

# Field-based competitive impacts between invaders and natives at varying resource supply

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## Summary

1. One line of thinking is that highly successful plant invaders achieve dominance in recipient communities via competitive superiority over natives. In contrast, it has been proposed that exotic species attain dominance not by competitive prowess but due to their colonizing abilities after disturbance. Interestingly, there have been relatively few attempts to quantify competitive effects of invaders on natives (and *vice versa*) in field settings.

2. We created monocultures of ten native perennial species and after two seasons of establishment we either left assemblages uninvaded or invaded them with seeds from one of three potent exotics; spotted knapweed (*Centaurea maculosa*), Dalmatian toadflax (*Lineria dalmatica*) and sulfur cinquefoil (*Potentilla recta*). Invasion was crossed with a supplemental water treatment to determine how increased resource supply might alter competitive outcomes. We also compared traits of exotics and natives to determine whether differences in height, lateral spread, shoot : root ratio and specific leaf area might shed light on competitive effects.

3. Exotics suppressed native biomass by an average of 51%. Water addition had no effect on invasibility or the competitive impact of exotics on natives. Although exotics decreased native biomass, invasion increased total above-ground biomass. Spotted knapweed was the most successful invader, and because of its greater abundance, it had the largest competitive impacts on natives. Spotted knapweed invasion also reduced plant-available soil nitrogen, water and light.

4. The majority of native species did not differ in their resistance to weed invasion, although *Achillea millefolium* and *Festuca idahoensis* monocultures were more resistant to invasion than monocultures of *Antennaria rosea*. Exotic biomass was either unaffected by competition with natives (knapweed) or was moderately suppressed by natives (cinquefoil and toadflax). Native species did not differ significantly in their competitive impacts on exotics and resource supply only influenced the competitive impacts of natives on spotted knapweed. Knapweed and toadflax, in particular, differed from all the natives in combined growth and leaf traits.

5. *Synthesis*. Our results show that exotics exert strong competitive dominance over individual native species with competitive effects relatively unaltered by increased resource supply. These effects occurred in undisturbed assemblages, suggesting that invader-native competitive outcomes can drive invasion dynamics for the species studied.

**Key-words:** dalmation toadflax, exotic plants, invasion, native-exotic competition, native plant monocultures, resource addition, spotted knapweed, sulfur cinquefoil

## Introduction

Introduced plants are thought to attain dominance in their new range by dint of their superior competitive ability (Levine *et al.* 2003). This competitive supremacy has been postulated to occur for several reasons. One oft-mentioned hypothesis is

that exotics gain a competitive edge over natives because they are liberated from specialist natural enemies (Elton 1958). By receiving less herbivore and pathogen attack than natives, the competitive balance is thought to tip in favour of exotics. Another hypothesis is that exotics gain the competitive upper hand against natives by exuding allelopathic compounds that natives have not evolved with (Callaway & Ridenour 2004). Finally, it has been postulated that exotics outcompete natives

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because they possess unique life-history attributes that change ecosystem properties in ways that feed back to benefit exotics (Vitousek & Walker 1989; D'Antonio *et al.* 2001), or enable exotics to access resources unavailable to natives (Mack *et al.* 2000).

Although competition is often invoked in traditional explanations of invader success, a recent alternative framework places less emphasis on competitive superiority 'driving' exotic dominance. Instead, exotics are seen as 'passengers' that capitalize on disturbance to gain advantage in recipient systems. Disturbance, pre-emption of space by exotics, and subsequent severe seed limitation of natives hinders their ability to re-assert themselves within invaded sites (Seabloom *et al.* 2003a; MacDougall & Turkington 2005). According to this view, competition may play a role, but a subsidiary one, in perpetuating exotic dominance (MacDougall & Turkington 2005; but see Seabloom *et al.* 2003b).

Despite the importance of competition in traditional explanations of exotic success, and more recent scepticism about the sole importance of competition in 'driver' vs. 'passenger' models for invasion, few field experiments have actually quantified the strength of competition between exotics and natives (Parker & Reichard 1998; Vilá & Weiner 2004). The majority of research that has examined native-exotic competition has been short-term, often in a greenhouse, and usually involving competition between seedlings (but see Booth *et al.* 2003). The few field studies that have been conducted have mostly focused on competition between exotic and native grasses (Wedin & Tilman 1996; Bakker & Wilson 2001; Corbin & D'Antonio 2004; MacDougall & Turkington 2005), examined how entrenched exotics influence native establishment (Gordon *et al.* 1989; Dunbar & Facelli 1999; Gorchoff & Trisell 2003; Miller & Gorchoff 2004) or explored how exotic removal influences subsequent community response (D'Antonio *et al.* 1998; Alvarez & Cushman 2002). Multi-year, larger-scale field experiments that determine competition intensity between established natives and invading exotics are still rare. Because of this, our understanding of the role of competitive interactions between natives and exotics during the ontogeny of an invasion is surprisingly limited.

For many systems, there are a host of important questions relating to native-exotic competition that remain outstanding. First, the extents to which individual native species (as opposed to groups of species) differ in their competitive resistance to different invaders are not clear (but see Dukes 2002). We know that increasing species diversity can enhance invasion resistance (Levine 2000; Naeem *et al.* 2000; Prieur-Richard *et al.* 2000; Symstad 2000; Dukes 2002; Kennedy *et al.* 2002; Fargione *et al.* 2003; van Ruijven *et al.* 2003; Zavaleta & Hulvey 2004; Maron & Marler 2007), and that greater functional overlap between resident and invading species can importantly contribute to this invasion resistance (Prieur-Richard *et al.* 2000; Fargione *et al.* 2003). Yet the magnitude of variation in competitive effects of single native species against particular exotics in field settings is often not known. Secondly, how different co-occurring invaders compare in their competitive ability against natives is unclear. Whether

differences in local abundance among exotics (even those that are dominant) are due to the variability in invader competitive ability, variation in propagule pressure, initial colonization success, or other historical factors is often unknown. Thirdly, although exotics can depress native biomass at the individual plant level (reviewed by Vilá & Weiner 2004), how invasion in the field influences overall productivity, and how this varies depending on the identity of the native and the identity of the exotic, is not well understood for most systems. Although Ehrenfeld (2003) found that invasion increased total above-ground community biomass in 78% of cases reviewed, most of these studies were observational comparisons of invaded and uninvaded sites where the contribution of particular exotic species to this pattern was not quantified. Furthermore, whether differences in productivity between natives and exotics are underpinned by differences in traits that might influence resource capture is still not well resolved. In one of the few experimental tests, Wilsey & Polley (2006) found that a suite of exotic grasses had greater above-ground productivity, higher shoot : root ratios, and lower deep root biomass than native grasses. Such comparisons have not been made between native and invasive forbs.

A fourth issue concerns the role of resource supply in mediating native-exotic competitive interactions. Increasing resource supply often enhances the competitive dominance of exotics (Hobbs & Mooney 1991; Milchunas & Lauenroth 1995; Burke & Grime 1996; Maron & Connors 1996; Wedin & Tilman 1996; Thomsen *et al.* 2006). These results suggest that anthropogenic global change, and the concomitant increase in resource supply (CO<sub>2</sub>, water and nitrogen) that it creates, may facilitate greater exotic dominance (Dukes & Mooney 1999). Yet, whether increasing resource supply primarily acts to enhance the dominance of exotics that are already entrenched (i.e. increases the competitiveness of exotics) or actually leads to more successful exotic colonization and subsequently new invasions is not clear. Resource supply is not usually manipulated in the context of field-based competition experiments between natives and exotics (but see Wedin & Tilman 1993, 1996).

To shed light on these issues, we examined competitive interactions between established natives and invading exotics under field conditions where we varied resource supply. We established field plots with each composed of one of ten naturally co-occurring native perennial grassland plant species that are constituents of Palouse grassland in the western Rocky Mountains. We either invaded or did not invade these assemblages with one of three perennial exotic forbs that increasingly dominate these grasslands, spotted knapweed, *Centaurea maculosa*, Dalmatian toadflax, *Linaria dalmatica*, and sulfur cinquefoil, *Potentilla recta*. We crossed invasion treatment with water addition to determine how water, a major limiting resource in dry grasslands of the intermountain west (Sheley *et al.* 1999), might influence competitive interactions. We addressed the following questions: (i) what is the competitive effect of each exotic on native biomass and how does this vary depending on both native and exotic identity and resource supply? (ii) For knapweed in particular (because it was the most potent competitor), are competitive effects on natives

mediated by resource depletion (light, soil nitrogen and water)? (iii) What is the competitive effect of each native species on each exotic, and how is this influenced by resource supply or native species identity? (iv) Does invasion increase or decrease total productivity, how does this vary among exotics, and are there consistent differences between natives and invaders in particular traits that might influence this pattern?

## Methods

### PLOT SET-UP

Plots were established at a site that had previously been an organic farm but had been fallow for at least 3 years before the experiment was initiated. Despite not being farmed for several years, soil fertility was high. In summer 2002, prior to initiating the experiment, we tilled and watered the site to stimulate weed germination out of the seed bank. We subsequently killed weeds with the herbicide Roundup®. In April 2003 we created monocultures of 10 native perennial plant species that commonly co-occur in grasslands in the intermountain west. Species planted were (i) grasses (*Festuca idahoensis* and *Koeleria macrantha*), (ii) early flowering forbs that branch with short rhizomes, stolons or at the root crown (*Geum triflorum*, *Antennaria rosea*, and *Penstemon procerus*), (iii) mid-season forbs with woody root crowns (*Penstemon wilcoxii*, *Potentilla arguta*, and *Gaillardia aristata*) and (iv) mid-season forbs with spreading rhizomes (*Achillea millefolium* and *Monarda fistulosa*). These plants are common, and therefore likely represent species with 'average' competitive abilities compared to rarer species that might be inherently poor competitors.

To create monocultures we transplanted seedlings of each species into separate 3 × 3 m plots. Seedlings were grown from locally-collected seed in a greenhouse, starting in January 2003. Plots were arranged in three blocks separated by 6 m; plots within blocks were separated by 3 m. Each plot was divided into four 1.3 × 1.3 m subplots (separated by 0.2 m buffer strips), with each subplot planted with the same species at the same initial density (32 individuals/subplot). We further increased plant density by supplementing existing plants in subplots with an additional 16 individuals/subplot in April 2004. The ultimate density of species in subplots was higher than planted density because of copious seed production and subsequent natural recruitment of seedlings in spring 2004–2006. Subplots were randomly assigned to be invaded by one of three perennial exotics that are both regionally widespread as well as extremely abundant: spotted knapweed (hereafter 'knapweed', *C. maculosa*), Dalmatian toadflax (hereafter 'toadflax'; *L. dalmatica*), sulfur cinquefoil (hereafter 'cinquefoil'; *P. recta*), or remain as uninvaded controls.

In spring 2004 we established 6 additional 3 m × 3 m plots (three watered, three unwatered) on bare ground, where all pre-existing plants had been removed. We divided each plot into four subplots; into three of these we added seeds of the three exotics (at 7500 seeds m<sup>-2</sup>, the same seed density used to invade native monocultures; see below). All monocultures of natives and exotics were weeded continuously of species not assigned to the plot. Continuous weeding enabled us to remove plants when tiny, thereby minimizing disturbance.

We factorially crossed each monoculture with a ± water treatment (i.e. water addition vs. ambient); water supplementation began in May 2004 and was maintained through 2007. Each treatment combination was replicated three times (10 monocultures × 2 water treatments × 3 replicates = 60 plots total). We applied 1.25 cm of water per week to plots during the relatively wet months of May and

June. We generally watered at times when it was not raining and it had not rained for at least 24 h. We watered during May and June because we wanted to enhance the range of natural variability in rainfall during the normal wet season. The mean monthly rainfall in May and June during the years of this study were 7.3 and 6.47 cm, respectively (rainfall data for Missoula were obtained from the Western Regional Climate Center <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?mt5735>). If we had watered later in the summer, at a time that is normally dry, plant growth and phenology would have been altered in abnormal ways. See Maron & Marler (2007) for detailed description of how water was applied.

In September 2004, we randomly selected and invaded three of the four subplots within each plot with an equal number of seeds of a unique exotic. We added either 10.71 g of knapweed seeds, 0.76 g of toadflax seeds or 0.85 g of cinquefoil seeds to a randomly selected subplot within each plot. In September 2005 half the number of seeds added in 2004 were again added to the same subplots. We placed seeds in the central 1 m<sup>2</sup> of each subplot, and for each invader total seed weight added across both years corresponded to 7500 seeds.

### DATA COLLECTION

In September 2005 and July 2006 and 2007, we counted the number of flowering stems of each exotic within the central portion of each invaded subplot (1 m<sup>2</sup> in 2005 and 2006 and 0.56 m<sup>2</sup> in 2007). From late-June through mid-July 2007, at peak biomass production, we harvested all above-ground biomass rooted within a 0.75 × 0.75 m quadrat placed in the centre of uninvaded and invaded subplots within each plot (or in the planted monocultures of the exotics). Plants were cut at ground level, separated by species and bagged. Flowering and non-flowering exotics were also bagged separately. Harvested plants were dried at 60 °C and weighed.

We calculated a relative competition intensity index ( $RCI_{\text{exotic}}$ ) where  $RCI_{\text{exotic}} = (\text{Native Yield}_{\text{uninvaded}} - \text{Native Yield}_{\text{invaded}}) / \text{Native Yield}_{\text{uninvaded}}$ . Typically RCI is based on the outcome of competition between single individuals of two species. In our case,  $RCI_{\text{exotic}}$  can be influenced by: (i) the ability of exotics to invade (which determines their ultimate density) and (ii) the competitive effects of established exotics on resident natives. These competitive effects are, in-turn, influenced both by variation in (i) exotic density in native monocultures and (ii) per capita competitive impacts of exotics on particular natives. The effects can be partially teased apart by statistically controlling for exotic biomass in invaded subplots (see analysis below). We invaded established monocultures with exotic seeds rather than conducting competition experiments with equal numbers of natives and exotics, as a result  $RCI_{\text{exotic}}$  is likely to be very conservative. In the current context, this index represents a realistic assessment of competitive impacts that might be expected if exotics invade particular assemblages. We also calculated an  $RCI_{\text{natives}}$  for each native species monoculture (of the same water treatment), where  $RCI_{\text{natives}} = (\text{Exotic Yield}_{\text{invaded bare subplots}} - \text{Exotic Yield}_{\text{invaded native monocultures}}) / \text{Exotic Yield}_{\text{invaded bare subplots}}$ . As with  $RCI_{\text{exotic}}$ ,  $RCI_{\text{natives}}$  incorporates the competitive effects of natives on exotic establishment (which influences the density of exotics in invaded subplots) as well as the subsequent effects of natives on the individual biomass of established exotics. When calculating both  $RCI_{\text{natives}}$  and  $RCI_{\text{exotic}}$  we excluded native monocultures where there was no exotic establishment.

Because knapweed was the most successful invader (see Results), we focused on examining the mechanisms underlying the strong competitive effects of this species in particular. Specifically, we measured soil moisture, light and plant-available soil nitrogen in knapweed-invaded and uninvaded subplots to determine how

invasion influenced resource availability. During the peak growing season, from 22 May to 21 July 2006, we measured soil moisture approximately every 10 days. Soil moisture was measured at 5–15 cm and 35–50 cm depths with a TRIME FM TDR probe (Mesa systems, Medfield, MA) that was inserted down 5.1 cm diameter PVC access pipes. We assessed levels of  $\text{NO}_3^-$  and  $\text{NO}_4^+$  by burying (at a depth of 10 cm) two ion-exchange resin capsules (containing 1 g of ionic resin, Unibest, Bozeman, Montana) in the centre of each uninvaded and knapweed-invaded subplot in April 2007 and excavating these immediately before plant harvest in early July 2007. We transported resin capsules back to the lab on ice and subsequently extracted  $\text{NO}_3^-$  and  $\text{NO}_4^+$  by bathing each capsule in three sequential 1-h rinses of 2 M KCl (10 mL per rinse). Capsules were gently shaken on a shaker table during each rinse, after which KCl extracts were decanted to create a total extract volume of 30 mL. Extracts were frozen and then analyzed at the University of Colorado Kiowa Lab for  $\text{NO}_4^+$  and  $\text{NO}_3^-$  on an OI Analytical Flow Solution IV Spectrophotometric Analyzer. We used the mean of nitrogen values from the two resin capsules excavated from each subplot in analyses. Finally, we used an 86.5 cm long linear ceptometer (AccuPar-LP80, Decagon Devices, Pullman, WA, USA) to measure photosynthetically active solar radiation (PAR) in uninvaded and knapweed-invaded subplots. We took measurements at mid-day when there was minimal cloud cover in early July 2007, immediately before plant harvests. We recorded the percent decline in PAR from above to below the canopy (6–8 cm above ground level).

To compare traits of natives and exotics we randomly chose 20 individuals of each species (dispersed equally across the three control plots) and on each measured maximum height and lateral spread at peak growth in early July. We also measured specific leaf area (SLA) by harvesting two randomly selected fully expanded and illuminated, undamaged leaves on each of these plants. Leaves were dried in a plant press for at least 3 days and weighed. We determined leaf area for the same dry leaves by either measuring leaf area to the nearest 0.001 cm<sup>2</sup> on a calibrated Li-Cor 3100 or digitizing pressed leaves using a flatbed scanner and analyzing total area using NIH Image version 1.62 (available on the Internet at <http://rsb.info.nih.gov/nih-image/>). We calculated SLA for each leaf and used the mean of these measurements in subsequent analyses. Finally, to compare shoot : root ratios, we grew 20 individuals of all species in separate 1 gallon pots in a greenhouse for several months. Plants were grown from locally collected seed. Immediately before flowering, we harvested plants, carefully washing the soil from all roots. Plants were dried at 60 °C for several days and then weighed plants to obtain the ratio of shoot to root dry mass.

## ANALYSES

We first quantified the general extent of invasion by calculating the mean number of exotic flowering stems and mean exotic above-ground biomass (lumping the three exotic species into one group) across all native monocultures. To determine the overall strength of competitive effects imposed by exotics on natives, we first ran a split-plot ANOVA (PROC-Mixed module of SAS; ver. 9.1) where we compared the biomass of natives in uninvaded versus invaded subplots (where we grouped all exotics together). In this model, native identity, invasion status (invaded vs. uninvaded) and water treatment were fixed factors. Plots were considered split among invader types with water being applied at the whole plot level. We then used similar split-plot ANOVAs to examine how (i)  $\text{RCI}_{\text{native}}$ , (ii)  $\text{RCI}_{\text{exotic}}$  and (iii) exotic biomass within invaded monocultures differed based on exotic and native identity, water treatment and the interactions between these factors.

Biomass values used to calculate RCI were  $\ln + 1$  transformed. Tukey *post hoc* comparisons were used to decompose particular significant main effects. To examine how  $\text{RCI}_{\text{exotic}}$  varied on a per capita basis, we ran an identical split-plot model as above but as an ANCOVA with exotic biomass as a covariate. An alternative approach would have been to calculate per capita  $\text{RCI}_{\text{exotic}}$  by dividing  $\text{RCI}_{\text{exotic}}$  by exotic biomass. We could not use this approach, however, as this resulted in highly skewed values with heterogeneous variances that could not be normalized *via* transformation.

The final biomass attained by exotics within native monocultures could potentially be influenced by competitive processes that operate at different life stages of exotics. Natives could inhibit initial exotic colonization, which in turn could affect the ultimate biomass attained by exotics in monocultures. Natives could also limit the size and/or population growth of exotics after they colonize monocultures, and influence final biomass by this route. To partially tease these two effects apart we used ANCOVA to determine how water treatment and the change in the number of flowering stems of each exotic from 2005–2007 (used as a covariate) affected the ultimate biomass attained by each exotic in that monoculture. The change in number of flowering exotic stems represents both changes in plant size as well as changes in the number of genets per subplot. If final exotic biomass was solely dictated by initial colonization success, then this relationship should not be significant.

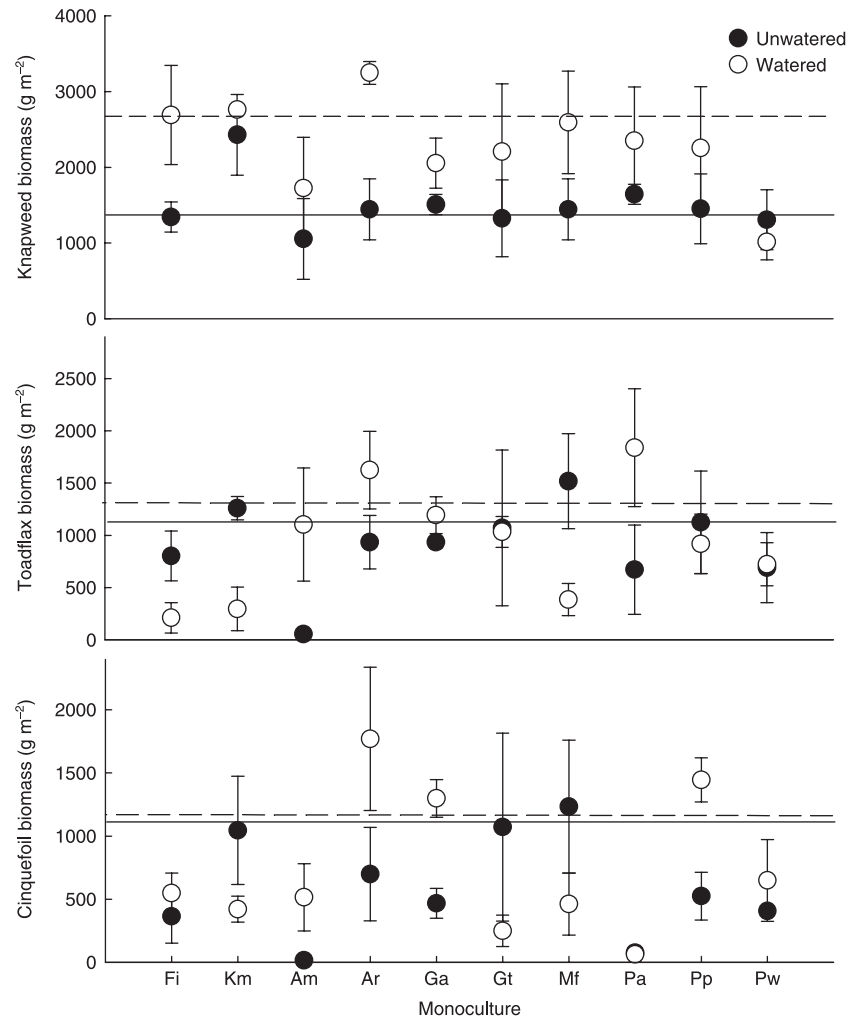
We also examined how competition between natives and knapweed influenced resource levels. We used separate split-plot ANOVAs to determine the effects of knapweed invasion on plant available: (i)  $\text{NO}_4^+$  and  $\text{NO}_3^-$  ( $\log + 1$  transformed) sorbed to resin capsules and (ii) the percent reduction in PAR from above to below the canopy (arc-sine square-root transformed). Water treatment (applied at the whole plot level), invasion ( $\pm$  knapweed invasion) and native species identity were fixed factors. To examine impacts of water addition and knapweed invasion on soil moisture, we performed a split-plot ANOVA as above but with the five measures of soil moisture taken at roughly equal intervals across the growing season in 2006 as a repeated measure. Finally, to determine how plant traits might differ between the natives and exotics, we performed a PCA (using Systat ver. 11) on maximum plant height, lateral spread, shoot : root ratio and SLA.

## Results

### VARIATION IN RESISTANCE TO INVASION

All three exotics successfully invaded monocultures of native plants. At the end of the experiment there were an average of 169 ( $\pm$  SEM 7.9) flowering exotic stems/m<sup>2</sup> within each monoculture, which equalled 1160 g m<sup>-2</sup> ( $\pm$  SEM 69 g) of biomass. The three exotics, however, differed in their ability to invade (Fig. 1, Table 1). Knapweed was the most potent invader, both in terms of the number of flowering stems (mean knapweed = 244 m<sup>-2</sup>, mean toadflax = 128 m<sup>-2</sup>, mean cinquefoil = 131 m<sup>-2</sup>; *post hoc* comparison  $P < 0.0001$ ) and total biomass (mean knapweed = 1918 g m<sup>-2</sup>; *post hoc* comparison  $P < 0.0001$ ). Toadflax biomass (mean = 894 g m<sup>-2</sup>) was greater than cinquefoil (mean = 667 g m<sup>-2</sup>; *post hoc* comparison  $P = 0.0001$ ) but this was not the case for flowering stems (*post hoc* comparison  $P < 0.05$ ).

Native species differed in their resistance to invasion (Fig. 1, Table 1). Both *Achillea millefolium* and *Penstemon wilcoxii*



**Fig. 1.** Competitive effects of natives on mean ( $\pm$  SEM) biomass ( $\text{g m}^{-2}$ ) of exotics. Horizontal lines denote mean exotic biomass ( $\text{g m}^{-2}$ ) within unwatered (solid line) and watered (dashed line) bare plots to which exotic seeds were added. Points below the horizontal lines represent competitive suppression of exotics by natives; points above the lines suggest facilitation. Codes for native species: Fi = *Festuca idahoensis*, Km = *Koeleria macrantha*, Am = *Achillea millefolium*, Ar = *Antennaria rosea*, Ga = *Gaillardia aristata*, Gt = *Geum triflorum*, Mf = *Monarda fistulosa*, Pa = *Potentilla arguta*, Pp = *Penstemon procerus*, and Pw = *Penstemon wilcoxii*.

**Table 1.** Results from split-plot ANOVA testing effects of water addition, invader identity, and native species identity on invader biomass within invaded assemblages and  $\text{RCI}_{\text{native}}$  (the percent reduction in exotic biomass due to competition with natives)

Source	d.f.	Invader biomass		$\text{RCI}_{\text{native}}$	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Water treatment	1, 2	3.43	0.20	0.21	0.69
Invader identity	2, 112	30.3	0.0001	25.78	0.0001
Native identity	9, 112	3.39	0.001	1.78	0.08
Invader $\times$ native	18, 112	1.42	0.13	1.02	0.44
Water treatment $\times$ invader	2, 112	0.53	0.59	3.06	0.051
Water treatment $\times$ native	9, 112	2.77	0.006	1.25	0.27
Water treatment $\times$ invader $\times$ native	18, 112	0.96	0.50	0.71	0.79

Denominator degrees of freedom for  $\text{RCI}_{\text{native}}$  = 109 rather than 112.

were significantly more resistant to invaders compared to *Antennaria rosea*, *Penstemon procerus*, *Gaillardia aristata*, *Monarda fistulosa*, and *Koeleria macrantha*. *Potentilla arguta* was more resistant than *Antennaria rosea* (*post hoc* comparisons,  $P < 0.05$ ). There was also a significant native species  $\times$  water treatment interaction (Table 1). Subsequent analyses of wet and dry plots separately revealed that in dry plots *A. millefolium* was again significantly more resistant to invasion than *A. rosea*,

*P. procerus*, *G. aristata*, *M. fistulosa*, and *K. macrantha*. All other natives were similar in invasion resistance. In wet plots, *A. millefolium* was only more resistant than *A. rosea* (*post hoc* comparison,  $P < 0.05$ ).

Subplots with greater change in the number of flowering exotic stems from 2005–07 had greater final exotic biomass (ANCOVA, knapweed;  $R^2 = 0.69$ ,  $F_{1,56} = 89.8$ ,  $P < 0.0001$ ; cinquefoil,  $R^2 = 0.46$ ,  $F_{1,56} = 43.6$ ,  $P < 0.0001$ ; toadflax,  $R^2 = 0.71$ ,

$F_{1,56} = 131.5$ ,  $P < 0.0001$ ). Thus, exotic biomass in monocultures was not solely dictated by initial differences in exotic colonization; subsequent increases in the number of stems (which could have been due to increases in size of plants as well as recruitment of new individuals) largely influenced final exotic biomass. For knapweed, the slope of this relationship varied depending on water treatment (invader growth  $\times$  water treatment interaction  $F_{1,56} = 21.3$ ,  $P < 0.0001$ ); this was not the case for the other two invaders (invader growth  $\times$  water treatment interaction  $P > 0.05$ ).

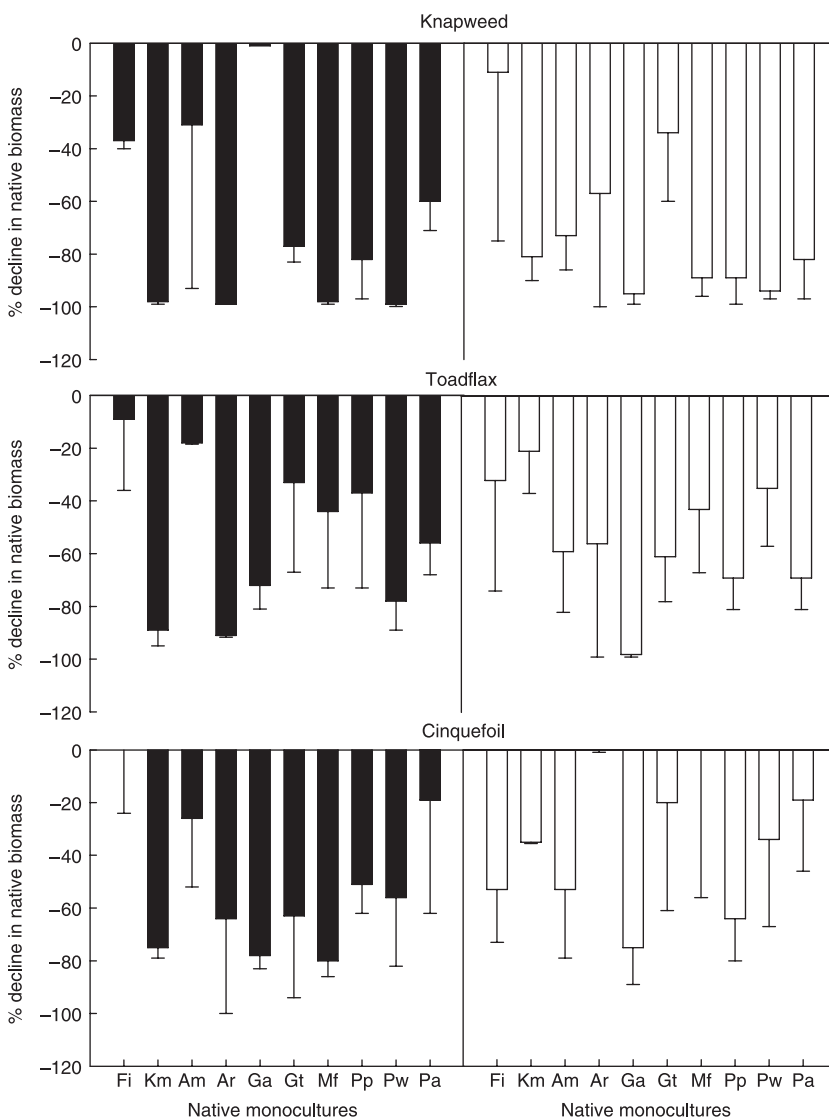
#### VARIATION IN COMPETITIVE EFFECTS OF NATIVES ON EXOTICS

Natives either exerted no competitive resistance to exotics (Fig. 1; knapweed biomass was an average of 77% greater in native monocultures compared to invaded bare plots without natives) or moderately suppressed exotics (Fig. 1; exotic biomass was an average of 33% and 19% lower in native monocultures compared to invaded bare plots for cinquefoil and toadflax,

respectively). These differences in impacts of natives on knapweed versus the other two exotics were significant (Table 1; *post hoc* comparisons,  $P < 0.0001$ ). Natives had similar impacts on cinquefoil and toadflax (*post hoc* comparisons,  $P > 0.05$ ). Native species did not differ in their competitive impacts on exotics (Table 1). The only significant interaction (a significant water treatment  $\times$  invader interaction, Table 1) indicated that natives had lower impacts on knapweed in watered versus unwatered plots, whereas this was not the case for the other two exotics (*post hoc* comparisons,  $P > 0.05$ ).

#### VARIATION IN COMPETITIVE EFFECTS OF EXOTICS ON NATIVES

In contrast to the limited effects of natives on exotics, exotics exerted strong competitive effects on natives. Exotics as a group depressed native biomass by an average of 51% ( $\pm$  SEM 6.7%), a significant reduction (Fig. 2;  $F_{1,190} = 99.2$ ,  $P < 0.0001$ ). The three exotics differed, however, in the magnitude of their competitive effects on natives (i.e.

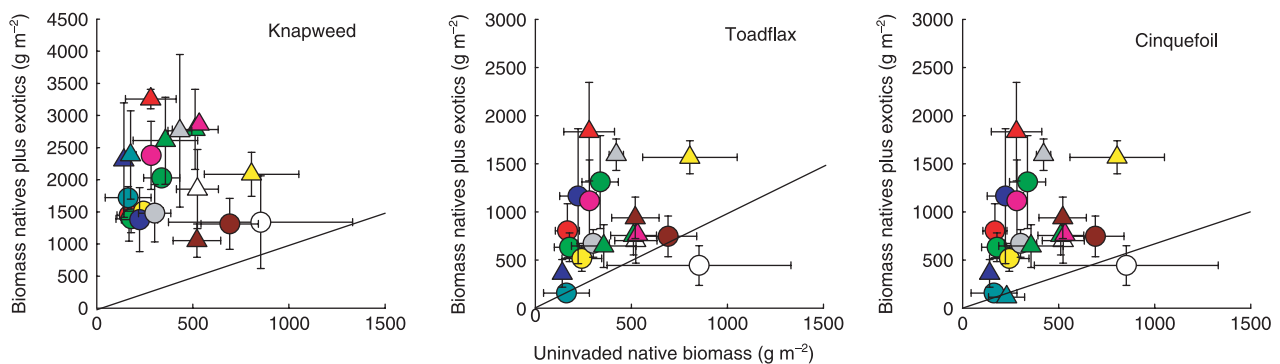


**Fig. 2.** Mean ( $\pm$ SEM) percent decline in native biomass due to competition from spotted knapweed (top panel), Dalmatian toadflax (middle panel) and sulfur cinquefoil (bottom panel). Left panels (black bars), unwatered plots, right panels (open bars), watered plots.

**Table 2.** Results from split-plot ANOVA testing effects of water addition, knapweed invasion, and native species identity on  $\text{NO}_3^-$  and  $\text{NO}_4^+$  sorbed to ion exchange resin capsules (mid-April–early July, 2007), and the % reduction in PAR (from above to below canopy, July 2007)

Source	d.f.	$\text{NO}_3^-$		$\text{NO}_4^+$		PAR	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Water treatment	1, 2	26.33	0.03	0.60	0.52	2.4	0.26
Knapweed invasion	1, 70	16.9	0.0001	1.77	0.19	210	0.0001
Native identity	9, 70	3.20	0.003	2.61	0.01	2.8	0.007
Knapweed invasion × native identity	9, 70	2.83	0.007	1.25	0.28	3.4	0.001
Water treatment × knapweed invasion	1, 70	6.44	0.013	0.50	0.48	0.13	0.72
Water treatment × native identity	9, 70	1.12	0.36	1.38	0.21	1.16	0.33
Water treatment × knapweed invasion × native identity	9, 70	0.96	0.48	0.49	0.88	1.04	0.42

Error degree of freedom for reduction in PAR is 74 rather than 70.



**Fig. 3.** Relationship between mean ( $\pm$  SEM) above-ground biomass in invaded assemblages (natives plus exotics) and mean ( $\pm$  SE) above-ground biomass of uninvaded assemblages (natives only). Means calculated for assemblages containing the same native (*Achillea millefolium* [white], *Antennaria rosea* [light red], *Festuca idahoensis* [light green], *Gaillardia aristata* [yellow], *Geum triflorum* [blue], *Koeleria macrantha* [pink], *Monarda fistulosa* [dark green], *Penstemon procerus* [grey], *Penstemon wilcoxii* [dark red], *Potentilla arguta* [teal]). Circles, dry assemblages, Triangles, wet assemblages. Diagonal represents the 1 : 1 line, where native biomass in uninvaded subplots equals the total biomass in invaded subplots.

$\text{RCI}_{\text{exotic}} F_{2,105} = 12.90, P < 0.0001$ ; Fig. 2). Spotted knapweed had larger competitive impacts on natives than did cinquefoil and toadflax (*post hoc* comparison,  $P < 0.0001$  for cinquefoil and toadflax, respectively). Cinquefoil and toadflax did not differ significantly in their competitive impacts (*post hoc* comparison  $P = 0.44$ ). Water addition did not significantly change the competitive impacts of exotics on natives ( $F_{1,2} = 0.60, P = 0.52$ ). The competitive impacts of exotics, however, did differ among a few natives ( $F_{9,105} = 2.82, P = 0.005$ ). Exotics had significantly greater competitive impacts on *A. rosea* compared to *A. millefolium* and *F. idahoensis* (*post hoc* comparisons,  $P < 0.05$ ). There were no significant interactions between native identity, exotic identity and water addition.

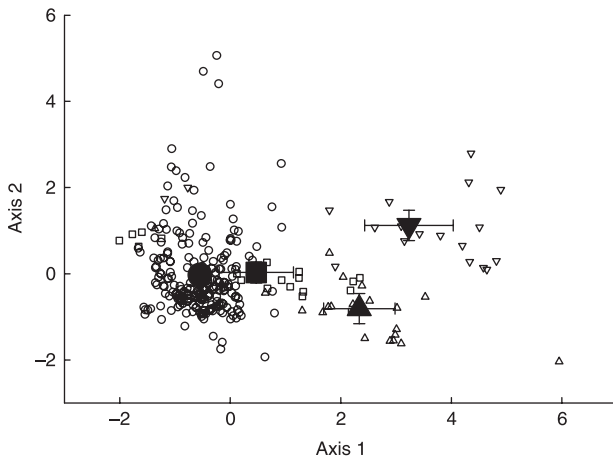
Variation among the three exotics in their competitive impacts on natives was a function of their abundance within invaded monocultures (ANCOVA,  $F_{1,104} = 12.26, P < 0.0008$ ). After exotic biomass was controlled for statistically, differences among exotics in their competitive impacts on native biomass disappeared (ANCOVA,  $F_{2,104} = 2.71, P = 0.07$ ), as did differences

among natives in how impacted they were by exotics (ANCOVA,  $F_{9,104} = 1.68, P = 0.10$ ).

The competitive suppression of natives by knapweed corresponded with declines in plant-available soil nitrate, PAR (Table 2) and water (shallow;  $\text{rMANOVA}, F_{1,438} = 12.0, P < 0.001$ ; deep;  $F_{1,428} = 53.9, P < 0.0001$ ). Water addition increased nitrate availability (Table 2) and shallow soil moisture (shallow:  $F_{1,2} = 209, P < 0.005$ , deep:  $F_{1,2} = 7.2, P = 0.11$ ) but had no significant effects on PAR or soil ammonium (Table 2). Resources also varied depending on native species identity (Table 2; shallow soil moisture,  $\text{rMANOVA}, F_{9,438} = 9.2, P < 0.0001$ , deep soil moisture =  $F_{9,428} = 4.6, P < 0.0001$ ). Soil moisture declined through the growing season (shallow soil moisture  $\text{rMANOVA}, F_{4,438} = 147, P < 0.0001$ , deep  $F_{4,428} = 48.7, P < 0.0001$ ).

Despite reducing native biomass, invasion increased total above-ground biomass (Fig. 3). The biomass of natives and exotics together within invaded subplots was greater than the biomass of natives within uninvaded subplots in the same plot (paired *t*-test,  $t = -12.85, -8.2$ , and  $-5.88$  for knapweed, toadflax and cinquefoil, respectively,  $P < 0.0001$ ).





**Fig. 4.** A Principle Component Analysis of traits (SLA, later spread, maximum height and shoot-root ratio) of ten native species (open circles,  $n = 20$  per species) and three exotics (*C. maculosa*, upward triangle, *L. dalmatica*, downward triangle, *P. recta*, square;  $n = 20$  per exotic). Large points represent the mean  $\pm$  95% CI axis scores for all natives combined and each exotic.

#### PLANT TRAITS

Principal components analysis revealed that the combined trait values of the ten native species were virtually non-overlapping with the two most potent exotics, spotted knapweed and Dalmatian toadflax (Fig. 4). Sulphur cinquefoil, a congener of one of the natives used in the experiment, had traits that were more similar to those of some of the natives. The first and second PCA axes accounted for 51.5% and 26.2% of the variance in traits, respectively. The trait that contributed the greatest to variation within axis one was SLA.

#### Discussion

Our study revealed several important outcomes regarding interactions between established native plants and invading exotics in a field setting. We found that common native perennials that co-occur in grasslands in western Montana generally provide weak competitive resistance to several exotics. We quantified competitive resistance in ways that in some respects were unconventional compared to traditional competition experiments. Rather than competing single plants against each other, we examined competition in the context of a simulated invasion, where competitive interactions were allowed to play out over several years. This enabled us to determine competitive resistance at a coarse level, by measuring the ability of exotics to invade existing native monocultures, and at a finer level, by determining how invader biomass varied between invaded bare subplots (where colonization from seed occurred in the absence of competitors) and invaded monocultures containing different native competitors. We recognize that competition, as we measured it, includes both effects of natives on exotic establishment as well as the negative effects on the biomass of established individuals.

In terms of colonization, we found that native monocultures were easily invaded. Monocultures were substantially more invaded than mixed-species assemblages that received identical initial additions of exotic seeds (Maron & Marler 2008). Despite the fact that seeds were added to solid carpets of natives in monoculture, exotics both penetrated these assemblages and then subsequently increased through time. Part of the success of exotics may be due to the fact that we invaded monocultures with a high density of seeds. On the other hand, monocultures are often easily invaded, especially in comparison to more diverse mixtures (Levine 2000; Naeem *et al.* 2000; Dukes 2002).

At a finer level, we again found that natives exerted extremely weak competitive effects on exotics. Averaged together, the biomass of knapweed, cinquefoil and toadflax was, on average, 8% greater in native monocultures than in bare soil lacking competitors. Natives had their greatest negative effects on cinquefoil biomass; at the other end of the spectrum knapweed biomass was actually 77% greater within solid carpets of natives than in bare soil lacking competitors. The apparent facilitation of knapweed by natives may have occurred because it was easier for knapweed seeds to germinate within existing vegetation compared to bare plots (as opposed to a true lack of competitive effects of established natives on established knapweed). Unlike effects on invasibility, there were no differences among natives in their competitive impacts on exotics. Moreover, resource supply generally had limited effects on  $RCI_{\text{native}}$ . The only exception to this was that natives had lower impacts on knapweed in watered versus unwatered plots. Taken together, our results lend additional insight into the nature of native-exotic competition that cannot be gleaned from existing diversity-invasibility experiments because these experiments typically have: (i) used natives rather than exotics as 'model invaders' (Knops *et al.* 1999; Lavorel *et al.* 1999; Symstad 2000), (ii) used exotics and natives in resident assemblages (Dukes 2002; Zavaleta & Hulvey 2004) and (iii) not had treatments where invaders are grown in isolation from resident species (and *vice versa*) so that native-exotic competitive effects could be quantified.

The fact that natives had very weak competitive effects on spotted knapweed is at odds with previous research showing that in one-on-one competition experiments natives can have significant suppressive effects on spotted knapweed (Callaway *et al.* 2004). Why might these two sets of results be incongruent? One reason might have to do with the scale of these experiments. Unlike a traditional competition experiment where individuals are forced to interact in small pots, our experiment involved invading larger plots with exotic seeds. Perhaps at this larger scale there are more opportunities for species to avoid competition. A second reason for these divergent results may have to do with the fact that we invaded with seeds rather than forcing juvenile plants to compete one-on-one. Knapweed seeds undergo a significant amount of germination in early fall, when adult native plants are senesced and when there are only low levels of native seed germination (Maron & Marler 2007, unpublished data). Thus, in late fall, knapweed seedlings can become abundant even in high diversity native assemblages



due to this mismatch in germination timing with natives (Maron & Marler 2007). It may be that natives exert little competition with knapweed simply because knapweed can abundantly establish in monocultures at a time when native growth is limited, and then rapidly overwhelm natives in above-ground competition for light. Finally, the limited competitive impacts of natives on exotics in our experiment may have to do with the physical environment where we conducted this experiment. We established our plots in a field that had in years past been used as an organic farm, where the soil was still high in nutrients (Maron & Marler unpublished data). As such, perhaps below-ground resources were not limiting to plant growth for plants invading monocultures. This could have acted to shift competition from below to above-ground, favouring rapidly growing exotics. Interestingly, however, in contrast to the situation in monocultures, in high diversity mixed-species plots natives had large negative effects on exotic establishment, with below-ground nutrient and water availability being strong predictors of exotic abundance (Maron & Marler 2007).

Across invaded monocultures, exotics reduced native biomass by an average of 51%, with these negative impacts scaling in direct proportion to exotic abundance. In a review of competitive impacts of exotics on natives Vilá & Weiner (2004) found that native biomass was reduced by an average of 46.6% when competing with exotics. Our estimate of the impact of exotics on natives is very conservative with respect to Vilá & Weiner's (2004) results because our study incorporates both the vagaries of initial colonization of monocultures and then subsequent competition between established exotics and established natives. In contrast to the very strong competitive impacts of *C. maculosa* on natives, Suding *et al.* (2004) found that the related exotic, *Centaurea diffusa* (diffuse knapweed), had minimal competitive effects on natives.

Although the three exotic species we used differed in their colonization success, we found no differences among these species in their per capita competitive impacts on natives. Thus, although knapweed is allelopathic (Callaway & Aschehoug 2000; Bais *et al.* 2003), this does not in relation to the other two exotic species, appear to boost its per capita competitive impacts on natives. In mixed-species assemblages, we found similar results, with exotic impacts on natives scaling to their biomass and knapweed being a better invader than the other two exotics (Maron & Marler 2008). More generally, whether invasibility and impact scale linearly for other 'strong invaders' (*sensu* Ortega & Pearson 2005) or whether per capita effects of invaders differ is unclear (Levine *et al.* 2003), as few studies have experimentally examined the impacts of invaders on recipient assemblages (Parker *et al.* 1999; but see Dukes 2002).

Our results indicating that exotics can both successfully invade undisturbed native monocultures as well as substantially reduce native biomass strongly suggests that these invading species are not mere 'passengers' in the invasion process (*sensu* MacDougall & Turkington 2005). While they can clearly be facilitated by disturbance (Maron personal observation), they are also quite capable of establishing in undisturbed vegetation, and once established, they can reduce native

biomass. Previous studies that have examined exotic-native competition in the field have produced mixed results. Experiments that have examined competition between invading annual exotic grasses and native perennials have suggested that exotics may be poorer competitors in relation to natives (Seabloom *et al.* 2003b; Corbin & D'Antonio 2004; and MacDougall & Turkington 2005). In some cases exotics may have difficulty establishing within intact native vegetation, but once there they can effectively compete with natives (Hager 2004). Yet many greenhouse studies and some field studies (reviewed by Vilá & Weiner 2004) have indicated that exotics may be superior competitors to natives. Our study was not designed to address the question of whether invaders, *as a class*, are better competitors than natives. Our results do imply, however, that several very potent invaders in grasslands in the intermountain west are successful by dint of their superior competitive ability over natives. We note, however, that tests of the broader question of how exotics compare to natives in competitive ability remain scarce (Levine *et al.* 2003; Vilá & Weiner 2004).

Davis *et al.* (2000) have argued that communities should become more invisable as resource supply increases. The idea is that pulses in resource supply lead to 'free' resources not taken up by resident vegetation, thereby increasing opportunities for invaders. Although we did not add resources in a pulsed manner, our results did show that: 1) water addition increased soil moisture and soil nitrogen but 2) elevated resource supply had surprisingly little effect on either the competitive impact of exotics on native biomass or *vice versa*. However, increased resource supply did change invasion resistance for particular natives. The most resistant native species (*A. millefolium*) in dry assemblages lost its resistance in wet plots. Suding *et al.* (2004) found that diffuse knapweed (*Centaurea diffusa*) could better tolerate competition from natives under high versus low resource levels, and reducing soil phosphorus increased the competitive effects that natives exerted on diffuse knapweed. The lack of a substantial effect of water addition in our experiment may have been influenced by the fact that we added water to plots during May and June, a time of year that is typically wet. Thus, resource addition may have occurred at a time of the season when soil moisture was not limiting to plant growth. However, adding water to plots later in the season, in July or August when conditions are drier, would have made little biological sense and would have likely shifted plant size and phenology in unnatural ways, making for results that would be extremely difficult to interpret. Moreover, since models predict that western Montana may experience wetter springs under global climate change (Houghton *et al.* 2001), our intention was to explore how this might influence invasion dynamics.

In previous research where we examined invasion by knapweed, cinquefoil and toadflax into multispecies native assemblages we found that increased water supply increased invasibility to knapweed but had no effect on invasibility (or impact) of cinquefoil or toadflax. Bradford *et al.* (2007) also found that increased CO<sub>2</sub> and N did not benefit exotic competitors when competing with multispecies mixes of natives

and Walker *et al.* (2005) found that invasion did not increase in response to periodic pulses of fertilizer and water in New Zealand grasslands.

Interestingly, the two most potent invaders in our study, spotted knapweed and Dalmatian toadflax, had traits that were substantially different from all the other natives that were grown in monoculture (Fig. 4). Moreover, univariate analyses revealed that the single trait that was most distinct between exotics and natives was specific leaf area (SLA). In a phylogenetically controlled set of contrasts, Grotkopp & Rejmánek (2007) similarly found positive associations between high SLA and invasiveness among a group of 28 woody plants, half of which were invasive. SLA is often closely tied to relative growth rate, which is a key difference between non-invasive and invasive pines (Grotkopp *et al.* 2002). These results notwithstanding, the quest to identify unique traits shared among widely divergent groups of successful invaders has generally been unsatisfying (Roy 1990; Mack *et al.* 2000; Colautti *et al.* 2006). Rather than attempting such a global analysis, a more fruitful approach might be to compare traits between co-occurring invasive exotics and natives on a community by community basis (Moles *et al.* 2008). That is, successful exotics within a particular community may differ from co-occurring natives in trait values, but the specific traits that differ between the invader and natives may vary from community to community. Indeed, to the extent that exotics naturalize more readily in recipient communities that do not contain abundant native congeners (Daehler 2001), this may be indicative of the importance of this mismatch in traits between natives and successful exotics.

One striking pattern is that total productivity often is greater in invaded than non-invaded communities (Ehrenfeld 2003). However, such trends have been difficult to interpret, as they are usually observational comparisons of invaded and uninvaded communities, where confounding factors are not controlled (but see Zavaleta & Hulvey 2004). In a setting where we could control for confounding factors, we found that invasion substantially increased total above-ground biomass (Fig. 3). That is, exotics added more biomass to the native assemblages they invaded than they took away by suppressing resident native biomass. We found similar effects in mixed species assemblages (Maron & Marler 2008). This raises the question of whether the impacts of invaders on community productivity are tied to differences between exotics and natives in traits that affect resource capture and hence above-ground productivity. It also raises the question of how differences in below-ground biomass might differ between invaded and uninvaded plots. At this juncture, we lack definitive answers to these questions but they are topics we are currently investigating.

The overall implications of our results are that single species of natives offer very little competitive resistance to three widespread and abundant exotic forbs. Thus, to the extent that a variety of anthropogenic factors continue to degrade native grassland diversity, these systems may become more vulnerable to invasion. Moreover, because our results suggest that competitive impacts of exotics on natives scale to

exotic biomass (this study, Maron & Marler 2008), highly invasible systems (at least those invaded by 'strong invaders'; Ortega & Pearson 2005) will be heavily impacted, which in-turn will feed back to make native systems even more open to invasion. Determining the magnitude of this feedback, and developing restoration strategies, perhaps involving augmenting plant diversity of degraded grasslands with diverse mixes of native seed, should be major research priorities.

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