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# Impact of *Acroptilon repens* on co-occurring native plants is greater in the invader's non-native range

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**Abstract** Concern over exotic invasions is fueled in part by the observation that some exotic species appear to be more abundant and have stronger impacts on other species in their non-native ranges than in their native ranges. Past studies have addressed biogeographic differences in abundance, productivity, biomass, density and demography between plants in their native and non-native ranges, but despite widespread observations of biogeographic differences in impact these have been virtually untested. In a comparison of three sites in each range, we found that the abundance of *Acroptilon repens* in North America where it is invasive was almost twice that in Uzbekistan where it is native. However, this difference in abundance translated to far greater differences between regions in the apparent impacts of *Acroptilon* on native species. The biomass of native species in *Acroptilon* stands was 25–30 times lower in the non-native range than in the native range. Experimental addition of native species as seeds significantly increased the abundance of natives at one North American site, but the proportion of native biomass even with seed addition remained over an order of magnitude lower than that of native species in *Acroptilon* stands in Uzbekistan. Experimental disturbance had no long-term effect on *Acroptilon* abundance or impact in North America, but *Acroptilon* increased slightly in abundance after disturbance in Uzbekistan. In a long-term experiment in Uzbekistan, suppression of invertebrate herbivores and pathogens did not result in either consistent increases in *Acroptilon* biomass across years or declines in the biomass of other native species, as one might expect if the low impact of *Acroptilon* in the native range was due to its strong top–down regulation by natural enemies. Our local scale measurements do not represent all patterns of *Acroptilon* distribution and abundance that might exist at the scale of landscapes in either range, but they do suggest the possibility of fundamental biogeographic differences in the way a highly successful invader interacts with other species, differences that are not simply related to greater biomass or reduced top–down regulation of the invader in its non-native range.

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## Introduction

A hallmark of strong invaders (sensu Ortega and Pearson 2005) is their ability to attain high population abundances over large spatial and long temporal scales and disproportionally dominate communities in their non-native ranges. Interestingly, these patterns often do not occur in the native ranges of invaders. This general observation has long intrigued ecologists (Darwin 1872; Elton 1958) and hypotheses to explain invasive success have proliferated as a result (reviewed by Mack et al. 2000; Hierro et al. 2005). However, despite a growing number of studies that have compared the productivity, biomass, density or demography between plants in their native and non-native ranges (Woodburn and Sheppard 1996; Grigulis et al. 2001; deWalt et al. 2004; Jakobs et al. 2004; Beckmann et al. 2009; Williams et al. 2010), very little is known about how these differences in abundances between ranges quantitatively translate into impacts on other species.

Many studies have been conducted in communities in the non-native ranges of invaders that correlate native abundance, productivity, community structure or some ecosystem-level process between invaded and uninvaded sites (Bruce et al. 1997; Ridenour et al. 2008; Ehrenfeld 2004; Ortega and Pearson 2005; Lu and Ma 2005; Jäger et al. 2007; Liao et al. 2008; Hejda et al. 2009). These studies are crucial for understanding invasions, but it is often difficult to determine whether differences between invaded and uninvaded sites are due to the impact of an invader per se, or due to site conditions that predispose certain areas to different degrees of invasion. Experimental studies circumvent this problem, but these are still surprisingly rare (but see Dukes 2002; Zavaleta and Hulvey 2004; Maron and Marler 2007). Rarer still are studies that quantify differences in the impacts that an invasive has on natives in its native and introduced ranges. That is, we still lack quantitative information on both: (1) the difference in relative abundance of invaders in their native versus introduced ranges, coupled with (2) how this difference in dominance influences the abundance of co-occurring plant species or overall community structure in both ranges. To our knowledge only one study has quantified the impact of an invasive species on the productivity or diversity of its neighbors in the field in both its native and non-native ranges. Inderjit et al. (2011) found that the canopies of *Ageratina*

*adenophora*, a widespread and aggressive subtropical invader, had facilitative effects on other species in its native Mexico but highly inhibitory effects in its non-native ranges in China and India. These differences were correlated with differences in the allelopathic effects of volatile organic compounds on species native to the different ranges.

Such biogeographic comparisons are a crucial starting point for understanding invasions because they shed light on the extent to which some exotics behave differently at home and abroad. For example, disturbance has long been thought to contribute to invader success (Baker 1974; Hobbs 1989; Davis et al. 2000; Mack et al. 2000). Yet whether exotics actually respond differently to disturbance in their native versus introduced ranges is unclear as biogeographic comparisons that manipulate disturbance and examine effects on exotic and native abundance in both ranges are still few (but see Hierro et al. 2006; Williams et al. 2010). If exotics respond similarly to disturbance both at home and abroad then disturbance cannot explain invader success unless the frequencies of disturbances are different between ranges (Williams et al. 2010). Alternatively, if disturbance has a more positive effect on invader abundance in the introduced than the native range, this tells us something very interesting about how the biology of an invader may differ between ranges (Hierro et al. 2006). Ultimately, these types of studies are necessary in order to lay the groundwork for testing more specific mechanistic hypotheses for what may account for differences in abundance, and impact, between ranges.

Differences in abundance or impact of an invasive species between the native and the invaded range may not only stem from different competitive effects of the invasive plant on the resident plant communities, but also from differences in other biotic interactions or in abiotic factors. One idea that has been repeatedly put forward to explain the invasion success of exotic plant species is that an invasive plant species encounters a different and usually impoverished complex of natural enemies in the introduced range, compared to the native range, and that the release of top–down regulation results in a rapid increase in distribution and abundance (Maron and Vila 2001; Keane and Crawley 2002). While studies have shown that invasive plant species harbor a smaller complex of natural enemies in the introduced than in the native range (Mitchell and Power 2003; Keane and Crawley 2002;

Liu and Stiling 2006, Wikström et al. 2006; Schaffner et al. 2011) surprisingly few studies have actually attempted to document the effect of natural enemies on the abundance and competitive ability of an invasive species in its native range (Carson and Root 2000; deWalt et al. 2004; Vilà et al. 2005; Parker and Gilbert 2007; Williams et al. 2010).

Here we compare the biomass and impact of the herbaceous perennial *Acroptilon repens* (L.) DC. (Russian knapweed) in its native and introduced ranges. *Acroptilon repens* (hereafter *Acroptilon*) is native to Turkey, central Asia and China where it can be a problematic weed in agricultural settings (Kolören et al. 2008). *Acroptilon* has been introduced throughout much of western North America and has been declared noxious in 16 western states (http://plants.usda.gov). *Acroptilon* appears to be highly competitive in its non-native range; nearly pure monocultures of this invader are not uncommon at local scales (Watson 1980), and strong competitive and allelopathic effects of the species on North American natives have been reported (Grant et al. 2003). *Acroptilon* produces a polyacetelene which inhibits the growth of other species (Watson 1980; Stevens 1986). With the exception of regularly plowed orchards and highly disturbed roadsides, such pure stands are not common in at least two parts of *Acroptilon's* native range, Uzbekistan and Turkey (U. Schaffner & J. Littlefield, *unpublished data*), suggesting that *Acroptilon* may have lower impacts on its neighbors at home. This is supported by greenhouse experiments indicating that *Acroptilon* may have stronger competitive effects on native North American species than on congeneric or confamilial native species in the native range of *Acroptilon* (Ni et al. 2010). Yet, while *Acroptilon* is almost free of herbivory in its introduced range, some 100 invertebrate herbivores have been recorded feeding on *Acroptilon* in the native range (U. Schaffner and J. Littlefield, unpublished results). The higher diversity and load of natural enemies in the native range may offer an alternative explanation for the absence of pure stands in undisturbed habitats in the native range. We compared the impact of *Acroptilon* on the diversity and biomass of native species in both ranges and explored whether the response of this invader to experimental disturbances was fundamentally different between regions. We also added native seeds to plots in both ranges to explore how the ability of natives to establish and co-occur

with *Acroptilon* might vary biogeographically. Based on the observation that *Acroptilon* tends to build up lower densities in the native than in the introduced range, we also set up a natural enemy exclosure experiment in the native range to assess the role of top–down regulation on abundance and impact of *Acroptilon*.

## Methods

In order to explore potential fundamental biogeographical differences in invader abundance and impact, in 2005 we initiated field experiments and measurements at two sites in the native range and two sites in the non-native range. Following this, in 2008 we set up similar experiments in one more site in each of the two ranges.

*Invader biomass and impact: Kattakurgan/Urgut versus Yakima, Washington*

In September and October 2005, we set up a field experiment at two sites at the Yakima Military Training Center in Yakima, Washington, USA, and at two sites near Samarkand, Uzbekistan. The two sites in Uzbekistan had to be completely re-established in April 2006, due to the destruction of plots. Sites at Yakima were "Pond" (UTM 10T 0695048 5171732) and "M.A.T.E." (UTM 10T 0695699 5172563), and each was within a different multi-hectare patch of *Acroptilon* in which the density of the invader varied substantially. Sites in Uzbekistan were "Kattakurgan" (UTM 42S 4421937 266189) and "Urgut" (UTM 42S 4371127 330525) and both were characterized by grassland which had not been disturbed for at least 10 years. The cover of *Acroptilon* at the two sites in Uzbekistan was among the highest we could find in habitats that were not continuously plowed. At the Pond and M.A.T.E. sites we randomly located 80 and 40 permanently marked $1 \times 1$ m plots, respectively, and these plots were randomly allocated to one of four treatments: (1) an unaltered control, (2) disturbance, (3) no disturbance and seeded with a native seed mix, and (4) disturbance and seeded with a native seed mix. The Pond site had 20 replicates of each treatment spread over $\approx 1$ ha and the M.A.T.E. had 10 replicates of each treatment spread over $\approx 1$ ha. Similarly, at the Kattakurgan and Urgut sites 80 and 40 $1 \times 1$ m plots

were permanently marked, respectively, and subjected to the same treatments (20 replicates of each treatment at Kattakurgan, and 10 replicates at Urgut, and at each site plots were spread over spread over ≈ 1 ha). Plots were disturbed by clipping all vegetation and then manually turning over and mixing the top 10 cm of soil and seeds were applied by hand broadcasting followed by a light raking of the seeds into the soil. For the North American sites, we added *Achillea millefolium* (yarrow; 7 g; ∼ 40,000 seeds), *Poa sandbergii* (Sandberg's bluegrass; 7 g; ∼ 15,800 seeds), *Psuedoroegneria spicata* (bluebunch wheatgrass; 25 g; ∼ 7,600 seeds), and *Lupinus sericeus* (silky lupine; 8 g; ∼ 1,000 seeds) to plots. These seeds were purchased from Landmark Native Seeds, Spokane WA. It is important to note that commercial production of native seeds may select for traits that may not fully reflect how natural interactions or other ecological responses in the field. For the Uzbek sites, we locally collected and used the following native species: *Alhagi pseudalhagi* (∼ 500 seeds each in autumn 2005 and spring 2006), *Poa bulbosa* (∼ 2,000/ ∼ 2,000 seeds), *Cynodon dactylon* (∼ 1,000/ ∼ 1,000 seeds) and *Medicago sativa* (alfalfa; ∼ 2,500 seeds/ ∼ 2,500 seeds).

At Yakima, plots were sampled on 8 September 2005, 11 April 2006, 11 July 2006, 1 April 2007, 28 June 2007, and 27 June 2008. In Uzbekistan, plots were sampled on 4 October 2005, 6 April 2006, 18 May 2006, 28 September 2006, 6 May 2007, 26 September 2007, and 15 May 2008. On 8 September 2005 at the Yakima sites and on 4 October 2005 at the Uzbek sites only *Acroptilon* was sampled because so many other species had senesced, but at all other sample dates all species were recorded. At the Yakima sites plots were disturbed and seeded on 8 September 2005 after *Acroptilon* cover was recorded, and at the Uzbek sites plots were disturbed and seeded on 6 October 2005 and again on 18 April 2006.

At all sites, to sample the cover of each species we placed a 1 × 1 m quadrat over each plot that was gridded into one hundred 10 × 10 cm squares. We measured cover as the number of squares occupied by a species. At the Kattakurgan and Urgut sites, on 16 May 2008, we harvested *Acroptilon* and native vegetation and dried them at 60°C and then weighed the biomass of each vegetation type in each plot. At Yakima, on 27 June 2008, we harvested *Acroptilon*, other exotics, and natives from 1/3 of the plots in each

treatment, dried the plants for 72 h at 60°C, and weighed them and separated each type by plot. We estimated the biomass of *Acroptilon* and natives for all plots with cover-biomass regressions.

Invader biomass and impact: Tashkent versus Whitehall, Montana

We established a second shorter term field experiment in different parts of the native and non-native ranges to see if some of the general patterns found in the first field experiment were consistent.

In early May 2008, we set up a new experiment at the Tashkent Sea, Uzbekistan (42T 4533510 5288020). In randomly located 1 × 1 m plots spread over ≈ 1 ha; the cover of *Acroptilon* and of native cover was estimated using the method described above. Subsequently, 15 plots each were randomly allocated to one of two treatments: (1) no disturbance and seeded with a native seed mix, and (2) disturbance and seeded with a native seed mix. On 3 May, the 15 plots of treatment 2 were plowed, and then the same four native species were sown into all plots at the same density as in experiment 1. On 16 September 2008, cover of all individual plant species was again estimated on all 30 plots.

On 12 December 2007, we set up a new experiment near Whitehall, Montana (12T 4047020 5083165) using the design described above. On 28 July 2009, cover of all individual plant species was estimated on all 30 plots. At Tashkent, we then harvested *Acroptilon* and all other native vegetation; whereas at Whitehall we harvested *Acroptilon* from half of the plots divided evenly among treatments and biomass was dried for 72 h at 60°C and weighed. We estimated the biomass of *Acroptilon* from cover-biomass regressions, and the biomass of natives at Whitehall from percent cover and regression equations for cover and biomass from plots at Yakima.

Impact of natural enemies in the native range

Herbivory may suppress and indirectly attenuate the competitive dominance of invaders in their native range. Therefore, in autumn 2004 we set up an experiment to exclude native natural insect herbivores and pathogenic fungi that might attack *Acroptilon* at the Kattakurgan field site. For this experiment we set up plots in *Acroptilon* patches keeping *Acroptilon*

cover at approximately 50%, a relatively high level for the native range. To assess the impact of native herbivores on *Acroptilon* performance, 36 1-m$^2$ plots were permanently marked with 12 plots each randomly assigned to following treatments: (a) control plots where only the surface of the soil around the perimeter of the plots was disturbed, (b) plots where rhizomes were cut around the perimeter of the plots to minimize effects of clonal connections on experimental results, (c) plots where rhizomes were cut around the perimeter of the plots and plants sprayed every 2 weeks between April and September, alternatively, with the systemic insecticide 'Imidachlopride' (Confidor®, Bayer, Germany) and the contact insecticide 'Dimethoate' (Rogor 40®, Omya AG, Switzerland). The two insecticides affect a slightly different spectrum of insects, and Imidachlopride also acts as acaricide and nematocide. A towel was placed below the *Acroptilon* shoots prior to insecticide application to minimize insecticide drift onto the other vegetation. The plots that were not treated with insecticides received the same amount of water as plots treated with insecticides. In a separate pot experiment conducted at the CABI Europe-Switzerland Centre in Delémont, Switzerland, we found no negative or positive direct effects of the two insecticides on *Acroptilon* above-ground biomass (U. Schaffner, *unpublished results*). The efficacy of the herbivore exclosure treatment was confirmed during the first season in 2004; the density of the gall wasp *Aulacidea acroptilonica* on the sprayed plots was zero with insecticide versus 6.4 galls/m$^2$ in the control plots (reduction 100%), the density of the mite *Aceria acroptiloni* was 2.1 infested shoots/m$^2$ versus 8.5 infested shoots/m$^2$ in the control (reduction 75%), and the density of an unidentified seed head fly was 0.5 larvae/seed head with insecticide versus 2.7 larvae/ seed head in the controls (reduction 81%). In late 2005, an additional 12 experimental plots were randomly interspersed into the ongoing herbivore exclosure experiment to test the effect of fungicide on the relative abundance of *Acroptilon* and natives; rhizomes were cut around the perimeter of the plots, and from April 2006 the *Acroptilon* plants in these plots were regularly sprayed with the systemic fungicide 'Benomyl' (Benlate®, DuPont, France). Benomyl has been shown to have minimal direct effects on plants in some studies (Paul et al. 1989) and is a recommended method for manipulating soil fungi in experiments with plants (Smith et al. 2000). However, Benomyl is a broad-spectrum fungicide that will not only reduce the abundance of pathogenic fungi, but also that of mutualistic mycorrhizal fungi. Therefore, in this experiment the effect of Benomyl should be interpreted as the overall effect of fungi on *Acroptilon*. Total above-ground vegetation was harvested each year on all experimental plots in September to determine dry biomass and seed output of *Acroptilon*, as well as the biomass of all other vegetation.

Analyses

To examine how *Acroptilon* and surrounding native plant biomass varied between North America and Uzbekistan we used a mixed model ANOVA (in proc mixed module, SAS ver. 9.2) with region (North America vs. Uzbekistan) a fixed factor and experimental location within each region as a random factor, and *Acroptilon* biomass and native biomass as dependent variables. Biomass was log + 1 transformed to meet assumptions of ANOVA. We tested the effects of disturbance and seeding on *Acroptilon* and total native cover at each of the four sites independently using two way ANOVA with disturbance and seeding as fixed factors (SPSS 19, 2010). We tested changes in total native diversity at Yakima for all seeded plots combined between April, 2006 and June 2008 (the end of the experiment) with one way ANOVA using disturbance, seeding, and date as fixed factors (SPSS 19, 2010). We tested the effects of disturbance and seeding as fixed factors on *Acroptilon* cover and native cover at each site independently with two way ANOVA.

In the natural enemy exclosure experiment in the native range, we tested the effects of herbivore exclosure and above-ground fungal exclosure on *Acroptilon* seed output, *Acroptilon* biomass, and the biomass of other species as dependent variables in Repeated Measure ANOVAs with insecticide treatment and fungicide treatment as between-subjects factors, respectively and year as a within-subjects factor.

Results

In an analysis of all sites in both ranges, *Acroptilon* biomass was approximately twice as high in plots with all treatments combined in North America compared

to plots in Uzbekistan (ANOVA, $F_{region} = 7.55$; 1,199; $P = 0.0065$). For all plots at all sites, native plant biomass was far higher in Uzbekistan than in Washington and Montana ($F_{region} = 158.5$, $df = 12.09$, $P < 0.005$). Thus the ratio of *Acroptilon* to native biomass was 25–30 times higher in the non-native range than in the native range.

Invader biomass and impact: Kattakurgan/Urgut versus Yakima

In the non-native range, with both sites from the first field experiment combined due to very quantitatively similar patterns at each site and for simplicity (hereafter we refer to these combined sites as the "Yakima site"), *Acroptilon* reached a maximum mean cover value of $86.8 \pm 1.4\%$ for all treatments combined (Fig. 1). The mean biomass at the Yakima site at the end of the multi-year experimental period was $339$ g/m$^2$ (Table 1). *Acroptilon* attained very similar mean aboveground biomass across all seeding and disturbance treatments, and there were no differences among treatment in any year. In the native range, with both sites combined (also due to very similar quantitative patterns; and hereafter we refer to these combined sites as the "Kattakurgan/Urgut site"), at the end of the experimental period the mean cover of *Acroptilon* across all treatments at the Kattakurgan/Urgut site was $24.2 \pm 1.8\%$ with a mean total biomass at the end of the experiment for both sites and all treatments combined of $158 \pm 12$ g/m$^2$ (Table 1). At the Kattakurgan/Urgut site in Uzbekistan, *Acroptilon* reached maximum mean cover values of $46.2 \pm 4.0\%$ and $45.7 \pm 5.1\%$ for the disturbance-no seeding and the disturbance-seeding treatments, respectively (Fig. 1).

Regional differences for the cover and biomass of native species (not including *Acroptilon* in its native range) were more striking. In April 2006, *before* the emergence of *Acroptilon* shoots, total summed cover for all North American native species in seeded plots was $84.4 \pm 8.8\%$ and $74.2 \pm 8.6\%$ for the disturbance-seeding and the no disturbance-seeding treatments, respectively (Fig. 1). However, after *Acroptilon* re-merged in the summer and in successive years the total summed cover of North American native species in the seeded treatments dropped to $11.0 \pm 2.4\%$ and $25.2 \pm 4.0\%$ (ANOVA testing total natives in seeded plots in April 2006 versus end of experiment, $F = 8.924$; $df = 1.93$; $P = 0.004$) with a mean cover

over the experimental period for all treatments of $9.8 \pm 4.8\%$. The mean biomass of North American natives at the Yakima site at the end of the experimental periods was $11 \pm 7$ g/m$^2$ (Table 1). In Uzbekistan, the summed cover of native species other than *Acroptilon* averaged $234.9 \pm 6.8\%$ (>10 times higher than at Yakima) for all treatments combined in May 2007, and there were no effects of seeding at any point in the experiment. At the end of the experiment the mean summed cover of all Uzbek natives other than *Acroptilon* was $159.4 \pm 4.7\%$ and the mean cover of all Uzbek natives across the duration of the experiment was $165 \pm 8.2\%$. The mean biomass of Uzbek natives, other than *Acroptilon*, was $314 \pm 28$ g/m$^2$, approximately 30 times greater than for North American natives at the Yakima sites. In North America, the mean ratio of *Acroptilon* biomass to native biomass was 30:1; whereas in the native range of *Acroptilon* in Uzbekistan the ratio was 1:2.

There were no effects of disturbance at the Yakima site on either *Acroptilon* or native cover (Fig. 1). In Uzbekistan, disturbance in April 2006 decreased *Acroptilon* cover in September 2006 from $23.3 \pm 2.9\%$ and $26.7 \pm 2.9\%$ in the no disturbance-seeding and no disturbance-no seeding treatments, respectively, to $14.4 \pm 1.8\%$ and $12.4 \pm 1.3\%$ in the same treatments (two way ANOVA, $F_{disturbance} = 20.813$; $df = 1,115$; $P < 0.001$). One year after disturbance these relationships switched so that *Acroptilon* cover in the disturbance treatments was higher than in the no disturbance treatments ($46.2 \pm 4.0\%$ and $45.7 \pm 5.1\%$ for seeding and no seeding treatments, versus $34.4 \pm 4.1\%$ and $32.6 \pm 4.0\%$ in the same treatments; two way ANOVA, $F_{disturbance} = 9.371$; $df = 1,115$; $P = 0.003$). Disturbance reduced the cover of all native Uzbek species soon after the disturbance event (For May 2006, $F_{disturbance} = 13.009$; $df = 1,115$; $P < 0.001$), and disturbed plots tended to sustain slightly lower native cover than undisturbed plots for the duration of the experiment, suggesting that in contrast to the absence of disturbance effects in its non-native range at our sites, *Acroptilon* may have acquired a relative advantage from disturbance in its native range.

As noted above, seeding had strong effects on the cover of native North American species, increasing the mean cover during the first season from $0.3 \pm 0.3\%$ and $2.4 \pm 0.4\%$ in the no disturbance-seeded and disturbance-seeded plots to 70 and 80% cover in the same treatment combinations in the first spring before

**Fig. 1** Cover of *Acroptilon repens* and total cover and species richness of native species (other than *Acroptilon* in the native range) in factorial treatments with disturbance and native seeding as factorial treatments, the Kattakuran/Urgut site in Uzbekistan and the Yakima site in Washington, USA. *Arrows* denote time at which distrubance and seeds were applied. Error bars show 1 SE
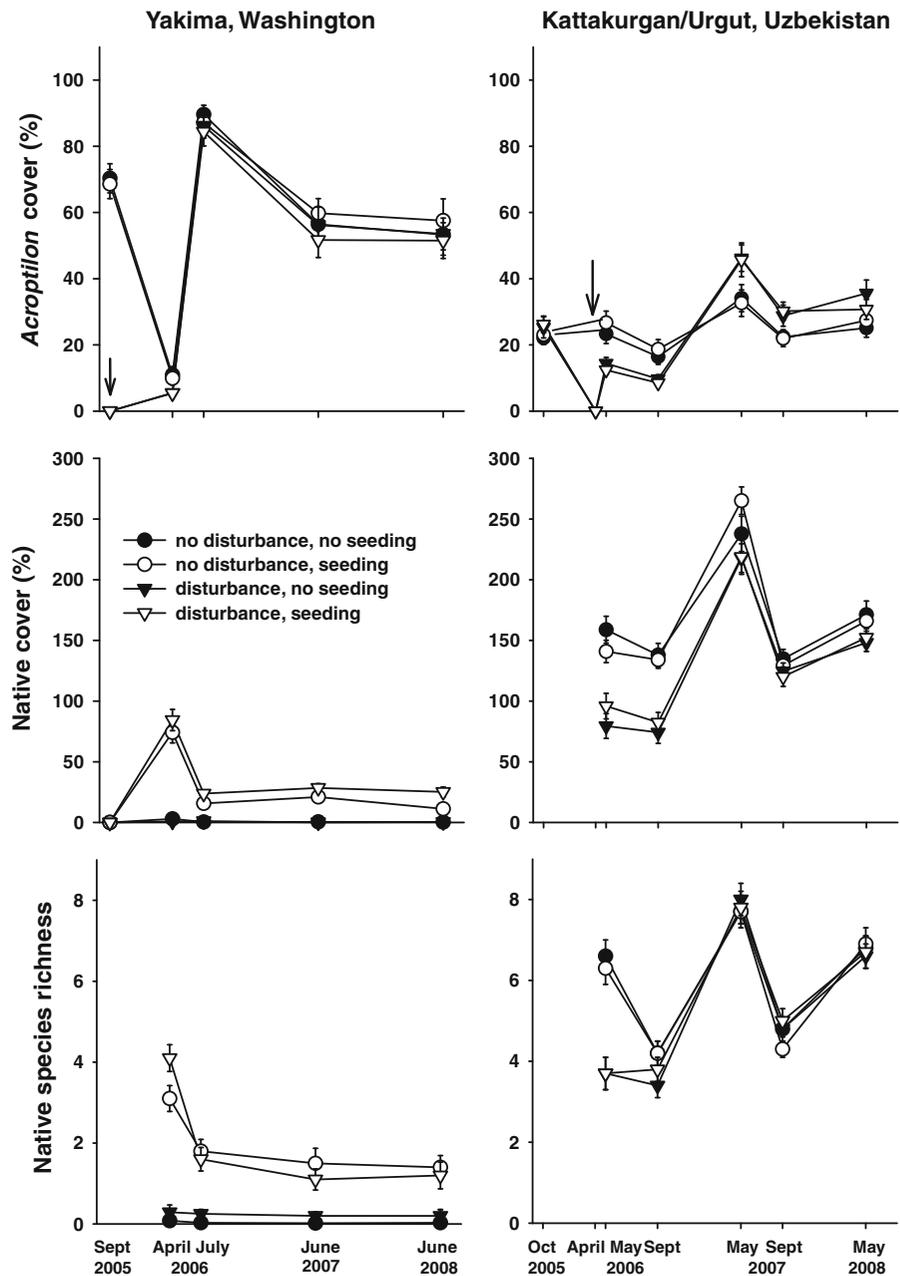


*Acroptilon* re-emerged. The cover of natives dropped substantially at the end of the first growing season after the emergence of *Acroptilon* shoots, but cover in the seeding treatments remained higher at the end of the experiment (11.2 ± 2.4% and 25.2 ± 4.0% in the no disturbance-seeded and disturbance-seeded plots). However, surviving native species were very small in size, usually existing beneath a canopy of *Acroptilon*. This is reflected in the dramatic differences in biomass

between the native and non-native ranges (Table 1). Seeding increased mean species richness of North American natives from 0.03 and 0.2 species per m² to 1.4 and 1.2 species per m². The total number of North American species found in plots (all plots contained *Acroptilon*) at the Yakima sites was 7, including those that were seeded. Seeding had no effect on the species diversity in plots in Uzbekistan, and the total number of species in plots at the Uzbek sites was 45.

**Table 1** Comparisons of the biomass of *Acroptilon repens*, natives, and other exotics among sites in the native range of Uzbekistan and the non-native range of North America for *Acroptilon* (see Figs. 1, 2)

|  | North America | | Uzbekistan | |
|---|---|---|---|---|
|  | Yakima | Whitehall | Kattakurgan/Urgut | Tashkent |
| Acroptilon biomass (g/m$^2$) | 339 ± 45 | 178 ± 20 | 158 ± 12 | 116 ± 18 |
| Total number of native species | 7 | 8 | 45 | 31 |
| Summed native cover (%) | 23 ± 6 | 15 ± 3 | 165 ± 9 | 146 ± 13 |
| Native biomass (g/m$^2$) | 11 ± 7 | 7 ± 5* | 314 ± 28 | 282 ± 53 |
| Summed biomass of other exotics (g/m$^2$) | 56 ± 11 | 28 ± 9 | – | – |
| *Acroptilon*/native biomass ratio | 31:1 | 25:1 | 1:2 | 1:2 |
| *Acroptilon*/"other" biomass ratio | 9:1 | 3:1 | – | – |

* Native biomass was derived from cover measured at Whitehall, but cover-biomass regressions calculated from Yakima data

Total native cover 3 years after the treatments were imposed was not correlated with *Acroptilon* cover, neither at the Yakima site (Fig. 2, $R^2 = 0.018$; $P = 0.372$) nor at the Kattakurgan/Urgut site ($R^2 = 0.007$; $P = 0.392$).

**Invader biomass and impact: Tashkent versus Whitehall**

In the second and shorter term field experiment most basic biogeographic differences observed in the first experiment were consistent qualitatively but somewhat different quantitatively. The strongest exception to this was the lack of a significant effect for seeding at either the Whitehall, Montana or the Tashkent, Uzbekistan sites. So few individual plants were found for seeded native species in either region we could not include this treatment in the analyses or figures. There was no effect of disturbance on the cover of *Acroptilon* at the Whitehall, Montana site, and the total cover of *Acroptilon* across all treatments was 88.0 ± 2.4%, with a mean biomass of 178 ± 20 g/m$^2$ (Fig. 3, Table 1). There was also no effect of disturbance on the cover of *Acroptilon* at the Tashkent site, and the cover of *Acroptilon* across all treatments was 26.8 ± 5.4% with a mean biomass of *Acroptilon* across all treatments of 116 ± 18 g/m$^2$.

Native abundance at the Whitehall site was low; 5.6 ± 1.9% cover and 1.1 ± 0.3 species in undisturbed plots and 19.6 ± 7.0% cover and 1.4 ± 0.4 species in disturbed plots (Table 1), and there was no effect of disturbance on the mean summed native cover per plot. The total number of native species found in all Whitehall plots combined was 8. Native
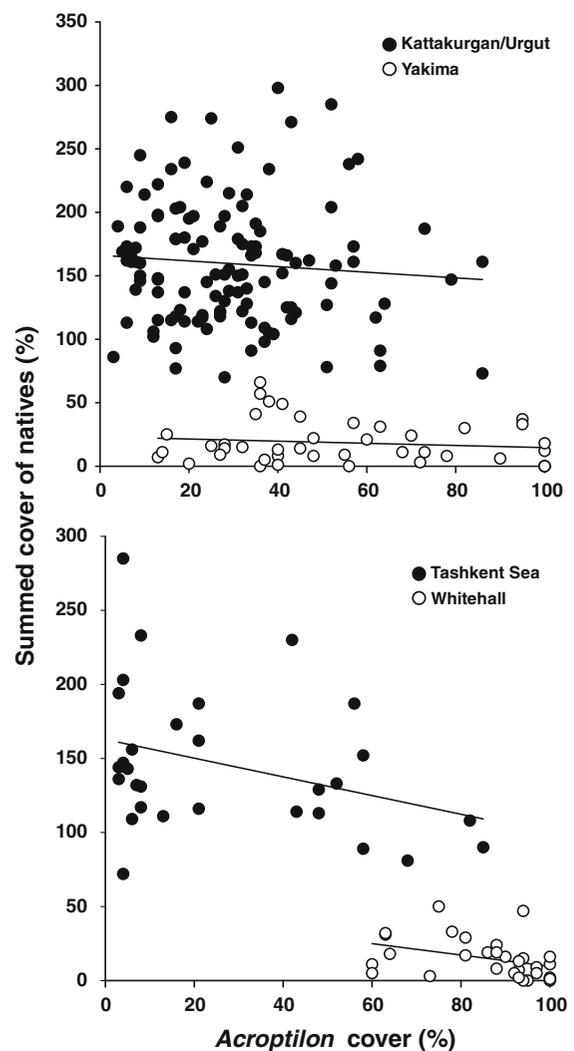


**Fig. 2** Relationships between *Acroptilon repens* cover and the total cover of natives at two sites in the native range and two sites in the non-native range
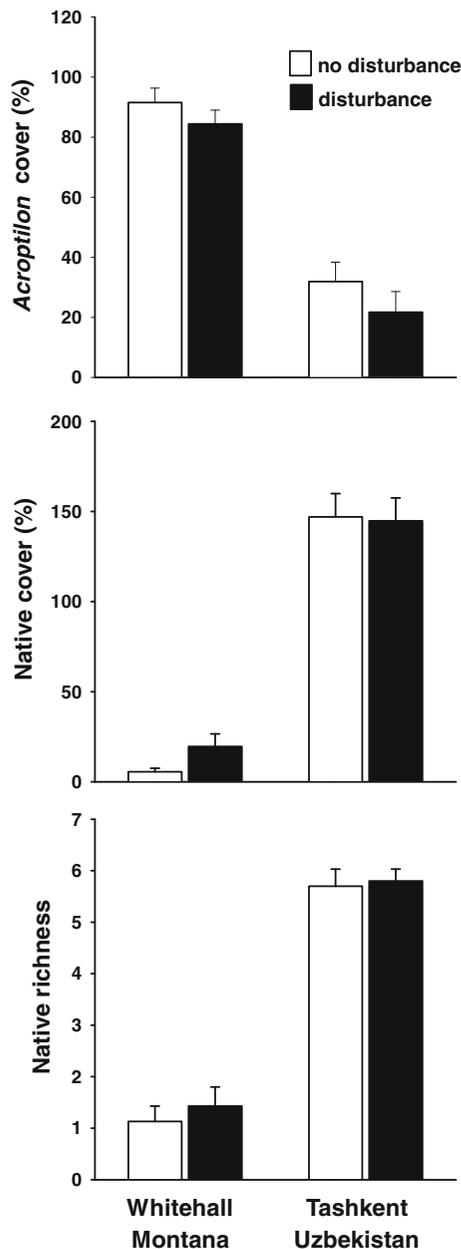
**Fig. 3** Cover of *Acroptilon repens* and total cover and species richness of native species (other than *Acroptilon* in the native range) with and without disturbance, at the Tashkent site in Uzbekistan and the Whitehall site in Montana, USA. *Error bars* show 1 SE

cover at the Tashkent site was roughly 10 times higher than at Whitehall; $147 \pm 12.9\%$ with $5.7 \pm 0.3$ species per plot in the disturbed plots and $144.8 \pm 12.7\%$ cover and $5.8 \pm 0.2$ species per plot in the undisturbed plots. There was no effect of disturbance

on native species cover at the Tashkent site. Using the cover-biomass regression equations from Yakima we estimated the mean native biomass at Whitehall to be $7 \pm 5$ g/m$^2$. In contrast the mean native biomass at Tashkent was $282 \pm 53$ g/m$^2$. The total number of species in the plots at the Tashkent site was 31. At Whitehall, the mean ratio of *Acroptilon* biomass to native biomass was 25:1; whereas in Tashkent the ratio was 1:2.

After one season, total native cover was weakly negatively correlated with *Acroptilon* cover at the Whitehall site in Montana (Fig. 2, $R^2 = 0.140$; $P = 0.042$), and marginally negatively correlated with *Acroptilon* cover at the Tashkent Sea site in Uzbekistan ($R^2 = 0.115$, $P = 0.066$). Total native cover was much lower across all cover values of *Acroptilon* at the Yakima site in Washington than the Kattakurgan/Urgut site in Uzbekistan.

Impact of natural enemies in the native range

Excluding native herbivores led to a consistently higher seed output of *Acroptilon* throughout the experiment (Repeated Measures ANOVA, $F_{insecticide} = 23.72$; $df = 1.22$; $P < 0.001$; Fig. 4). Above-ground biomass of *Acroptilon* was also significantly affected by the insecticide treatment (Repeated Measures ANOVA, $F_{insecticide} = 16.04$; $df = 1.22$; $P = 0.001$). When analyzing individual years separately, *Acroptilon* above-ground biomass was only significantly higher on insecticide-treated plots in 2006 (ANOVA for 2006, $F_{insecticide} = 7.31$; $df = 1.22$; $P = 0.013$). Biomass of the native vegetation (excluding *Acroptilon*) did not differ between insecticide-treated and control plots (Repeated Measures ANOVA, $F_{insecticide} = 0.17$; $df = 1.22$; $P = 0.898$).

Excluding leaf and shoot pathogens during two growing seasons did not affect biomass or seed output of *Acroptilon*, nor did it affect the biomass of the native plant species (Repeated Measures ANOVA, all $P > 0.4$).

**Discussion**

The most striking results from our biogeographic comparison of the community-scale impacts of *Acroptilon* was that the biomass of *Acroptilon* was about twice as high in the non-native range as in the native range, and
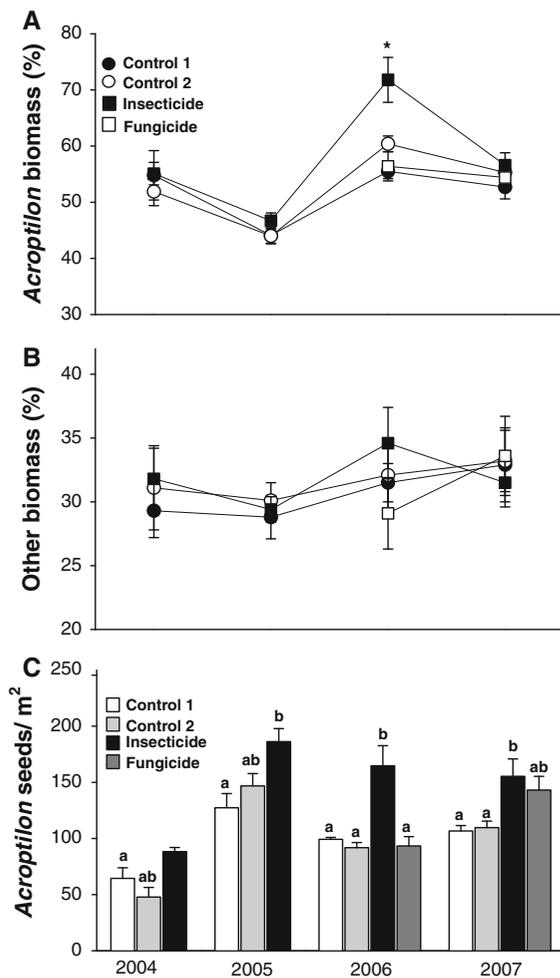
**Fig. 4** (**A**) Biomass of *Acroptilon repens*, (**B**) biomass of other vegetation, and (**C**) seed production of *Acroptilon* in controls and experimental treatments excluding invertebrate herbivores or fungal pathogens. *Error bars* show 1 SE

that the biomass of native species was roughly 30 times lower in the non-native range than in the native range of *Acroptilon*. This correlative pattern could have been caused by any number of mechanistic processes that we have not addressed: e.g. unknown historical events such as difference in disturbance events or disturbance type, enemy release, or differences in the fundamental competitive interactions between *Acroptilon* and the natives of the different regions. However, the suppression of insect herbivores in the native range did not lead to the consistent and dramatic effects that one might predict if *Acroptilon* density or biomass in the native range is controlled by natural enemies. Release from seed predation may contribute to *Acroptilon's* success

but is unlikely to account for the dramatic differences in *Acroptilon* densities between the two ranges. The reason for this is that seedling recruitment may be fairly rare for this species, as we never observed recruitment in *Acroptilon* patches in the native or the invaded range (U. Schaffner and J. Littlefield, pers. obs., R.M. Callaway pers. obs.). The difference in *Acroptilon* impact between the native and introduced range was not driven entirely by the divergence between continents in *Acroptilon* biomass. The abundance of native species *per unit biomass* of *Acroptilon* was an order of magnitude lower in the non-native range. Also, in the introduced range the cover of native vegetation did not increase to any substantial degree with reduced *Acroptilon* biomass or cover. Such strikingly different behavior in the native and non-native ranges suggests that either *Acroptilon* is dramatically favored over natives at the North American site by greater access to resources untapped by natives or release from strong competitors that affect the distribution and abundance of *Acroptilon* in its native communities. Additionally, release from natural enemies could allow *Acroptilon* to increase its competitive effects. However, the natural enemy exclosure experiment carried out in the native range did not provide evidence that the lower abundance and competitive ability of *Acroptilon* in the native range is due to significant top–down regulation by natural enemies, and we did not find a negative correlation between *Acroptilon* abundance and native species abundance in the native range. Rather, our results and those reported by Ni et al. (2010) suggest that the different behavior of *Acroptilon* in the native and non-native ranges is due to inherent differences in the way the invader competes with species in the two ranges.

We want to emphasize that measurements such as ours at a local scale cannot possibly represent all patterns that might exist at the scale of landscapes. As an extreme example, at the scale of the states of Montana or Washington, *Acroptilon* has almost certainly only increased species richness via the addition of itself to regional species pool; to our knowledge evidence for invasive plant species driving the complete extinction of any native species is exceedingly rare (Sax et al. 2002). At more local scales in North America (hectares perhaps) *Acroptilon* may either exist at very low densities and have minimal impacts, or exist at densities or biomasses that appear to be even higher than at our field sites. It is important to recognize the limitations of extrapolating from small field

experiments to continents; however, other biogeographic comparisons of *Acroptilon* abundance are even more dramatic than ours. For example, Watson (1980) reported *Acroptilon* stem densities in North America from 100 to 300 shoot per m$^2$; whereas even in agricultural settings in its native range in Turkey stem densities were measured at 5.8–26.8 shoots per m$^2$ (Kolören et al. 2008). Regardless, variation at local scales may be even more extreme and difficult to quantify in the native ranges of *Acroptilon* because it appears to be even patchier than in many parts of its non-native range. Thus we are not arguing that our results are representative of large landscapes in either the native or the non-native range, but instead that they represent reasonably comparable sites in the two ranges and at these two sites abundance and impact of the invader is far greater in the non-native range. But since all invasions are essentially local, it makes sense to assess competitive interactions and impacts at this scale. The challenge for the field of invasion biology is to assess the constancy of local biogeographic differences in the ecology of invaders when scaled up to regional levels.

In a meta-analysis of 42 studies, Liao et al. (2008) found that exotic invasion correlated with a mean 83% increase in annual net primary productivity (ANPP) (also see Rout and Callaway 2009). Similarly, Maron and Marler (2008) found that experimental invasion of constructed native communities substantially increased total plot biomass. At our Yakima site, the mean live aboveground biomass, a close approximation of ANPP, was 350 g/m$^2$ in 2008, much higher than the mean annual productivity of Palouse prairie in eastern Oregon (28–104 g/m$^2$ depending on rainfall; Sneva and Hyder 1962), ANPP in Palouse grassland at near Richland, Washington (80 g/m$^2$; Sims et al. 1978), or that of intermountain prairie in the Blackfoot Valley of Montana (160 g/m$^2$; J. M. Maron, *unpublished data*). In contrast, the total live aboveground biomass of *Acroptilon*-invaded plots at Whitehall, Montana was 190 g/m$^2$ in 2009, very similar to the ANPP of 188 g/m$^2$ measured for the same mixed grass prairie type at Fort Keogh Livestock and Range Research Laboratory, Miles City, Montana (Vermeire et al. 2009) suggesting that *Acroptilon* may not always increase total ANPP.

The virtual absence of native recruitment at Yakima without very heavy seeding, even immediately after disturbance, suggests that *Acroptilon* may ultimately exhaust the seed bank of natives. Seed limitation can have strong effects on community composition in native communities (Tilman 1997; Zobel et al. 2000; Martin and Wilsey 2006) and invaders may strongly exacerbate seed limitation. Bard et al. (2004) and Sheley and Half (2006) found that seeding, with supplemental watering, substantially improved the establishment of natives after suppression of *Centaurea stoebe*. Seabloom et al. (2003) found that native annual forbs in Californian serpentine grassland were strongly seed limited; suggesting that dominance by exotic species may not be only due to direct competitive interactions, or for that matter any process in which these exotic act as "drivers" of invasion. However, in all such cases direct competition may be what ultimately eliminated native seeds from the seed bank. In the field, Grant et al. (2003) found that natives started from experimentally applied seed were more suppressed in *Acroptilon* stands in Colorado, USA than natives started as seedlings.

If the strong competitive effects of *Acroptilon* on other plant species are important for the impact of the invader in its non-native range, might *Acroptilon* act as a selective agent on native North American species? Mealor and Hild (2006) compared a large number of gene loci for populations of the natives *Hesperostipa comata* and *Sporobolus airoides* collected in old *Acroptilon* patches to those for populations collected outside the patches. Their results indicated that a small portion of loci may be linked to genes undergoing selection caused by *Acroptilon* invasion. In a second experiment, *S. airoides* genets collected from old *Acroptilon* patches showed consistently greater growth when transplanted into other patches of *Acroptilon* than genets collected patches with no *Acroptilon*, suggesting that some native species have the potential for adaptation to coexist with this invader (Mealor and Hild 2007; also see Callaway et al. 2005).

Experimentally applied disturbance moderately increased *Acroptilon* cover in the last year of the experiment in Kattakurgan/Urgut (but not in Tashkent), but without a corresponding response by the other species. This positive response to disturbance is in line with the perceived early successional life history of *Acroptilon* in its native range. Furthermore, despite the lack of a disturbance effect in our already highly invaded experimental systems in Montana and Washington, *Acroptilon* invasion in North America appears to be much more intense in highly disturbed

communities (Maddox et al. 1985). We suspect that the lack of a disturbance effect in the non-native range ranges in our experiments is because the dominance and impact of *Acroptilon* at our sites was so strong that disturbance effects were overwhelmed. Hierro et al. (2006) found that disturbance increased *Centaurea solstitialis* abundance and performance far more in nonnative ranges than in the native range, a response that appeared to be related to stronger inhibitory effects of soil biota in the native range.

Our results are among the few to indicate a strong biogeographic shift in the basic community ecology of an invader—its abundance and how it interacts with other species (but see Inderjit et al. 2011). This does not mean that *Acroptilon*, or other invaders, are somehow fundamentally "different" than other species, but instead, because of different suites of abiotic and biotic constraints and factors they participate in strikingly different ecological processes in their native and non-native ranges. Patterns such as these indicate important biogeographic differences in the community ecology of invaders (Brooker et al. 2009). Our results (also see Ni et al. 2010), suggest that disproportionally strong competitive ability may contribute to the competitive success of *Acroptilon* in North America, which adds to the growing body of evidence that some exotic invasions involve biogeographic shifts in how the invader interacts with other species.

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