other studies (Marler et al. 1999; Callaway and Aschehoug 2000; Ridenour and Callaway 2001; Blicker et al. 2002; Zabinski et al. 2002), we believe spotted knapweed may possess characteristics that allow it to dominate a plant community even though its R* for N is higher than that of co-existing species. R* theory alone may not be an appropriate mechanism for explaining plant community dynamics between vastly different functional groups or when nonindigenous invasive species such as spotted knapweed are present. To successfully predict plant community dynamics on semi-arid rangeland with and without the presence of a nonindigenous invasive species, a more comprehensive model that includes mechanisms in addition to competition should be considered. Instead of relying on one parameter like R* to predict plant community dynamics, we should continue to research additional mechanisms, such as changes in species' morphology and resource use efficiency, and how the relative importance of resource versus non-resource mechanisms changes in response to resource availability.

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