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Phenology as a basis for management of exotic annual plants in desert invasions

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Summary

1. Exotic annual plants are an increasingly important ecological issue and new, creative approaches to management are required. In desert ecosystems of the southwestern USA, the forbs *Brassica tournefortii, Erodium cicutarium* and *Schismus* spp. dominate and alter native annual communities. Hand weeding *B. tournefortii* is currently the most common control method employed, but weeding is inadequate and expensive for managing large-scale invasions. New methods must be developed to conserve and restore desert ecosystems.

2. Exotic annuals in desert systems have rapid germination and phenology compared to natives, indicating that a window for selective control of exotic annuals may occur immediately after exotic seedling emergence. We tested the role of timing in control methods by comparing a cotyledon-stage glyphosate application to a bolting-stage application and to hand weeding *B. tournefortii*, plus an untreated check. Treatments were tested at two sites dominated by either exotic or native annuals and followed for 2 years; early application was repeated the second year. Cover and richness were evaluated during seedling and peak flowering stages underneath and between shrubs.

3. Early glyphosate application did not affect native cover, but did reduce exotic cover. Late herbicide negatively impacted both exotics and natives. Natives had little positive response, and then only through hand weeding under shrubs, but the same treatment caused an increase in the exotic *E. cicutarium.*

4. *Synthesis and applications*. The rapid phenology of exotic annuals may be exploited to control exotics while minimizing impacts on native plants in desert communities. This approach may be useful for other invasions in other ecosystems by species with rapid, early germination, or may act as a supplement to improve the efficacy of existing management regimes.

Keywords: *Brassica tournefortii*, ephemerals, *Erodium cicutarium*, forb, grass, herbicide, Sahara mustard, *Schismus*, timing

Introduction

Exotic annual plants have invaded and transformed ecosystems world-wide, and continue to threaten the structure and function of native communities (Lonsdale 1999; Ricciardi 2007). Plant invasions are often attributed to trait differences between the invader and members of the invaded plant community including differences in reproduction (Gurvich, Tecco & Diaz 2005), competitive ability (van Kleunen, Weber & Fischer 2010), resource use (Funk & Vitousek 2007) and phenology (Godoy *et al.* 2009), among others. Targeting these differences can improve management efforts and minimize impacts to native communities (Byers *et al.* 2002).

Desert biomes have traditionally been among the least impacted by invasions (Lonsdale 1999), but exotic annuals have rapidly invaded some deserts in the last two decades and are now a major source of concern (Schiermeier 2005; Craig *et al.* 2010). Although exotic annuals have been shown to have negative impacts on native annual species and alter ecosystem function in deserts (Brooks 2000; Barrows *et al.* 2009), land managers are concerned that control methods will impact the native plant community more than will competition with exotics. Few options are available for controlling these species, and most methods have not been rigorously tested. However, neglecting control of exotic species increases invasive populations, perpetuating the risk of widespread invasion and altered landscapes.

Impacts on native forbs in the southwest deserts of the USA occur from a small group of exotic species, including *Schismus* spp. (*S. barbatus* and *S. arabicus*, annual grasses), *Brassica*

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tournefortii and *Erodium cicutarium* (annual forbs). Barrows *et al.* (2009) found that *B. tournefortii* had negative effects on all native annual plants measured in Coachella Valley dunes, including an 80–90% reduction of flowers and fruits in native forbs. *Erodium cicutarium* and *Schismus* spp. also impact native annual plants in the Colorado Desert (Steers 2008). Furthermore, shrubs are known to facilitate these species by creating resource-rich islands in the landscape (Holzapfel & Mahall 1999). As beneficial microsites, undershrub annual communities are most prone to invasion (Fowler & Whitford 1996; Brooks 1999b).

Although *Schismus* spp. and *E. cicutarium* are common, *B. tournefortii* is still infrequent or absent in much of the southwest, offering a unique opportunity to prevent it from further spread. Management of *B. tournefortii* is essential to remove it from sensitive areas, such as the critical sand dune habitat of the Coachella Valley of California (Barrows *et al.* 2009). Hand weeding is currently used to control small infestations of *B. tournefortii* in desert ecosystems (Brooks, Draper & Trader 2006). Hand weeding has also been used in experiments to study the effects of *B. tournefortii* on native communities in the Coachella Valley (Barrows *et al.* 2009). However, hand weeding is labour-intensive, expensive, and cannot easily be applied to large (> 1 ha) areas. Moreover, hand weeding produces large amounts of biomass that requires disposal elsewhere to prevent local reseeding. Finally, only *B. tournefortii* can be hand weeded effectively because other exotics, such as *E. cicutarium* or *Schismus* spp., are too small and widespread. For these reasons, other effective strategies must be vigorously pursued.

Herbicides are consistently more cost-effective than hand weeding but their use in desert wildlands has been limited by concerns about impacts on sensitive species (California Native Plant Society, 2008). However, herbicides disturb the soil less than hand weeding, and as soil disturbance often promotes invasive exotic plants, hand weeding can encourage rather than discourage some exotic species (Hobbs & Huenneke 1992; Steers & Allen 2009). While herbicides may impact native species, they can reduce exotic species in the desert for years following application (Allen *et al.* 2005).

Exotic annuals in desert ecosystems, such as *Erodium* spp., generally have more rapid phenology than native annual species (Burk 1982; Jennings 2001; DeFalco *et al.* 2003; Marushia 2009). They often germinate rapidly (Bartolome 1979) and emerge before most native forbs (DiTomaso 2007). Native desert forbs often have particular environmental requirements for germination (Beatley 1967, 1974; Venable, Pake & Caprio 1993; Adondakis & Venable 2004). In contrast, invasive species that are not native to the desert may have broad germination requirements and/or rapid emergence (Blackshaw 1992; Gutterman 1996, 2001; Bangle, Walker & Powell 2008; J.S. Holt & R. Tayyar, unpublished data). Inouye, Byers & Brown (1980) found that *E. cicutarium* was among the first cohort to germinate and contributed to a large, early proportion of biomass. *B. tournefortii* has high rates of rapid, early emergence (Marushia 2009). This difference in phenology between exotic and native species could create a window of opportunity for management during the period between exotic and native emergence (Steers & Allen 2009). Removing exotic species just after emergence could prevent impacts to natives from competition and reduce the number of exotic plants overall, even if later rain events produced new cohorts (Steers 2008; Steers & Allen 2009).

Although invasive plants in other ecosystems may also have rapid germination and emergence, differential emergence patterns between exotics and natives in deserts, as well as sparseness of vegetation overall and the critical need for control of invasives make this ecosystem particularly well suited for testing a phenologically based approach to management. The purpose of this research was to test the most common method of *B. tournefortii* control, hand weeding, against two herbicide application methods using glyphosate. These included an early application intended to take advantage of rapid phenology in exotic species and a bolting-stage application intended to prevent seed set. We tested these treatments in resource-rich shrub understorey and resource-poor shrub interspace microsites, and also contrasted treatments in one heavily invaded desert community and one less invaded community that has the same exotic species present. We hypothesized that early application would preferentially remove exotic annuals with little impact on native forbs, but that late application would impact all species equally. We hypothesized that hand weeding would have the least impact on the native annual community, but would also have no effect or an increasing effect on exotic annuals in the following year due to disturbance.

Materials and methods

STUDY SITES

Two *Larrea tridentata* communities were chosen. Snow Creek is located at the western edge of the Colorado Desert in the Coachella Valley (33°54′04.00″ N, 116°40′42.98″ W) and often has greater precipitation than much of the low desert, an average of 12–23 cm from October to April (Western Regional Climate Data Center, 2009). This site is heavily invaded by the exotic species *Schismus* spp., *E. cicutarium,* and *B. tournefortii*. The second site, Willow Hole (33°53′29.76″ N, 116°27′31.63″ W) is also in the Coachella Valley; its average precipitation is 11 cm during the winter (Western Regional Climate Data Center, 2009). Willow Hole is dominated primarily by native species and *B. tournefortii*, with varying cover of *Schismus* spp. and infrequent patches of *E. cicutarium*. Both sites are essentially flat, located in stabilized dunes with sandy soils, and experience some human disturbance.

Temperature and rainfall were recorded with two HOBO temperature sensors (Onset Computer Corporation, PO Box 3450, Pocasset, MA 02559-3450, USA) and two tipping-bucket rain gauges connected to a HOBO event recorder. Data for Willow Hole in 2007–08 was collected from the nearby north Palm Springs NOAA weather centre (Western Regional Climate Data Center, 2009).

EXPERIMENTAL DESIGN

Exotic weed control experiments were conducted at each site in the winters of 2007–08 (year 1) and 2008–09 (year 2). The experiments were arranged as randomized complete block designs with four treatments (including an untreated check) in 12 blocks for a total of 48 plots per site. Treatments included hand weeding, early herbicide application, and late herbicide application. Blocks consisted of four loosely grouped 8 m^2 plots, each plot centered on a creosote shrub and laid with perimeters parallel to the compass directions. Plots were a minimum of 2 m from each other, usually *c.* 15 m apart.

Previous research has shown differences between annual communities underneath creosote shrubs (undershrubs) vs. between shrubs (interspaces) (Brooks 1999b, 2000); therefore, these two microsites were sampled and analysed separately. In each plot, four 1 × 0·5 m subplots were placed, two in the interspace and two under shrubs. Undershrub subplots were placed on the north and south creosote canopy edges to control for solar angle. Large bare patches of poor soil occur naturally between shrubs, so interspace subplots were deliberately placed in vegetated patches to record the maximum treatment response. Untreated and early herbicide plots were especially heterogeneous in year 1; therefore, random subplots were added by tossing a plot frame into plot interspaces and orienting the frame to the nearest vegetated patch. For untreated plots, one subplot was added (three total); for early herbicide treatments, two subplots were added (four total).

All plots from year 1 were followed in year 2 using the marked subplots. In addition, the early herbicide treatment was repeated in a new plot added to each block at each site, with two marked subplots in each shrub understorey and interspace. No random subplots were added in year 2.

MANAGEMENT TREATMENTS

Year 1

The first rain event was *c.* 4 cm at Snow Creek and *c.* 2·8 cm at Willow Hole on 30 November 2007 (Fig. S1 Supporting Information). Early herbicide treatments were applied on 21 and 22 December at Willow Hole and Snow Creek, respectively. All seedlings were at the cotyledon stage at the time the early glyphosate treatment was applied. Some native seedlings were observed, although a formal census of seedlings present was not taken. Glyphosate (Roundup Pro, Monsanto Co., St Louis, MO, USA; 41% a.i.) was mixed at 21 mL L^{-1} water with a blue dye added to mark the spray pattern. Hand-pump sprayers (Solo 456 sprayers, 5100 Chestnut Ave., Newport News, VA 23605, USA) were used to apply a light, even mist over the entire treated plot, avoiding shrubs but spraying underneath canopy edges. At Snow Creek, one block was omitted due to lack of herbicide; the 11 treated plots received a total of 2589 mL a.i. ha^{-1}.

Brassica tournefortii hand weeding occurred at the same stage favoured by land managers, when rosettes were flowering and beginning to set seed, but before seeds were viable. Rosettes pre-bolting are difficult to pull, and rosettes pulled post-seed set must be removed to prevent reseeding the site. Hand weeding was limited to subplots plus a 0·5-m^2 weeded buffer zone. Willow Hole was weeded on 21 February while Snow Creek was weeded on 22 February 2008.

Late herbicide application occurred at the same rosette stage as hand weeding, the typical stage recommended for treating annual forbs with glyphosate. All *B. tournefortii* and *E. cicutarium* were sprayed before seeds were viable. Plants were sprayed with the same concentration of glyphosate as the early herbicide treatment using a pressurized gas backpack sprayer (R&D Sprayers, Model C., 419 Hwy 104, Opelousas, LA 70570, USA). The gas sprayer delivered a finer, more consistent mist of 3955 mL a.i. ha^{-1}. The entire 8 m^2 plot area was sprayed at Snow Creek, while at Willow Hole only the patches with exotic annuals were sprayed, again avoiding large bare patches. Both sites were treated on 23 February 2008.

Year 2

Initial rainfall occurred on 25 November 2008. Snow Creek received 2·4 cm, while Willow Hole received only 1·1 cm (Fig. S1). Herbicide was applied in the newly established plots at Snow Creek on 4 December. However, limited germination and high winds delayed the application date at Willow Hole to 27 December 2008. Both treatments used the same glyphosate concentration, backpack sprayer and rate as in year 1.

DATA COLLECTION AND ANALYSIS

Year 1

Richness and percentage cover of all species, bare ground and litter were collected on all subplots at the peak of native forb flowering. Percentage cover was collected by estimating the total cover per species per subplot. Estimations were calibrated among data collectors to the lead investigator's estimates at the beginning of each collection day, and re-checked frequently throughout data collection. Consensus was considered acceptable if estimates were within *c.* 1% error for cover under 10%, *c.* 5% error for 10–50%, and *c.* 10% error for 50–100%. The same investigator led all data collection. Data were collected at Willow Hole on 6 and 7 March 2008 and at Snow Creek on 10, 11 and 13 March 2008. Data for late herbicide treatments were collected on 15 March. Data were not collected at the seedling stage.

Year 2

Data were collected at the seedling stage during the early herbicide treatment in addition to data collection at peak flowering. For seedling data, 0·25 m^2 frames were placed at the centre of each untreated subplot. Species richness was collected for all seedlings in each subplot. Seedling data were collected on 5 December 2008 at Snow Creek and on 27 December 2008 at Willow Hole.

Because the subplot size used at peak flowering was larger than the subplots used for seedling data, comparisons of richness composition were made by calculating the proportion of native richness per plot at both the seedling and mature flowering stages. Proportions were arcsine transformed and analysed using a *t*-test with stage of data collection as the independent variable. Differences between sites and north/south plots were tested using them as grouping variables within the analysis.

Post-treatment data were collected on all plots at peak native flowering, including all of the plots treated in year 1 and the new early treatment from year 2. Richness and percentage cover were collected on 9–13 March 2009 at Willow Hole and 16–17 March 2009 at Snow Creek.

Data were analysed in JMP (SAS Institute, SAS Campus Drive, Building S, Cary, NC 27513, USA) using analysis of variance (ANOVA) after meeting assumptions of the test. The first model was a mixed-model ANOVA constructed using year of data collection, site (Willow Hole vs. Snow Creek), treatment (early and late herbicide, hand weeding, and untreated control) and microsite (shrub interspaces and under shrubs) as independent variables and block as a random effect nested within all of the above independent variables. Absolute percentage cover of bare ground, litter, *B. tournefortii, E. cicutarium, Schismus* spp., total exotic cover and total native cover were independently tested as dependent variables. Because several two and three-way interactions occurred between independent variables (Table S1), data were then analysed separately for each year, site, and microsite. Interspace subplot cover values were averaged within plots and treatments within years and sites, and compared across treatments using ANOVA with treatment as the independent variable. North vs. south undershrub values were tested as a nested independent variable within treatment, analysed with ANOVA across treatments. Early glyphosate treatments that were repeated in new plots during year 2 were not included in ANOVAS because they were not comparable to treatments from year 1. Instead, year 2 early glyphosate was compared only to year 2 untreated plots. Mean separations between plant types and treatments were tested using a *t*-test or Tukey's HSD test for multiple comparisons. Because some subplots in year 2 could not be definitively matched to subplots in year 1, change in cover of each variable across years was tested using *t*-tests rather than repeated measures.

Results

SEEDLING CENSUS, YEAR 2

The seedling census at each site showed that there were differences in proportions of native richness at the seedling stage, when plants were treated with the early herbicide, compared to richness at peak flowering at both sites (Table 1). The proportion of exotic richness at the time of herbicide treatment was comparable to peak flowering, but there was an increase in native species richness after early treatment, especially at Willow Hole (Table 1).

INTERSPACE MICROSITES

Year 1

At the time of peak native flowering and data collection, exotics were the dominant ground cover between shrubs at Snow Creek, while natives were dominant at Willow Hole (Figs 1a,b and 2a,b). Of the exotic species at each site, Snow Creek interspaces were dominated by *Schismus* spp. and *E. cicutarium* as much or more than *B. tournefortii* (Fig. 3a–c). In contrast, *B. tournefortii* was the dominant exotic at Willow Hole both underneath and between shrubs (Fig. 4).

Exotic cover was reduced in all treatments at both sites, except for hand weeding in interspaces at Snow Creek (Figs 1–4a to c, Tables 2 and 3). Interspace subplots at Snow Creek had layers of *Schismus* spp. and *E. cicutarium* underneath the *B. tournefortii*; therefore hand weeding *B. tournefortii* had little impact on the overall cover of exotic species (Figs 1b and 3b,c). However, hand weeding removed nearly all exotic cover between shrubs at Willow Hole (Figs 2b and 4b,c). Herbicide increased bare ground at both sites ($F_{3,283}$ = 5·54, P = 0·001, data not shown).

Total native cover was not reduced by early glyphosate at either Snow Creek or Willow Hole, nor was it increased by any of the exotic control techniques in shrub interspaces (Figs 1a and 2a, Table 2). At Snow Creek, native cover was retained in the late glyphosate treatment compared to the untreated control but was lower than native cover in hand weeded subplots (Fig. 1a). Native cover was reduced by late glyphosate application at Willow Hole (Fig. 2a). Early herbicide was less effective than late herbicide in removing exotic cover (Figs 1b and 2b, Tables 2 and 3). Late herbicide removed all three exotic species at both sites (Figs 3a–c and 4a–c), but also reduced native cover (Figs 1a and 2a). *Erodium cicutarium* was controlled by early glyphosate application, while *Schismus* spp. were best controlled by late glyphosate (Figs 3b,c and 4c). Early glyphosate did not differ from late in reducing *B. tournefortii* at Snow Creek, but *B. tournefortii* mortality was greater in late treatments than early at Willow Hole, indicating that some *B. tournefortii* emerged after or survived early application there (Figs 3a and 4a). Early herbicide treatment also produced some shifts in the dominance of different native annual species (data not shown). Although height and density were not recorded, observations suggested that native plants were larger and less dense in early glyphosate plots than in control plots (R. G. Marushia, pers. obs.).

Hand weeding removed only *B. tournefortii* and had no effect on either *E. cicutarium* or *Schismus* spp. at Snow Creek (Fig. 3a–c). The same removal treatment at Willow Hole resulted in an additional small decrease in *Schismus* spp. (Fig. 4c).

Table 1. Proportion of native richness at seedling and flowering stages in untreated plots at both sites in 2008–09. *T*-tests between seedling and mature stage native richness are given, significant comparisons are in bold. Average values at each stage are given below the *t*-test

	Snow Creek		Willow Hole	
	Intershrub	Undershrub	Intershrub	Undershrub
Seedling richness ratio (native:total)	0·51 ± 0·18*	0·40 ± 0·20	0·90 ± 0·13	0·75 ± 0·21
Mature richness ratio (native:total)	0·34 ± 0·16	0·24 ± 0·22	0·74 ± 0·11	0·69 ± 0·14
$F_{1,22}$	9·78	5·02	25·22	1·70
R^2	0·31	0·19	0·53	0·07
P	**0·005**	**0·036**	**< 0·001**	0·206
Native seedling richness	1·63 ± 0·92	0·92 ± 0·93	3·79 ± 0·83	3·42 ± 1·35
Exotic seedling richness	3·04 ± 0·36	2·21 ± 1·06	1·92 ± 0·72	1·92 ± 0·58
Native mature richness	2·83 ± 1·17	2·21 ± 1·35	8·00 ± 2·4	5·13 ± 2·44
Exotic mature richness	2·88 ± 0·80	3·08 ± 0·58	2·19 ± 0·76	2·04 ± 0·55

*Ratios arc-sine transformed.

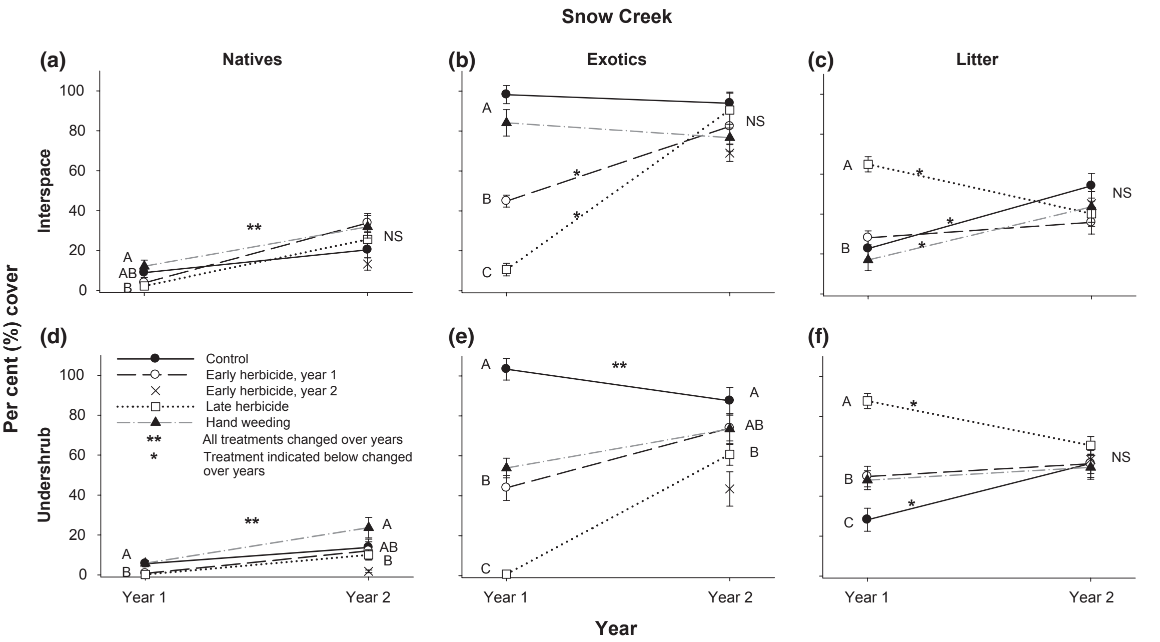

Fig. 1. Absolute per cent (%) cover of natives, exotics, and litter between and underneath shrubs at Snow Creek post-treatment in 2007–08 and 2008–09. Differences within year are noted by letters next to symbols representing treatments. NS, no significant differences. Stars indicate significant change in cover within treatment across years.

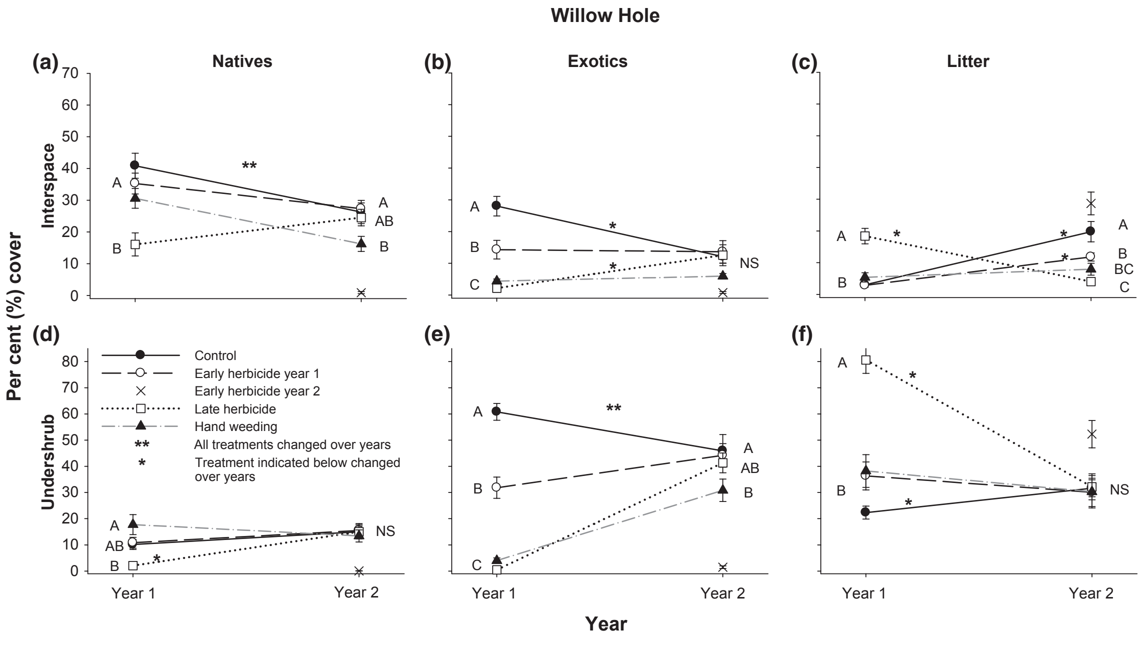

Fig. 2. Absolute per cent (%) cover of natives, exotics, and litter between and underneath shrubs at Willow Hole post-treatment in 2007–08 and 2008–09. Differences within year are noted by letters next to symbols representing treatments. NS, no significant differences. Stars indicate significant change in cover within treatment across years.

Year 2

At Snow Creek, differences in cover of natives, exotics, and litter disappeared in the second year (Fig. 1a–c, Table 2). At Willow Hole, legacy effects were apparent (Table 2). Hand weeded plots at Willow Hole had the lowest native cover in the second year (Fig. 2a). Late herbicide produced the most *B. tournefortii* at Snow Creek, but not more than early herbicide (Fig. 3a). Early herbicide continued to reduce *E. cicutarium* in the second year at Snow Creek, but caused significantly more *Schismus* spp. than in hand weeded plots (Fig. 3b,c). There was no difference in cover of exotics in interspaces at Willow Hole (Figs 2b and 4a–c, Table 3).

The new application of early herbicide did not increase or decrease native cover at Snow Creek ($F_{1,22}$ = 1·36, P = 0·256, Fig. 1a), but nearly eliminated *E. cicutarium* ($F_{1,22}$ =

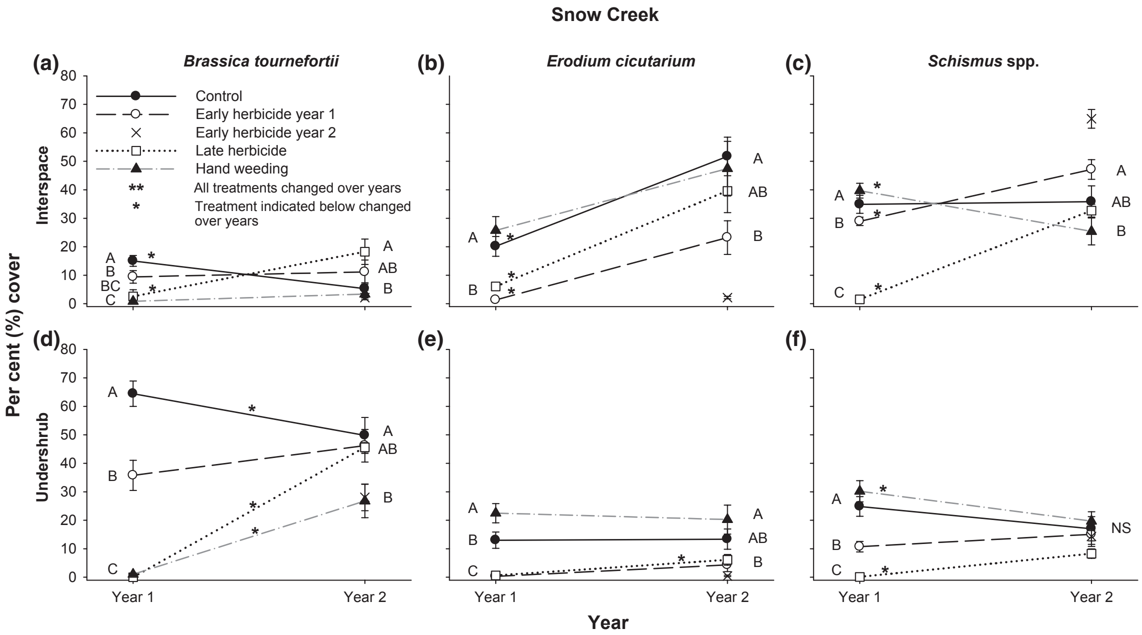

Fig. 3. Absolute per cent (%) cover of *Brassica tournefortii, Erodium cicutarium*, and *Schismus* spp. between and underneath shrubs at Snow Creek post-treatment in 2007–08 and 2008–09. Differences within year are noted by letters next to symbols representing treatments. NS, no significant differences. Stars indicate significant change in cover within treatment across years.

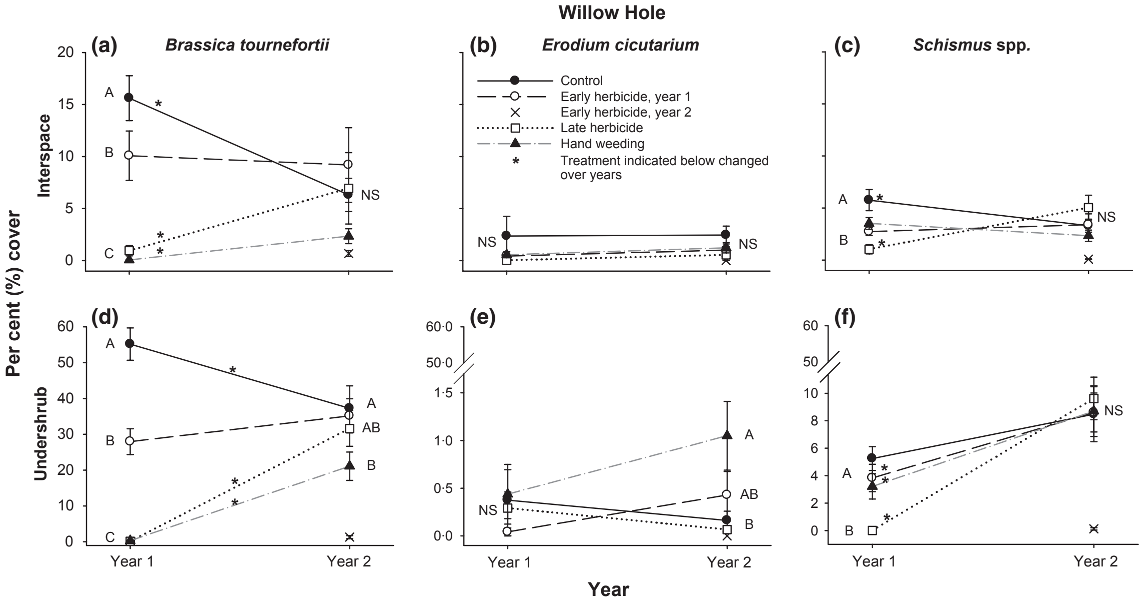

Fig. 4. Absolute per cent (%) cover of *Brassica tournefortii, Erodium cicutarium*, and *Schismus* spp. between and underneath shrubs at Willow Hole post-treatment in 2007–08 and 2008–09. Differences within year are noted by letters next to symbols representing treatments. NS, no significant differences. Stars indicate significant change in cover within treatment across years.

54·88, $P < 0{\cdot}001$, Fig. 3b). However, *Schismus* spp. nearly doubled in cover in response ($F_{1,22} = 20{\cdot}05$, $P < 0{\cdot}001$, Fig. 3c). *Brassica tournefortii* was unaffected at Snow Creek.

The year 2 early herbicide treatment at Willow Hole was phenologically late and resulted in reductions of both native and exotic cover ($P < 0{\cdot}01$ for all cover types and exotic species, Figs 2a–c and 4a–c), and was comparable to the late herbicide treatment in year 1.

UNDERSHRUB MICROSITES

Year 1

Both sites were heavily invaded underneath shrubs (Figs 1e and 2e), largely by *B. tournefortii* (Figs 3d–f and 4d–f). As in interspace plots, early glyphosate reduced exotic cover but did not reduce natives at Willow Hole (Fig. 2d,e). However,

Table 2. ANOVA tests across treatments within each site and microsite, and within years for cover types. Early herbicide treatments in year 2 are not included in 2008–09 tests or tests across years. Significant effects of treatments are in bold

			Natives				Exotics				Litter			
			F	R^2	P	Year	F	R^2	P	Year	F	R^2	P	Year
Snow Creek	Interspace	Year 1	**3,44 = 5·03**	**0·26**	**0·004**	***P* = 0·005**	**3,44 = 75·7**	**0·84**	**< 0·001**	***P* = 0·003**	**3,44 = 22·3**	**0·6**	**< 0·001**	***P* = 0·019**
		Year 2	3,43 = 1·72	0·07	0·36		3,43 = 1·15	0·06	0·47		3,43 = 1·64	0·15	0·07	
	Understorey	Year 1	**3,89 = 8·7**	**0·29**	**< 0·001**	***P* < 0·001**	**3,89 = 81·2**	**0·74**	**< 0·001**	***P* < 0·001**	**3,89 = 27·6**	**0·52**	**< 0·001**	P = 0·28
		Year 2	3,90 = 1·97	0·09	0·125		**3,90 = 2·79**	**0·17**	**0·046**		3,90 = 0·7	0·09	0·54	
Willow Hole	Interspace	Year 1	**3,44 = 9·2**	**0·38**	**< 0·001**	***P* = 0·010**	**3,44 = 29·0**	**0·66**	**< 0·001**	P = 0·626	**3,44 = 25·1**	**0·63**	**< 0·001**	***P* = 0·047**
		Year 2	**3,42 = 3·2**	**0·19**	**0·032**		3,44 = 1·3	0·08	0·3		**3,44 = 12·2**	**0·45**	**< 0·001**	
	Understorey	Year 1	**3,91 = 7·0**	**0·25**	**< 0·001**	***P* = 0·016**	**3,91 = 120**	**0·81**	**< 0·001**	***P* < 0·001**	**3,91 = 26·3**	**0·49**	**< 0·001**	***P* = 0·001**
		Year 2	3,92 = 0·03	0·13	0·99		**3,92 = 4·4**	**0·22**	**0·007**		3,92 = 0·10	0·17	0·96	

Table 3. ANOVA tests across treatments within each site and microsite, and within years for cover of exotic annuals. Early herbicide treatments in year 2 are not included in 2008–09 tests or tests across years. Significant effects of treatments are in bold

			Brassica tournefortii				*Erodium cicutarium*				*Schismus* spp.			
			F	R^2	P	Year	F	R^2	P	*Year*	F	R^2	P	Year
Snow Creek	Interspace	Year 1	**3,44 = 16·4**	**0·53**	**< 0·001**	P = 0·872	**3,44 = 15·3**	**0·51**	**< 0·001**	***P* < 0·001**	**3,44 = 79·0**	**0·84**	**< 0·001**	P = 0·466
		Year 2	**3,43 = 4·13**	**0·22**	**0·012**		3,43 = 2·5	0·15	0·071		**3,43 = 4·0**	**0·22**	**0·0314**	
	Understorey	Year 1	**3,89 = 81·2**	**0·75**	**< 0·001**	***P* < 0·001**	**3,89 = 22·9**	**0·45**	**< 0·001**	P = 0·325	**3,89 = 30·4**	**0·52**	**< 0·001**	P = 0·682
		Year 2	**3,90 = 3·75**	**0·3**	**0·014**		**3,90 = 4·24**	**0·17**	**0·008**		**3,90 = 2·89**	**0·1**	**0·04**	
Willow Hole	Interspace	Year 1	**3,44 = 20·9**	**0·59**	**< 0·001**	P = 0·459	3,44 = 1·23	0·08	0·31	P = 0·509	**3,44 = 10·5**	**0·42**	**< 0·001**	P = 0·879
		Year 2	3,44 = 1·2	0·07	0·33		3,44 = 2·2	0·13	0·101		3,44 = 1·6	0·1	0·211	
	Understorey	Year 1	**3,91 = 105**	**0·79**	**< 0·001**	***P* = 0·004**	3,91 = 0·65	0·03	0·59	P = 0·40	**3,91 = 7·1**	**0·26**	**< 0·001**	***P* < 0·001**
		Year 2	**3,92 = 4·3**	**0·2**	**0·007**		**3,92 = 3·6**	**0·14**	**0·017**		3,92 = 0·51	0·14	0·68	

natives were reduced at Snow Creek, where coverage was already low (Fig. 1d). Both herbicide applications successfully controlled *E. cicutarium* and *Schismus* spp. at Snow Creek (Fig. 3e,f), while late application was the only effective treatment for *Schismus* spp. under shrubs at Willow Hole (Fig. 4f). Late glyphosate produced a high cover of litter under shrubs at both sites (Figs 1f and 2f).

Hand weeding underneath shrubs was effective at Willow Hole, where *E. cicutarium* and *Schismus* spp. were not dominant (Figs 2e and 4d). Hand weeding somewhat increased native cover at Willow Hole (Fig. 2d). The increase was not significant; however, it was paired with an increase in native species richness (data not shown). In contrast, *E. cicutarium* increased in response to hand weeding at Snow Creek (Fig. 3d,e).

Year 2

There were more legacy effects from control treatments in the second year underneath shrubs than in interspaces (Tables 2 and 3). At Snow Creek, weeded plots had higher native cover in year 2 than untreated plots, but late herbicide plots had the lowest exotic cover (Fig. 1d,e, Table 2). Hand weeding continued to reduce *B. tournefortii*, but resulted in greater *E. cicutarium* cover than either herbicide treatment (Fig. 3d,e, Tables 2 and 3). Hand weeding at Willow Hole also reduced *B. tournefortii* in year 2 (Fig. 4d, Table 3). Despite the low occurrence of *E. cicutarium* at Willow Hole, there was a parallel increase in *E. cicutarium* cover in hand-weeded plots over untreated and late herbicide plots from year 1 (Fig. 4e, Table 3). There was no lasting effect of treatments on *Schismus* spp. at Willow Hole (Fig. 4f, Table 3).

The new early herbicide treatment functioned similarly at both sites underneath shrubs where native and exotic cover were reduced (Figs 1–4d to f). At Willow Hole, the year 2 herbicide treatment also increased litter underneath shrubs, similar to the late herbicide treatment in year 1 (Fig. 2f).

LABOUR CONSIDERATIONS

A major concern of land managers seeking to control invasive species is the time, effort, and cost required for treatments. For these experiments, both sites were sprayed in about 16 person-hours (ph) with each herbicide treatment (16 ph for early, 16 ph for late application). The maximum area sprayed was about 1500 m^2 across both sites for each treatment. Overall, each herbicide treatment required about 100 ph per hectare. In contrast, roughly 50 ph were required to hand weed about 290 m^2 total (including buffer zones around subplots) across both sites. Scaling up, about 1740 ph would be required to hand weed *B. tournefortii* from one hectare, nearly an order of magnitude increase in effort.

Discussion

Rapid phenology is a defining feature of ephemerals in desert systems (Beatley 1974; Burk 1982), and management of both native and exotic annuals in deserts must account for phenological responses to environmental conditions. The flora studied in this research responded differently to control methods depending on the timing of treatment, invasion level of the site and microsite. Our research also found that a single year of exotic control is inadequate to boost native annuals or cause dramatic, reproducible reductions in exotic annuals, highlighting the need for multi-year studies of emergence patterns of exotics and natives in order to adequately inform management decisions. However, results from this research also show that controlling exotic annuals by exploiting their rapid phenology is a promising technique.

Early herbicide treatment was a success in that it retained native cover while reducing exotic cover at both sites. However, exotics were not wholly removed from the system and native cover did not increase in most of the control treatments. Native annuals may not be able to respond positively except when there is complete removal of all exotic species (Steers 2008) or when control methods are combined with other restoration activities (Steers & Allen 2009). Alternatively, early herbicide treatment may have removed some native individuals, leaving fewer, larger plants that resulted in the same overall native cover as many smaller plants in other treatments. If the window between exotic and native emergence was longer, or the timing of herbicide application was earlier, it is possible that a positive cover response would result.

The few observed increases in native cover occurred from hand weeding, the method currently utilized by most desert land managers (Brooks, Draper & Trader 2006). However, it was the most labour-intensive option and only effective at a site where *B. tournefortii,* the target forb, was dominant. Counter to our hypotheses, hand weeding continued to diminish *B. tournefortii* cover in the second year, especially underneath shrubs. Our results suggest that hand weeding can be effective in sites invaded only by *B. tournefortii*, but that it may come at a cost both financially and ecologically. While native annuals experienced a slight increase in year 2 from weeding underneath shrubs in year 1, weeding also encouraged *E. cicutarium* in year 1, an effect that remained in year 2. *Erodium cicutarium* and *B. tournefortii* have similar rosette growth forms and may compete directly, replacing each other when one is removed (Brooks 2000). Rather than increased disturbance, the replacement effect may have occurred due to competitive release. Replacement effects result from competitive hierarchies in which exotic grasses and forbs are ranked above native forbs (Shipley & Keddy 1994; Allen *et al.* 2005), and are difficult to prevent. Herbicide treatments removed *E. cicutarium*, but encouraged *Schismus* spp. The composition, and consequently the dynamics, of the native and exotic annual commnity changed with control treatment, a potentially important outcome.

Adaptive management that combines methods (such as early glyphosate treatment combined with later grass-specific herbicide treatment ⁄ and/or hand weeding) can take advantage of site or climate characteristics from year to year (Krueger-Mangold, Sheley & Svejcar 2006). Our results show that either hand weeding or early herbicide treatment can be effective early control methods for sites that have just one or two invaders or may be recently invaded. Many landscapes will have two or more dominant exotics and management that removes many exotics or prevents future impacts will ultimately have the greatest benefits for native communities (Hobbs & Humphries 1995; Hulme 2006; Steers & Allen 2009). As a non-selective herbicide, glyphosate may remove multiple exotic species at the same time. This suggests that careful timing of herbicide application can take advantage of rapid phenology to reduce many exotic annuals, and may be a useful alternative to hand weeding a single exotic species. Reducing further impacts, seed set, and spread at less invaded sites, such as Willow Hole, may prevent them from becoming heavily invaded sites, such as Snow Creek, where control is not effective.

In this research, early herbicide also had several trade-offs. Early application removed only half the exotic cover at both sites and did not prevent all exotic annual seedbank inputs, although it probably reduced them. Also, early herbicide treatments are subject to inclement weather; in the second year applications, wind delayed treatment at Willow Hole to the point that natives were fully emerged. Survivorship of both native and exotic species was near zero. Finally, any exotics with late emergence (following early herbicide treatment) might be favoured and increase in dominance, as probably occurred in year 2 when *Schismus* spp. nearly doubled in cover with the removal of *E. cicutarium*. Since *Schismus* did not increase in year 1, this result indicates that exotic control is likely to differ across years depending on the unique emergence patterns within a season, and that it may be of greatest benefit to manage for those species of greatest concern at a given site and time. In this sense, early control regimes are ideal for adaptive management programs. In this experiment, we targeted *B. tournefortii* because previous research has shown that *Schismus* spp. are effectively controlled by grass-specific herbicide, which also impacts *E. cicutarium* (Steers & Allen 2009). Such herbicides might be applied after the early glyphosate application tested here, controlling grass species while leaving native forbs unharmed. A grass-specific follow-up application would not work for late-emerging forbs, but could be used for any grass invasion.

Exotic litter is a major fuel source for desert fires, and reducing fuel loads is a goal for land managers (Brooks 1999a; Brooks *et al.* 2004). Late herbicide resulted in high cover of litter underneath shrubs, potentially increasing fire hazard earlier in the year than normal. An alternative treatment to prevent seed set and reduce fuels would be a pre-bolting rosette herbicide application. As rosette litter breaks down rapidly, this would allow for maximum exotic seedbank depletion, but would remove exotics before they can create a fuel load. A rosette-stage application would not avoid native annuals, however.

Native annual forb germination is density-dependent, and may be inhibited by increasing densities of exotic annuals (Inouye 1980), thus reducing native annuals by inhibiting germination, even when an intact native seedbank exists. Native annual seedbanks are generally assumed to be healthy and intact in desert ecosystems because invasion and other disturbances have been low until relatively recently (Venable, Pake & Caprio 1993; Pake & Venable 1996). In a heavily invaded site where fire is increasing but native annuals have diminished, the benefits of preventing fuel loads and exotic seedbank inputs by controlling exotics could outweigh impacts of control measures on the native flora. Removing some of the exotic seedbank could, in time, stimulate germination in the native seedbank by reducing density-dependent inhibition. Either of the herbicide treatments in this research would accomplish this goal, although both application timings allowed some seed production by natives and/or exotics. Future research should assess which is greater over several years: impacts to the native annual community from invasive plants, or impacts from early herbicide application.

Initial rainfall and accompanying temperature regimes may drastically affect emergence patterns between exotic vs. native species from year to year (Bowers 1987). For instance, a series of small, warm rainfall events early in the autumn may produce a well-defined cohort of exotic annuals before native annuals meet germination requirements. In contrast, a large, cold rain event later may cause corresponding germination in both natives and exotics (Beatley 1974), removing the window for selective control. Even without treatment, our sites showed dramatic changes in species across years. Rainfall is unpredictable in southwestern deserts (Hereford, Webb & Longpre 2006), and may be subject to even greater extremes with climate change (Seager *et al.* 2007).

Our results show that heavily invaded sites are not easily controlled by either herbicide or hand weeding, and also suggest that one year of exotic control will not increase native annual success. However, the results from this research also demonstrate the potential to exploit rapid phenology among invasive species. Early control of invasive plants may be applicable to many ruderal plant invasions. Further research is required, especially in highly variable ecosystems such as deserts. Combined with further field tests, new herbicide timing techniques could be developed for annual communities. Herbicide timing techniques are likely to be effective in many situations where exotic species emerge earlier than natives, and therefore should also be tested outside of southwestern desert ecosystems.

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Supporting Information

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

Fig. S1. Temperature and precipitation at Snow Creek and Willow Hole study sites during annual growth seasons from 2007 to 09.

Table S1. Full-factorial mixed-model ANOVA results for the fixed effects of Year, Site (Willow Hole vs. Snow Creek), Treatment (control, early herbicide, late herbicide, and hand weeding), and Microsite (north side of shrub, south side of shrub, shrub interspaces).

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