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Disturbance, resource pulses and invasion: short-term shifts in competitive effects, not growth responses, favour exotic annuals

Levi M. Besaw[1], Giles C. Thelen[2], Steve Sutherland[3], Kerry Metlen[2] and Ragan M. Callaway[2]*

[1]Environmental Science, Salish-Kootenai College, Pablo, MT 59855, USA; [2]Division of Biological Sciences, The University of Montana, Missoula, MT 59812, USA; and [3]Forests and Woodlands Program, Rocky Mountain Research Station, USDA Forest Service, Missoula, MT 59807, USA

Summary

1. Increased resource availability and resource pulses often promote invasion by exotic invasive plants, but the relative importance of increased resource supply for invaders with different life histories is likely to vary. It is also unclear whether increased resources allow invaders to outgrow their native neighbours or alter the outcome of competition. Understanding mechanisms by which different invasive life histories respond to resource supply will help to target the most important species to control.

2. We found that aerially dropped wildfire retardant on intermountain grassland provided a very high pulse of N and P and caused dramatic increases in the abundance of annual exotic invaders already present in the system. Field experiments with retardant stimulated similar shifts to dominance by exotic annuals and decreases in native perennial grasses, but elicited no responses by native annual species.

3. In a greenhouse experiment, the growth response of both exotic and native species to retardant was not related to the intensity of mean competitive effects or responses. Concomitantly, gram per gram competitive effects differed substantially among species and treatments. N-caused shifts in the strength of competitive interactions were far better predictors than growth responses of the effects of retardant in the field. For example, *Centaurea stoebe*, an invasive perennial forb, grew disproportionally more than any other species in response to retardant when grown alone, but retardant significantly shifted competitive outcomes with this invader in favour of exotic annuals and the native bunch grass *Pseudoroegneria spicata*.

4. *Synthesis and applications*. Our results indicate that an extreme nutrient pulse did not create conditions whereby invaders outgrew native neighbours or other exotics, but instead altered the competitive playing field in ways that resulted in considerable changes in community composition. Given the minuscule scale of retardant drops on the landscape, our results do not suggest changing the way retardant is used to combat wildfire but do suggest that localized post-retardant weed control may be important so that retardant drops do not become point sources for exotic invasion. Furthermore, our results suggest that under high N conditions, invaders with annual life histories should be prioritized for control.

Key-words: annuals, competition, fire retardant, invasion, nutrient pulse, wildfire

Introduction

Disturbance, resource availability, resource competition and plant life history interact to affect the distribution and abundance of species in native ecosystems and the invasion of these ecosystems by exotics. Increased resource availability often promotes invasion by exotic plants (Huenneke *et al.* 1990; Burke & Grime 1996; Maron & Connors 1996; Davis, Grime & Thompson 2000; Thompson *et al.* 2001; Thomsen *et al.* 2006). For example, the rapid nutrient uptake capacity of invasive annual plants (Claassen & Marler 1998; Vasquez, Sheley

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*Correspondence author. E-mail: ray.callaway@mso.umt.edu

& Svejcar 2008) is thought to give them an advantage over native species. However, high resource-use-efficiency can also promote some invasive species (Funk & Vitousek 2007). It is not known whether life history (annuals vs. perennial) or nativity (exotic vs. native) is the primary determinant of a species' response to resource supply. Furthermore, the issue of whether increased resource supply simply increases the relative growth rates of exotics more than those of natives or more subtly alters competitive balances remains unresolved (Maron & Marler 2008).

Disturbance interacts in complex ways with the effects of resource availability and competitive abilities (Grime 1977) and is also a key factor in exotic plant invasions (D'Antonio & Vitousek 1992; Levine *et al.* 2003). Annuals often have advantages over perennials after disturbance because plant life-history traits affect response to disturbance (Grime 1977; Huston & Smith 1987). Neither disturbance nor resource-based processes are likely to explain the biogeographic patterns that define intercontinental invasions (Callaway & Maron 2006) unless non-native ranges on all continents inherently have more favourable combinations of the particular disturbance-resource set (than the native ranges) that limits a specific invasive species (see Hierro, Maron & Callaway 2005). However, within non-native ranges, understanding the interplay between resource availability, life history, competition and disturbance can yield crucial insight into the abundances and impacts of invaders (e.g. Davis, Grime & Thompson 2000; Daehler 2003; Levine *et al.* 2003).

Native intermountain grasslands in western Montana are dominated by perennial bunchgrasses and forbs but have been invaded by exotic grasses and forbs with annual or perennial life histories. Natural and anthropogenic disturbances are key aspects of successful invasion in these grasslands (Ferguson, Craig & Schneider 2007; Gundale, Sutherland & DeLuca 2008). Historically, one of the most important natural disturbances in intermontane grasslands and savannas has been wildfire (Arno 1980). In the absence of exotic plant propagules, burning can be beneficial for native annual and biennial forbs (Antos, McCune & Bara 1983; Huisinga *et al.* 2005; Dodson, Metlen & Fiedler 2008). However, fire can also promote exotic invasion in intermountain grasslands (Metlen & Fiedler 2006; Dodson & Fiedler 2006; Freeman *et al.* 2007; Gundale, Sutherland & DeLuca (2008).

Fire can directly affect soil nutrient status (Monleon, Cromack & Landsberg 1997; Wan, Hui & Luo 2001; Gundale, Sutherland & DeLuca 2008); however, current fire management using aerial retardant drops provides an unusual opportunity to explore the impact of resource supply on invasions because fire retardant is exceptionally high in ammonium and phosphorus (see Larson *et al.* 1999). While affecting miniscule proportions of intermontane grassland, the fertilizing effects of retardant can leave spectacular patches of green within seasonally senescing intermountain grassland for several growing seasons (Fig. S1, Supporting Information). We have also observed that these patches have very different species compositions compared with places where retardant did not land. These extraordinary pulses of nutrients provide the opportunity to explore the effects of competition theory within the context of a common disturbance regime and fire management and help to target-specific invasive life histories for control.

We explored the combined effects of very high rates of fertilization and wildfire in western Montana grasslands by correlating community composition with different combinations of fire and aerially dropped fire retardant in the field. We also carried out field experiments with the application of retardant and greenhouse experiments designed to compare the growth responses and competitive abilities of individual species in control and retardant fertilized soils.

Materials and methods

STUDY SYSTEM

Our research was conducted on Mount Jumbo, Missoula, MT USA (UTM 12T 0273610, 5194480), which is in the Sapphire Mountain Range. Almost all of the area is classified as an intermountain prairie. The biomass of intermountain prairies is dominated by perennial native bunchgrasses but the species richness consists primarily of perennial forbs. There are few native forbs and grasses on Mt Jumbo with annual life histories. Most of the annuals are non-native exotic plants, and there are also many non-native perennial forbs and grasses. On 4 July 2005, a wildfire was started accidentally, which spread across much of the mountain. Retardant drops were made on the west-facing side of the mountain on 5 July 2005 and the fire was contained on 6 July. The red coloured retardant created clearly demarked patterns of unburned grassland without retardant, burned grassland without retardant, unburned grassland with retardant and burned grassland with retardant. The retardant used was PHOS-CHEK Fire Retardant D-75F (http://phos-chek.com/), which contains 65% ammonium sulphate [$(NH_4)_2SO_4$], 15% ammonium phosphate [$(NH_4)_3PO_4$] and 5% diammonium hydrogen phosphate [$(NH_4)_2HPO_4$]. All of these ingredients are used as commercial fertilizers and thus provide a relatively environmentally friendly fire management tool; however, such highly concentrated nitrogen and phosphorus fertilizer has the potential to affect plant communities and promote exotic weeds.

FIELD MEASUREMENTS

On 14 July 2006, soil samples were collected from areas representing all four combinations of burn and retardant. Soil from 0 to 10 cm depth was collected at eight randomly located points for each burn-retardant combination in the same areas in which we sampled vegetation. Samples were not mixed, and each was analysed separately for NH_4^+ and NO_3^-. On 14 July 2006, we visually estimated the cover of all plant species to the nearest 5% (with the lowest category 1%) in 30 randomly located 1-m^2 plots in each of the four burn-retardant combinations for a total of 120 plots.

We first analysed field vegetation data with ordination, using the non-relativized cover of each species (non-metric multidimensional scaling, PC-ORD, McCune & Medford 1997). We then analysed the field data more directly, combining species into functional groups based on life history and nativity (exotic or native). It is important to note that the distinction between 'exotic' and 'invasive' is blurred here, as not all exotics in our plots would reasonably be classified as invasive. However, *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek (spotted knapweed; nee *C. maculosa* Lam.), *Bromus tectorum*

L., *Sisymbrium altissimum* L. and *Linaria dalmatica* (L.) Mill. constituted over 90% of exotic cover and these species are 'strong invaders' (see Ortega & Pearson 2005). We grouped species as 'exotic annual grasses', 'exotic perennial forbs', 'native perennial forbs' and 'native perennial grasses'. Other biogeographic origin–life-history combinations either did not occur in the plots or were very uncommon. We analysed the effects of fire and retardant with the combinations as predictor variables with two-way ANOVAS and *post hoc* Tukey tests with normally distributed and untransformed data.

FIELD EXPERIMENT

In November 2007, when all species were dormant, we randomly selected thirty 1-m^2 unburned grassland plots on Mt Jumbo and treated half with retardant. It is important to note that we chose to apply retardant when *all* species were dormant, which was not the case for the post-fire-drop measurements described earlier. Our purpose was to avoid the potential toxic effects of retardant on perennial species such as may have occurred in the fire-based drop. We applied the same fire retardant used in the 2005 drop, composed of 1 : 12 ratio of PHOS-CHEK Fire Retardant grades D-75F to water. Using aerial photographs, we calculated the area affected by the drops on Mt Jumbo, estimated the volume dropped and thus estimated the average amount of retardant applied per metre. We then applied 4 L of our retardant mix to each plot which approximated the average rates in the original retardant drop. In July 2008, we recorded the percentage cover of annual exotic grasses, exotic annual forbs (almost exclusively *Sisymbrium*), exotic perennial forbs, native annual grasses, native annual forbs and native perennial grasses. Few native perennial forbs were in the plots and were not analysed. We analysed the effect of retardant with a one-way ANOVA. Data were normally distributed and were not transformed.

GREENHOUSE EXPERIMENT

We conducted a greenhouse experiment at The University of Montana to compare the growth responses of native and exotic species with different life histories to retardant and to compare growth responses to competitive effects and responses. A 50 : 50 mixture of local field soil and sand (20/30 grit, Lane Mt.) was put into 2·4-L pots. Retardant was mixed as in the field experiment and 100 mL was applied to half of the pots. Our target species were those that were most common in respective nativity-life-history groups in our original field measurements: the exotic annual grass *Bromus tectorum*, the annual exotic forb *Sisymbrium altissimum*, the exotic perennial forb *Centaurea stoebe*; the native perennial grass *Pseudoroegneria spicata* (Pursh) Á. Löve; and the native perennial forb *Artemisia frigida* Willd.. All seeds were collected in the field in the Missoula Valley area. Greenhouse temperatures were maintained between 15-30°C, corresponding roughly with natural summer temperatures. Natural light in the greenhouse was supplemented by metal halide bulbs and total photosynthetically active radiation during the day remained above 1200 μmol m^{-2} s^{-1}. The experiment lasted from 15 February 2008 to 27 July 2008. At the end of the experiment, all plants were harvested, washed and dried at 60°C for 3 days and then weighed. Each species was grown alone and in pairwise combination with the exception of *Centaurea-Artemisia*, and thus, these experiments do not take seed density into account. There were 10 replicates and the effects of each competitor species on each target species were tested using ANOVA with competition status and retardant treatment as predictor variables using normally distributed and thus untransformed data. We also calculated Relative Interaction Indices (RII) as 'competitive effect' for each species as a target and all competitor species following Armas, Ordiales & Pugnaire (2004) were:

$$\mathrm{RII} = \frac{B_{\mathrm{w}} - B_{\mathrm{o}}}{B_{\mathrm{w}} + B_{\mathrm{o}}}$$

where B_{o} = the total mass of a plant growing without a neighbour and B_{w} = the total mass of a plant growth with a neighbour.

Results

FIELD MEASUREMENTS

Wildfire increased soil nitrate levels across both retardant treatments (Fig. S2, Supporting Information; $F_{\mathrm{burn}} = 9{\cdot}27$, $P = 0{\cdot}005$) but retardant had no effect on nitrate ($F_{\mathrm{retardant}} = 1{\cdot}77$, $P = 0{\cdot}195$). In contrast, wildfire increased soil ammonium concentrations in the absence of retardant but decreased ammonium concentrations in the presence of retardant (Fig. S2, Supporting Information; $F_{\mathrm{burn\ \times\ retardant}} = 10{\cdot}73$, $P = 0{\cdot}003$). Most importantly, aerial drops of fire retardant increased soil ammonium by almost 100-fold, from 3·1 ± 0·4 to 240·5 ± 40·2 μg per dry g soil.

Considered separately, wildfire and retardant each had strong effects on plant community composition, shifting communities substantially on the *x*-axis of the ordination of sample plots but to different places on the *y*-axis (Fig. 1). Fire-related shifts appeared to be caused primarily by significant decreases in exotic perennial forbs (primarily *C. stoebe* and *L. dalmatica*; *t*-test, d.f. = 1,119; $P = 0{\cdot}007$), significant increases in native perennial forbs (*t*-test, $P < 0{\cdot}001$) and decreases in native perennial grasses (primarily *P. spicata* and *Festuca idahoensis* Elmer; *t*-test, $P = 0{\cdot}009$) with fire in the absence of retardant (Fig. 2). Fire had no effect on the abundance of exotic annuals either in the presence or in the absence of retardant. Retardant, however, significantly increased the cover of exotic annuals,

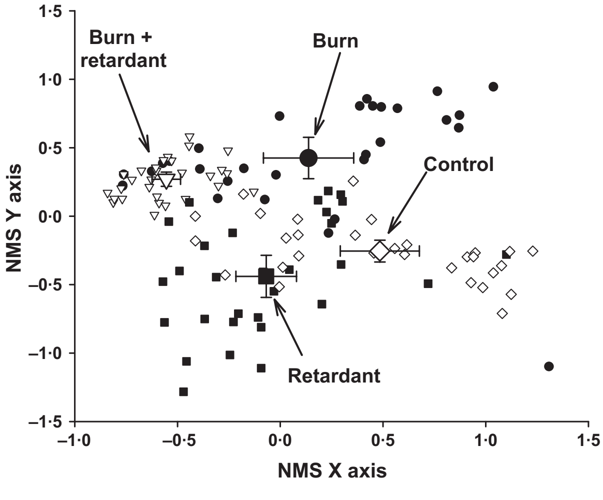

Fig. 1. Non-metric multidimensional scaling ordination of all species in field plots. Small symbols represent individual plots, large symbols represent the means of each of the four treatment combinations, and error bars around these means represent 95% confidence limits.

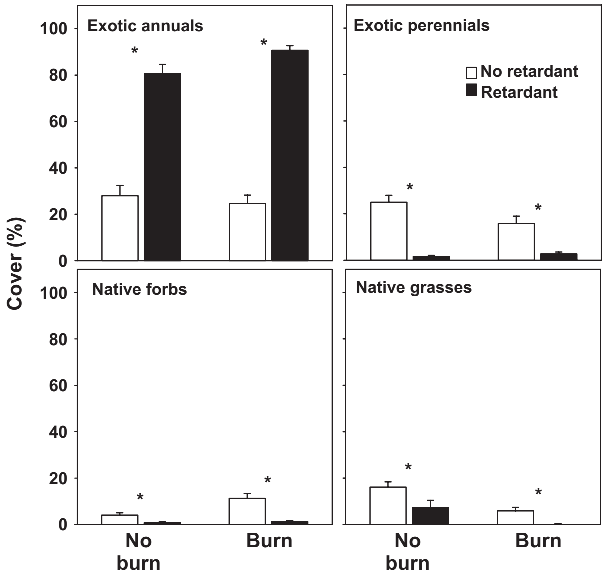

Fig. 2. Percentage cover of different functional groups in areas on Mt Jumbo burned by wildfire or not affected by fire and either with fire retardant aerially dropped in burned areas or unburned areas. Error bars represent 1 SE, and asterisks represent significant differences as determined by *post hoc* Tukey tests $P < 0{\cdot}01$.

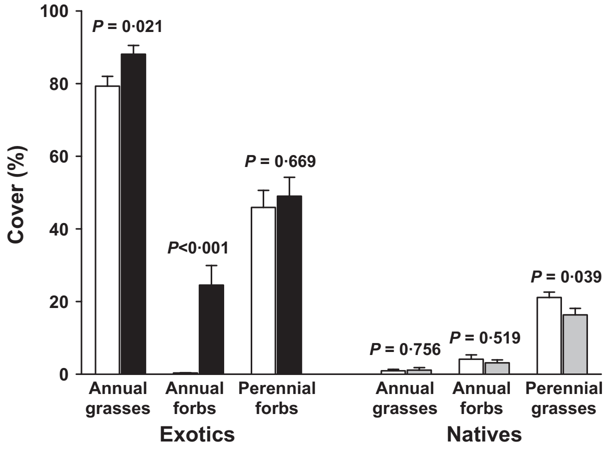

Fig. 3. Percentage cover of different functional groups in plots with and without experimentally added fire retardant. Error bars represent 1 SE, and *P* values for each functional group are from one-way ANOVAS.

primarily *B. tectorum* and *S. altissimum*, and significantly reduced all other functional groups (Fig. 2). The effects of fire and retardant together had the strongest effect on community composition, and this was primarily a very large increase in exotic annuals.

Field experiments with retardant qualitatively corroborated most field measurements and allowed a comparison of exotic and native annuals. Despite the fact that we randomly chose an experimental location already dominated by *B. tectorum* (cover was 80% without retardant), retardant increased the abundance of exotic annual grasses by 11% and the abundance of exotic annual forbs by almost two orders of magnitude. Exotic perennial forbs, native annual grasses and native annual forbs were not affected by retardant, and native perennial grasses were reduced by 22% (Fig. 3).

Experimentally applied retardant in the greenhouse experiment increased soil ammonium at the time seeds were planted from 4·7 ± 1·0 to 78·5 ± 9·5 μg per dry g soil (15 times higher), less than we measured in the field after the drop (76 times higher). Retardant increased nitrate in pots from 0·8 ± 0·1 to 1·2 ± 0·1 μg per dry g soil (*t*-test, d.f. = 1,14, $P = 0{\cdot}027$). In this experiment, the proportional responses of exotic annuals to retardant in the field (primarily *B. tectorum* and *S. altissimum*) were not correlated with their growth responses, relative to other species, in greenhouse experiments (Table S1, Fig. S3, Supporting Information). Of the five species tested, retardant increased the total mass of *B. tectorum* by 1,159%, *S. altissima* by 640%, *C. stoebe* by 1,886%, *A. frigida* by 1,558% and *P. spicata* by 465%. However, in competition, retardant increased the mean RII (their competitive effects) of the two exotic invasive annuals far more than any of the other species (Fig. 4; Table S1, Supporting Information, ANOVAS in Table S2, Supporting Information). For example, RII for the effect of *B. tectorum* increased significantly against all four of the other species, and for all other species combined, retardant more than doubled the competitive effect of *B. tectorum*, −0·33 ± 0·03 to −0·69 ± 0·08 (*t*-test, d.f. = 1,6; $P < 0{\cdot}001$). In contrast, retardant did not change the competitive effect of any other species against *B. tectorum* (Fig. 4). Retardant also significantly increased the competitive effect of the other annual invader, *S. altissima*, against each of three perennial species and for all other species combined from virtually zero without retardant (RII = −0·005 ± 0·06) to −0·28 ± 0·07 with retardant (*t*-test, d.f. = 1,6; $P < 0{\cdot}001$). Retardant did not increase the competitive effect of the perennial invader *C. stoebe* against any other species (Fig. 4), and when compared for all other species combined, it tended to *decrease* its overall competitive effect; RII changed from −0·33 ± 0·10 to −0·11 ± 0·03 (*t*-test, d.f. = 1,4; $P = 0{\cdot}113$). Retardant significantly increased the competitive effect of *A. frigida* on *S. altissima*, and *P. spicata* on *C. stoebe*, but retardant did not significantly affect the overall RII for either native perennial, *A. frigida* or *P. spicata* (Fig. 4). For *A. frigida*, the mean RII against other species combined without retardant was −0·23 ± 0·10 and with retardant −0·28 ± 0·20 (*t*-test, d.f. = 1,4, $P = 0{\cdot}844$). For *P. spicata*, the mean RII without retardant was −0·11 ± 0·03 and with retardant -0·10 ± 0·04 (*t*-test, d.f. = 1,6, $P = 0{\cdot}806$).

Discussion

A key finding of our work is that not all exotic invaders benefitted equally or at all, either in the field or in the competition experiments, from very large pulses in nutrient resources. In field measurements, field experiments and greenhouse experiments, invasive perennials either did not benefit or benefitted minimally from many-fold increases in *N* and *P* delivered as a single pulse through fire retardant.

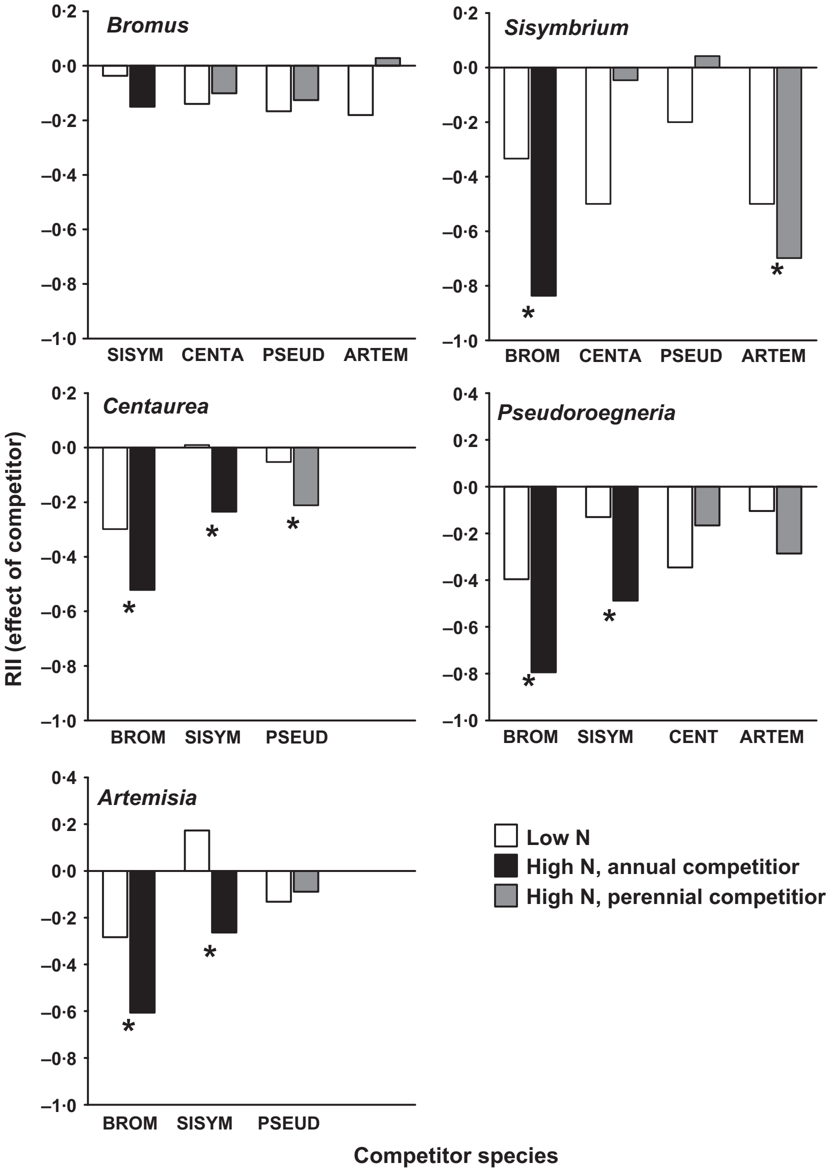

Fig. 4. Relative Interaction Indices (RII) for the competitive effects of different species on target species in greenhouse experiment. Lower RII indicates more intense competitive effect (competitors denoted on *y* axes). Asterisks denote a significant competitor × retardant interaction for specific competitor–target combinations (see Table S1, Supporting Information). SISYM – *S. altissium*, CENTA – *C. stoebe*, PSEUD – *P. spicata*, BROM – *B. tectorum*, ARTEM – *A. frigida.*

In contrast, exotic invasive annuals benefited substantially from fertilization through retardant in the field and in controlled experiments. Secondly, in our field experiment, native annual grasses and forbs did not increase in abundance with fertilization via fire retardant, whereas the abundance of exotic annuals and forbs increased dramatically. A third important result is that disturbance from wildfire and fertilization through retardant, in combination, had far greater transformative effects on communities in the field than did either factor in isolation. A fourth key finding was that the benefits gained by invasive annuals appeared to be almost exclusively through shifts in competitive advantages, not through relative higher growth responses to fertilization. The very strong competitive effects of exotic annuals at high retardant levels suggest that exotic perennials may have responded much more strongly to retardant in the field if exotic annuals were not present. We emphasize that our field results were measured over a very short time period, but our personal observations in 2010, 5 years after the burn, are that the patterns we describe here for native and exotic annuals and perennials remain clearly evident in the field.

Our results support the view that exotic plant species better invade areas with relatively high levels of soil nutrients or with periodic pulses of high nutrients (Burke & Grime 1996; Davis, Grime & Thompson 2000; Davis & Pelsor 2001; Yoder & Caldwell 2002; Maron & Marler 2007). However, we also found that nutrient addition altered *competitive outcomes* for both invaders and natives in ways that were not predictable from the growth responses of these species when grown alone. Thus, we did not find a classic ‘ruderal’ response but instead demonstrated an even greater shift towards competitive dominance by invaders. Importantly, our competition experiments were designed so that one individual interacted with one other individual and thus did not take seed or plant density into account. In contrast to results from other systems (Wilson & Shay 1990), the shifts in competitive responses in retardant treatments were better predictors of the changes measured in field and experiments than the responses of relative growth rates to retardant. It is particularly notable that when grown alone, the perennials *C. stoebe* and *A. frigida* had the largest proportional increases with added nutrients (*c.* 19 and 16 times larger, respectively), yet in the field and in experimental pairings with *B. tectorum* an *S. altissimum*, both perennials were much more competitively subordinate at high nutrient concentrations. Kolb *et al.* (2002) found that the exotic annual grass *Lolium multiflorum* grew at a faster rate *and* increased its competitive effect more than the perennial native grass *Hordeum brachyantherum*. Abraham, Corbin & D'Antonio (2009) also contrasted the performances of exotic and native plant species with annual and perennial life histories with increased *N* availability and found species-specific results. *Nassella pulchra* did not respond to *N* addition when grown alone and competed best against the exotic annual grass *Bromus diandrus* at low *N*. In their experiment, two native perennial grasses were suppressed more by *B. diandrus* than the exotic perennial grass *Holcus lanatus*, which had the greatest response of all the perennials to *N* additions when grown alone. Our finding that the relative abundance of different exotic and native species was affected strongly by competition suggests that management outcomes could be determined by which species are present at the time management is applied. For example, if annual invasive species such as *B. tectorum* are present, then resource pulses or disturbance might be unlikely to increase the abundance of invasive perennials. However, if annual invasive species are not present, resource pulses might then increase the abundance of invasive perennial.

We measured *N* fertilization in part to be consistent with many other studies of the effects of soil nutrients on exotic invasions. The fire retardant used here contains very large amounts of *P*, although we did not measure this specifically. Although *P* has been studied less than *N*, low levels of PO_4 have been shown to limit the growth of *B. tectorum* in the field (Miller *et al.* 2006; Gundale, Sutherland & DeLuca 2008) and *B. tectorum* tends to invade patches of high *P* availability (Bashkin *et al.* 2003). Because retardant has high concentrations of *both N* and *P*, our results are likely to be substantially different than studies that only examined the addition of *N*. Also, we conducted pairwise competition experiments in artificial greenhouse conditions. The results from these experiments corresponded well with field experiments and measurements, but experiments testing pairwise competitive outcomes would be another step towards understanding the role of competition in this system.

Different species respond in specific ways to the forms of available nitrogen. Relatively few species disproportionally utilize NH_4^+(the form present in our fire retardant) over NO_3^-, but perennials should benefit more from NH_4^+ (Kronzucker, Siddiqi & Glass 1997), whereas annuals should benefit more from NO_3^- (Young, Blank & Longland1995; Young *et al.* 1998). MacKown *et al.* (2009) found that the NO_3^- uptake rates of *Bromus tectorum* were 1·5–2·2 times greater than those of *Pseudoroegneria spicata* and *Elymus multisetus*, *E. elymoides*, native North American perennial grasses and that of *Taeniatherum caputmedusae*, an exotic invasive perennial grass. Surprisingly, the uptake of NH_4^+ by perennial grasses did not exceed that of *B. tectorum*. They concluded that the rapid seedling growth of *B. tectorum* coupled with greater NO_3^- uptake activity of *B. tectorum* appeared to drive superior competition against North American perennial grasses. These findings suggest that the highly positive effects of NH_4^+-based fire retardant on *B. tectorum* in our study were probably due to increased rates of nitrification made possible through high concentrations of total *N*, high uptake rates of NO_3^- by *B. tectorum* and the capacity for *B. tectorum* to utilize NH_4^+ despite its annual life history. Direct addition of NO_3^- would be expected to benefit *B. tectorum* even more.

We did not explicitly consider the potential toxic effects of high concentrations of retardant on leaf tissues. In July, when the fire and retardant drop occurred, most annuals would have been fully senesced, or close to senesced, whereas native and exotic perennials would have been in various states of partial activity. For example, based on our experience in these grasslands, *P. spicata* would be dormant with the exception of photosynthetically active tissue at the leaf bases, *A. frigida* would be minimally dormant, and *C. stoebe* would still have green cauline leaves and would have not yet produced viable seed. We do not know of tests of the toxic effects of the retardant we used on plants, but Bradstock, Sanders & Tegart (1987) reported short-term toxic effects on *Eucalyptus* leaves after aerial application of a different chemical fire retardant. Ammonium salts that are the key ingredient in most retardant solutions can alter germination for many species (Baskin & Baskin 1998), and Cruz *et al.* (2005) found that the retardant Fire Trol 934® (Fire Trol 934 ITRATECH, Gerasque, France) strongly inhibited seed germination. If direct application of retardant caused greater mortality of perennials, then the shift from perennials to annuals could have been stronger than that caused by fertilization effects alone. We experimentally applied retardant in November to eliminate the potential toxic effects of retardant (all plants are senesced or dormant in November), and the response of annual grasses to experimentally applied retardant was much less than in field measurements after the aerial drop in July. However, the proportional response of annual grasses was minimized by their high cover prior to establishing the experiment [see control (white) bars in Fig. 3] in the randomly chosen sample areas. Furthermore, the response of the annual forb *S. altissima* was even greater in the field experiment than in the post-drop field measurements. In this context, it is also important to note that the aerial drop and experimentally induced responses in the field occurred for life-history groups that were already present in the system; these species did not move into the system after disturbance and resource pulses.

Fertilization via fire retardant provides an extreme event, and the relative intensity of competition among species can be highly sensitive to the degree of fertilization. For example, natives can benefit from low levels of *N* fertilization, even when in competition with exotic annuals (Claassen & Marler 1998; Kolb *et al.* 2002). However, the balance of competition appears to consistently shift to favour annuals at higher levels of available *N*. Others have suggested that this occurs in part because perennial natives are physiologically incapable of utilizing excessive levels of *N* (Huenneke *et al.* 1990; Claassen & Marler 1998; Kolb *et al.* 2002; Vasquez, Sheley & Svejcar 2008). Our results indicated that at least some native perennial species are as physiologically capable of utilizing high *N* as two very invasive exotic annual species but lose badly to annuals when they are in competition.

Mass-based competitive effects were highly variable among species and treatments (0–5·59 g g^{-1}). Furthermore, competitive interactions were not simply decided on the basis of growth rates or competitor size, and mass-based effects did not consistently explain shifts in competition with fertilization by retardant. As an example, using *P. spicata* as a common target for all competitors, the mean gram per gram effect of the other species without retardant was as follows: *C. stoebe* – 0·85 g g^{-1} (1 gram of *C. stoebe* decreased the total mass of *P. spicata* by 0·85 g), *S. altissima* – 4·25 g g^{-1}, *B. tectorum* – 0·60 g g^{-1} and *A. frigida* – 0·48 g g^{-1}. Retardant increased the competitive effect (measured as RII, Fig. 4) of *B. tectorum* on all species, gram per gram effects were not the same against all competitors, and they were not affected by retardant in the same way for all competitors. Both sources of variation are important because they demonstrate that the competitive effects of species were not simply determined by how big they were. Retardant increased the gram per gram effect of *B. tectorum* on *A. spicata* from 0·28 to 0·41 g g^{-1} and on *C. stoebe* from 0·31 to 0·68 g g^{-1}. The gram per gram effect of *B. tectorum* on *S. altissima* was very weak under all conditions, 0·03 g g^{-1} without retardant and 0·04 g g^{-1} with retardant. In contrast, retardant *decreased* the gram per gram effect of *B. tectorum* on *P. spicata* from 0·60 to 0·39 g g^{-1}.

Such variation in gram per gram effects may be attributed to these species interacting with each other in ways that are not entirely dependent on resource uptake. For example, *C. stoebe*, which had the second strongest g/g effect on *P. spicata* in natural soil conditions, appears to be allelopathic (Ridenour & Callaway 2001; Pollock *et al.* 2009) and soil biota can have strong effects on how it competes with other species (Callaway *et al.* 2004). *Sysimbrium loeselii*, which is similar to *S. altissima* and also invasive, also appears to be allelopathic (Bainard, Brown & Upadhyaya 2009) and, interestingly, extracts were shown to inhibit *C. maculosa* (*stoebe*) and *P. spicata*. The very high gram per gram competitive effects of *S. altissima* in general and very low competitive gram per gram competitive responses may be related to such allelopathic effects.

Our results suggest that one of the most effective means of limiting wildfire – aerially applied fire retardant – has substantial potential to increase the abundance of exotic annuals already present in communities through the input of very large quantities of nutrients. By no means does this suggest that retardant should be not be used as a method for controlling wildfire, only that there may be an environmental cost to its use. Furthermore, by limiting the scope and intensity of fire, retardant may actually reduce fire-induced increases of some exotics. However, post-drop weed control may pay substantial dividends.

In our field plots (post-aerial drop), fire had no effect on the abundance of exotic annuals in the absence of retardant. However, our general observations and the results of others suggest that this is not generally the case for fires in intermontane grasslands or in other similar systems; fire often dramatically increases the abundance of *B. tectorum* or other exotic grasses (see D'Antonio & Vitousek 1992; Keeley & McGinnis 2007; Dodson, Metlen & Fiedler 2008; Gundale, Sutherland & DeLuca 2008). The relative benefits of limiting the scope of fires with nitrogen- and phosphorus-rich fire retardants at landscape scales may be even greater considering the dramatically increasing size and intensity of wildfires in some regions of North America (Arno & Fiedler 2005).

Soil nutrient-based shifts in competitive interactions such as we have described have the potential to dramatically alter the distribution and abundance of species in intermontane grasslands, as evidenced by our field results, and results from other systems suggest that such changes from pulse of resources may be long lasting (Milchunas & Laurenroth 1995). We illustrate retardant-caused shifts in competition in Fig. 5 with the two exotic annuals and the native *P. spicata.* Without retardant fertilization, the competitive effects of *B. tectorum* on *P. spicata* and *S. altissima* are moderate, and *S. altissima* has no effects on *P. spicata*, and *P. spicata* demonstrates a moderate competitive effect on *S. altissima.* However, in the very high nutrient conditions created by retardant, the competitive effects of *B. tectorum* on the other species doubled in intensity; *S. altissima* demonstrates moderate competitive effects on *P. spicata* and weak but significant effects on *B. tectorum*, and the competitive effect of *P. spicata* on *S. altissima* disappeared. These competitive scenarios correspond well with the dramatic increase in abundance of the exotic annuals and decrease in native perennials in the field. Our experimental measurements of competitive interactions technically demonstrate competitive 'intensity', not 'importance' (Brooker *et al.* 2005). However, the strong relationships between experimentally demonstrated intensity and shifts in dominance in field measurements and experiments indicate that competition is an important ecological process determining the relative abundance and distribution of plant species in our system and the expansion or decline of specific exotic invasive species. Retardant drops represent a very small impact on the landscape in general; thus, our results do not suggest changing the way retardant is used to combat wildfire. However, rapid weed control after retardant drop may prevent drop sites from becoming point sources for exotic invasion. Our results also suggest that under high *N* conditions, invaders with annual life histories should be prioritized for control.

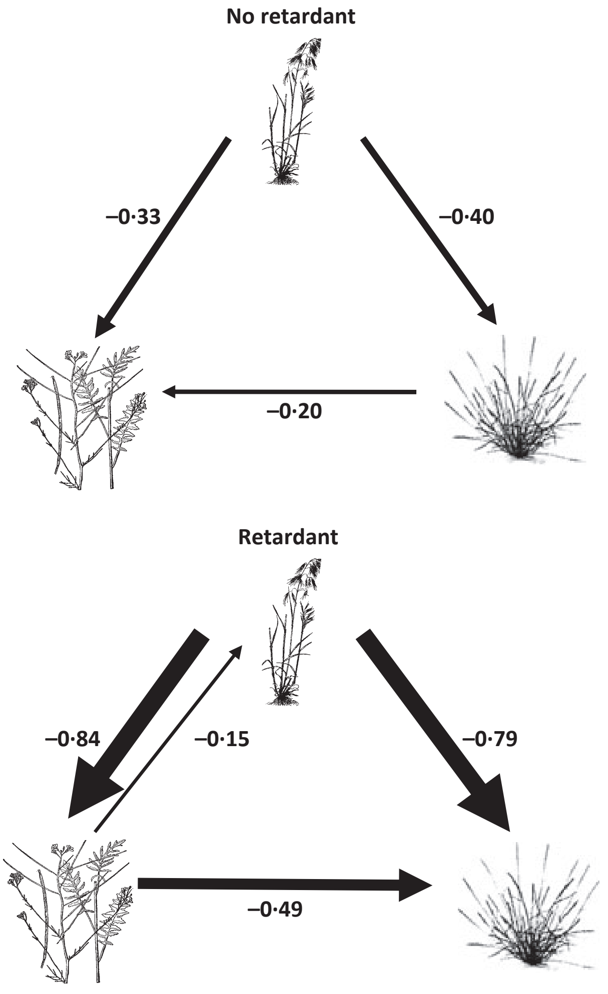

Fig. 5. Diagram illustrating differences in the networks of Relative Interaction Indices among *Bromus tectorum* (top), *Sisymbrium altissima* (bottom left) and *Pseudoroegneria spicata* (bottom right) with and without fire retardant.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Mount Jumbo with bright green strips marking where fire retardant was dropped.

Fig. S2. Soil nitrate and ammonium in burned areas and unburned areas on Mt. Jumbo with and without the aerial addition of fire retardant.

Fig. S3. Total mass of the five target species grown alone with and without fire retardant.

Table S1. Means and 1 SE for the total mass of species in competitive mixes.

Table S2. ANOVA tables for the greenhouse retardant competition experiment.