Biological Conservation 213 (2017) 106–114

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Secondary invasions of noxious weeds associated with control of invasive *Tamarix* are frequent, idiosyncratic and persistent

Eduardo González[a,b], Anna A. Sher[b,*], Robert M. Anderson[b], Robin F. Bay[b], Daniel W. Bean[c], Gabriel J. Bissonnete[d], David J. Cooper[f], Kara Dohrenwend[g], Kim D. Eichhorst[h], Hisham El Waer[b], Deborah K. Kennard[i], Rebecca Harms-Weissinger[j], Annie L. Henry[b], Lori J. Makarick[k,1], Steven M. Ostoja[l], Lindsay V. Reynolds[m], W. Wright Robinson[n], Patrick B. Shafroth[e], Eric Tabacchi[a]

[a] *EcoLab (Laboratoire Ecologie Fonctionnelle et Environnement), Université de Toulouse, CNRS; INPT, UPS, 118 Route de Narbonne Bâtiment 4R1, 31062 Toulouse Cedex 9, France*
[b] *Department of Biological Sciences, University of Denver, F. W. Olin Hall, 2190 E Iliff Ave, Denver, CO 80208-9010, USA*
[c] *Colorado Department of Agriculture, Biological Pest Control, Palisade Insectary, 750 37.8 Rd., Palisade, CO 81526, USA*
[d] *U.S. Bureau of Land Management, 82 East Dogwood, Moab, UT 84532, USA.*
[e] *U. S. Geological Survey, Fort Collins Science Center, 2150 Centre Ave., Bldg. C, Fort Collins, CO 80526, USA*
[f] *Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523, USA*
[g] *Rim to Rim Restoration. PO Box 297, Moab, UT 84532, USA*
[h] *Bosque Ecosystem Monitoring Program (BEMP), MSC 03 2020, Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*
[i] *Department of Physical and Environmental Sciences, Colorado Mesa University, Grand Junction, CO 81501, USA*
[j] *Northern Colorado Plateau Network, National Park Service, Moab, UT 84532, USA*
[k] *Grand Canyon National Park, 1824 S. Thompson Street, Suite 200, Flagstaff, AZ 86001, USA*
[l] *USDA California Climate Hub, Agricultural Research Service, University of California, Davis, 1 Shields Avenue, Davis, CA 95616, USA*
[m] *Department of Biology, Colorado State University, Fort Collins, CO 80523, USA*
[n] *Grand County Weed Department, 125 East Center Street, Moab, UT 84532, USA*

ARTICLE INFO

Keywords:
Ecological restoration
Invasive species management
Noxious weeds
Riparian systems
Secondary invasions
Tamarix control

ABSTRACT

Control of invasive species within ecosystems may induce *secondary invasions* of non-target invaders replacing the first alien. We used four plant species listed as noxious by local authorities in riparian systems to discern whether 1) the severity of these secondary invasions was related to the control method applied to the first alien; and 2) which species that were secondary invaders persisted over time. In a collaborative study by 16 research institutions, we monitored plant species composition following control of non-native *Tamarix* trees along southwestern U.S. rivers using defoliation by an introduced biocontrol beetle, and three physical removal methods: mechanical using saws, heavy machinery, and burning in 244 treated and 79 untreated sites across six U.S. states. Physical removal favored secondary invasions immediately after *Tamarix* removal (0–3 yrs.), while in the biocontrol treatment, secondary invasions manifested later (> 5 yrs.). Within this general trend, the response of weeds to control was idiosyncratic; dependent on treatment type and invader. Two annual tumbleweeds that only reproduce by seed (*Bassia scoparia* and *Salsola tragus*) peaked immediately after physical *Tamarix* removal and persisted over time, even after herbicide application. *Acroptilon repens*, a perennial forb that vigorously reproduces by rhizomes, and *Bromus tectorum*, a very frequent annual grass before removal that only reproduces by seed, were most successful at biocontrol sites, and progressively spread as the canopy layer opened. These results demonstrate that strategies to control *Tamarix* affect secondary invasions differently among species and that time since disturbance is an important, generally overlooked, factor affecting response.

---

[*] Corresponding author.
E-mail address: anna.sher@du.edu (A.A. Sher).
[1] Present address: Natural Resource Stewardship and Science, 1201 Oakridge Dr., Suite 200, Fort Collins, CO, 80525, USA.

http://dx.doi.org/10.1016/j.biocon.2017.06.043
Received 30 December 2016; Received in revised form 18 June 2017; Accepted 27 June 2017

1. Introduction

Ironically, human actions devoted to control of invaders often create additional anthropogenic disturbance that can result in secondary invasions, defined here as the proliferation of non-target invasive species, frequently referred as to weeds, after a complete or partial local eradication of the first, targeted alien (Pearson et al., 2016). The threat of secondary invasions is very high in most ecosystems, as these often contain multiple, subordinate exotic, potentially invasive species which can respond quickly once competitive pressure by the primary species is removed (Hulme and Bremner, 2006; Hulme et al., 2013; Kuebbing et al., 2013). For example, removal of invasive tree canopy layers may increase light resources in the understory and allow the proliferation of shade-intolerant invasive grasses that remained subdominant in the system before human intervention (e.g., Loo et al., 2009). However, soil disturbance during removal of targets has also been found to suppress secondary invaders one year later (Sher et al., 2008). Secondary invasions therefore represent an opportunity to understand how exotic species respond idiosyncratically to a given management-related disturbance. Unlike the initial invasion, the new disturbance will be deliberately imposed by humans when controlling the first invader, and therefore, easier to control in experimental designs. In a recently published meta-analysis of 60 cases of secondary plant invasions, Pearson et al. (2016) found that their severity was positively correlated to reductions in the target alien, but not to control method or intensity of disturbance. However, the authors also found that specific case studies revealed that management itself can foster secondary invasions.

Control of invasive *Tamarix* spp. (tamarisk, saltcedar) in riparian systems is an ideal case to study the effects of different types of anthropogenic disturbance on secondary invasions of different weeds. Eurasian species of the genus *Tamarix* and their hybrids have invaded extensively along southwestern U.S. rivers since they were introduced in the early 1800s for ornamental, windbreak and erosion control purposes, and are now the third most frequent and second most abundant in cover of riparian trees in western North America (Friedman et al., 2005). Although *Tamarix* were establishing and spreading before the advent of the dam-building era in the western U.S. (Birken and Cooper, 2006), their naturalization and rapid expansion was partly facilitated by hydro-geomorphic regime alterations caused by dam regulation and exploitation of water resources in the twentieth century (Stromberg et al., 2007; Merritt and Poff, 2010). Once established, *Tamarix* can contribute further to riparian habitat alteration, for example by altering abiotic and biotic conditions (e.g., floodplain aggradation, salt accumulation, change of microbial soil communities and light availability), which has led to its characterization as both passenger and driver of ecosystem change (Johnson, 2013).

Efforts to control *Tamarix* invasion in the U.S. have been very intense in recent decades. Years of trials with diverse mechanical, chemical and biological techniques have gradually kept stable and even reduced *Tamarix* populations in many locations (Harms and Hiebert, 2006; Belote et al., 2010; Hultine et al., 2010; Ostoja et al., 2014, Kennard et al., 2016; González et al., 2017). However, even if *Tamarix* is successfully controlled, legacy effects on the ecosystem combined with the conditions that allowed the initial invasion may favor the establishment and proliferation of several other exotic weeds (Shafroth et al., 2008; Hultine et al., 2010; González et al., 2017).

Despite its great potential for helping to understand biological invasions and informing management of riverscapes, quantitative reports of the severity of secondary invasions in post *Tamarix*-treated riparian systems remain local, often from single sites or river reaches (e.g., Sher et al., 2008; Ransom et al., 2012; Douglass, 2013; Ostoja et al., 2014; Kennard et al., 2016) or with too few site replicates to evaluate the scale of their impact at a regional level (Harms and Hiebert, 2006; Bay and Sher, 2008). This contrasts to a significant effort by the scientific community to investigate the spatial scope of primary invasions, notably of *Tamarix* spp. and *Elaeagnus angustifolia* (Russian olive), in southwestern U.S. rivers (e.g., Friedman et al., 2005; Nagler et al., 2011; Jarnevich et al., 2013; McShane et al., 2015). In addition, studies exploring the causes underlying the existence and severity of secondary invasions in southwestern U.S. rivers following *Tamarix* control are surprisingly rare. In particular, the weed-specific responses to the wide array of existing techniques for *Tamarix* control remain largely unexplored. To our knowledge, only Sher et al. (2008) found a (negative) relationship between the intensity of control related-disturbance and response of one exotic weed: *Bromus tectorum* (cheatgrass), but their observations were limited to only one year after removal. In one study including 244 removal sites, González et al. (2017) found that some physical removal methods (i.e., burning and mechanical removal using heavy machinery) created site conditions more prone to invasions of exotic forbs than saw-cutting and biocontrol, but did not make any distinction between species of invaders.

With few long-term studies, even less attention has been placed on the persistence of secondary invasions over time (Pearson et al., 2016). This has important consequences for management, as fewer resources for eradication should be allocated if the weeds will disappear naturally in the absence of further disturbance of the same type or intensity that facilitated their arrival and/or proliferation. In the case of *Tamarix* control, González et al. (2017) found that the abundance of exotic weeds decreased in ten sites that received only biological control over three years of monitoring but was stable or even increased in sites subjected to physical removal methods (mechanical cutting, heavy machinery and burning) and when larger spatial (i.e., river catchment) and temporal (i.e., 5 years on average) scales were taken into account. They suggested that the inherently disturbed riparian systems, the weak recovery of competing native species, and the inefficiency of follow-up herbicide treatments could explain the persistence of weeds. However, the specific responses of the multiple secondary invaders over time were not explored.

Here, we assessed vegetation response across *Tamarix* control treatments and selected the exotic weed species with the highest potential to become secondary invaders in the context of *Tamarix* control along southwestern U.S. rivers. We used this information to answer the following questions: 1) How does control method influence the severity of secondary invasions? 2) How does the severity of secondary invasions change over time and does the temporal trajectory differ as a function of control method?

2. Materials and methods

2.1. Study sites

Vegetation response after *Tamarix* control was monitored in 244 sites distributed on floodplains and streambanks of two of the largest catchments in the American West, the Colorado River and Rio Grande, and some of their major and minor tributaries (Fig. 1). The sites spanned ca. 350,000 km^2 across six U.S. states: Arizona, California, Colorado, Nevada, New Mexico and Utah. To be included in the study, a site must have been subjected to *Tamarix* control by at least one of the following four methods: prescribed or accidental burning of *Tamarix* stands (“burn”, 33 sites); mechanical removal using heavy machinery such as root plows, mowers or bulldozers (“heavy machinery”, 57 sites); or using chain or hand saws (“cut”, 99 sites), and defoliation by the biocontrol beetle, *Diorhabda* spp. (“biocontrol”, 55 sites). When sites were subject to more than one method, the site was labeled with the method of the highest disturbance (i.e., burn > heavy > cut > biocontrol). It is important to note that they are different *types* of disturbance, with different effects on secondary plant invaders. Biocontrol, for example, does not cause soil physical disturbance but its effects on vegetation are cumulative over time with successive defoliations. Burning was considered to have the greatest disturbance because it affects both chemical and physical fluxes of nutrients (Sher and Hyatt, 1999; González et al., 2017), even though the effects on soil physical

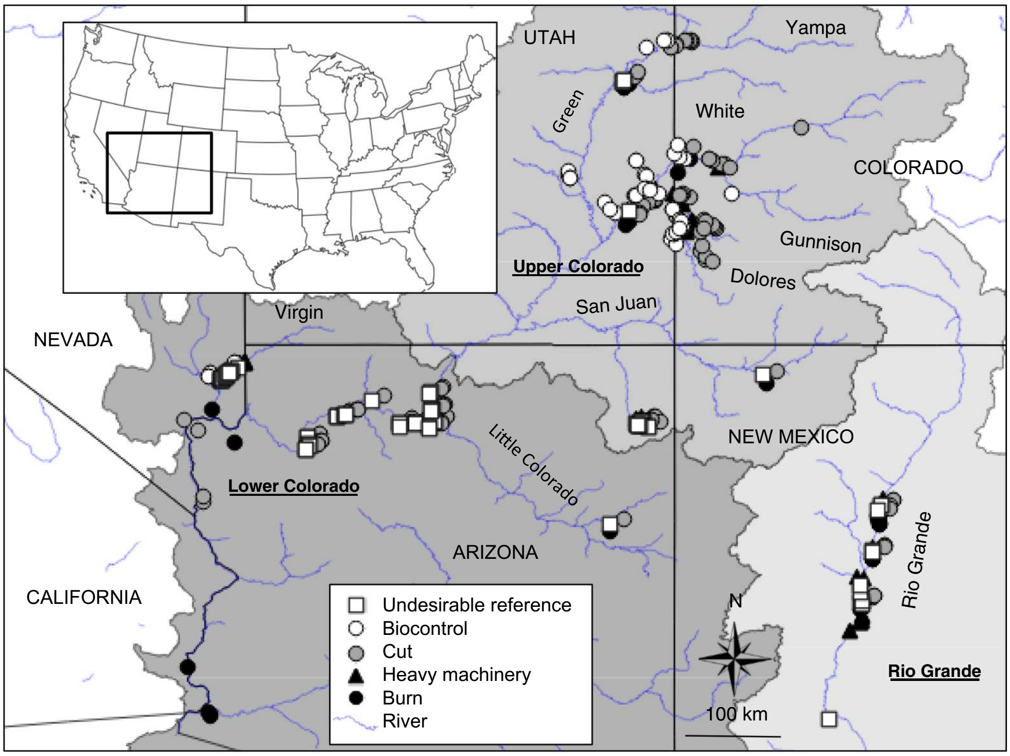

Fig. 1. Colorado River (Upper and Lower) and Rio Grande River catchments showing locations of the 244 sites analyzed in this paper where invasive *Tamarix* has been treated using different control methods: burning *Tamarix* stands, mechanical removal using heavy machinery, mechanical removal using chain- or hand-saws and defoliation of the biocontrol agent, the *Tamarix* beetle *Diorhabda* spp.; and 79 reference sites, representing undesirable conditions, the starting point for *Tamarix* control.

disturbance in particular may be higher for the heavy machinery treatment. Biocontrol was frequently combined with any of the three physical removal methods, but combining burning, heavy machinery and saw-cutting was very rare. *Tamarix* control was sometimes followed up with chemical treatment of noxious weeds (aerially or from the ground; 56 sites). On-site burning of the *Tamarix* stems and debris stacked in piles after removal to reduce transportation costs was a common practice but not considered either as a treatment for controlling *Tamarix* or as a follow-up method. The treatments could be applied simultaneously during the same year or in sequential steps over several years, but homogeneously across the entire site.

Vegetation was also sampled in 79 reference sites that represented a starting point for *Tamarix* control (undesirable reference sites hereafter), either theoretically (i.e., model site with undesired abundance of *Tamarix*, 36 sites) or practically (i.e., site before *Tamarix* control, 43 sites). Most of the undesirable reference sites were paired with treated sites. Each site, treated and undesirable reference, corresponded to a single geomorphic unit (i.e., a distinctive fluvial landform such as a gravel or sand bar, flood deposit, channel margin, abandoned channel, off-channel depression, floodplain terrace, etc.). Some treated (93) and some undesirable reference (11) sites were sampled several years, making a total of 598 observations (i.e., site sampled at a given year; Table 1).

2.2. *Vegetation surveys*

Vegetation surveys measured cover of *all* plant species at each site estimated visually in rectangular or circular plots or using the point or line intercept method along transects (Table A).

2.3. *Selection of exotic weeds with potential to become secondary invasions*

A total of 547 taxa were identified, 535 to the species level, 32 of which (including *Tamarix* spp.) are considered noxious species in at least one of the six states where the study sites were located (legal status, PLANTS Database of the U.S. Department of Agriculture, USDA-NRCS, 2014; Table B). Noxious species are exotic species that are "weedy or invasive" (USDA-NRCS, 2014). They are usually agricultural pests or harmful for livestock. From the 32 noxious species, we selected potential secondary invaders in southwestern U.S. rivers based on the following five criteria: 1) plant was not a target of primary control (e.g., *Tamarix* and *Elaeagnus angustifolia*) 2) plant had a frequency (i.e., proportion of observations with presence) > 5%, 3) plant had a mean cover when present > 5%, 4) plant's cover was the same or higher in the treated than in the undesirable sites, 5) plant was widespread, defined as present in at least one third (11) of the 34 geomorphically homogeneous river reaches that were sampled. From the remaining non-native species, additional criteria for potential secondary invaders were: any species that were considered noxious anywhere in the U.S.,

Table 1
Summary of sites and observations for treated and undesirable reference sites. Observations are the sum of sites sampled at a given year. NA – not applicable.

	Biocontrol only	Cut	Heavy machinery	Burning	Undesirable reference	Total
Total number of sites	55	99	57	33	79	323
Total number of observations	72	219	95	78	134	598
Number of sites with only one observation over time	45	46	39	21	68	219
Number of sites with two or more observations over time	10	53	18	12	11	104
When two or more observations, median number and range (in parenthesis)	3 (2–3)	2 (2–5)	3 (2–7)	5 (2–9)	4 (3–11)	
Time (yr.) since end of *Tamarix* physical removal (time since beetle arrival at biocontrol only sites) at the last observation, median (range)	7 (1–9)	5 (0–13)	3.5 (0–18)	3 (0–18)	NA	

met the five criteria, and had high frequencies (> 50%). These criteria were intentionally restrictive as we believed the strength of our database was its great spatial extent, which allowed generalisations for southwestern U.S. rivers. Some secondary invaders may be present in few sites only but a very high cover (e.g., *Bromus rubens*, Supplementary material Table B), but modeling their response to control treatments would have required a different experimental design due to zero-inflated data. Restricting our analysis to the most frequent species across our large spatial scale allowed for the broadest analysis in space and time and therefore the most widely applicable results. Detailed inventories of weeds and local analysis of their responses to management may help to predict and set up follow-up treatments for mitigating secondary invaders locally (see for example Sher et al., 2008, Ransom et al., 2012 and Perkins et al., 2015 in our study area).

2.4. Data analysis

We used Kruskal-Wallis tests and pairwise Mann-Whitney comparisons (SPSS, v. 13.0) to explore the effects of *Tamarix* control treatments (fixed factor, four levels) on the abundance of each weed species selected.

We were also interested in the effects of time since *Tamarix* control on the abundance of secondary invaders. The time since *Tamarix* control refers to the number of years since the end of removal for the cutting, heavy machinery and burning treatments, and to the time since the arrival of the defoliating beetle for the biocontrol treatment (the year of arrival equates to the first defoliation event). However, in the first three physical removal categories, *Tamarix* removal-related disturbance has a pulse at time of removal (i.e., year = 0), then presumably decreases over time; while in the biocontrol, the disturbance is cumulative with successive number of defoliations by the biocontrol beetle (even though the bulk of defoliation normally occurs during the first few years after the arrival of beetles and stabilizes afterwards; Hultine et al., 2010; Kennard et al., 2016). This consideration is important because, when analyzing species abundance patterns during preliminary analyses, interactions between control method and time since *Tamarix* control were observed. Therefore, we ran one Kruskal-Wallis test and six pairwise Mann-Whitney comparisons across the different control methods for each time period: from zero years since removal, i.e., site monitored immediately after *Tamarix* removal or since beetle establishment, to eight or more years, with observations being the replicates. As sites were neither monitored for the same number of years nor for the same duration (see Table 1), the number of replicates used to run the tests at each time period was different and lower than the total number of treated sites – 244 (see Fig. 2 caption). When sites were subjected to two or more treatments (e.g., cut and biocontrol), the control method for that site was considered as the highest disturbance category (i.e., cut in the example). Following these criteria, among the 244 restored sites 33 were burned, 57 heavy machinery, 99 cut and 55 biocontrol (Table 1). Biocontrol sites for years 0, 1, 2 and 3 were merged into a single category as the number of observations for each time period was too low to perform the analyses.

The change in severity of the secondary invasions over time was assessed for each weed and control method separately, using Spearman correlations ($P < 0.05$) between time and weed abundance. To avoid problems related to pseudoreplication, for the 93 sites that had multiple years of post-*Tamarix* control weed abundance data, we only used the last year of observations. The time scale was therefore a chronosequence.

3. Results

3.1. Four exotic species officially listed as noxious as the main secondary invasions in the context of Tamarix control in the southwestern U.S. rivers

Considered as a group, the weeds defined as noxious by the USDA appeared in 89.2% of the observations in the treated sites, with a mean cover when present of 22.0% ± 1.1% (1 SE). Among the 31 species listed as noxious in the study area (excluding *Tamarix* spp.), only three met our five criteria: *Acroptilon repens* (Russian knapweed), *Bromus tectorum* (cheatgrass) and *Salsola tragus* s.l. (= *kali*) (Russian thistle). Among the remaining species considered noxious in other states, *Bassia scoparia* (common kochia) was very frequent (> 50%) in the *Tamarix* treated sites of our database and thus included in our analyses.

Of those four species that were retained for further analyses, *A. repens* and *B. scoparia* appeared at very high frequencies, in at least one third of the sites, and usually with a dominant mean cover when present of ca. 17%. *Bromus tectorum* and *S. tragus* were also very frequent (ca. 40%) but rarely dominant (mean cover < 10%). *A. repens*, *B. scoparia* and *S. tragus* had a significantly higher abundance following *Tamarix* control, compared to pre-treated or undesirable reference sites (Mann-Whitney tests, $P < 0.05$, see Supplementary material Table B). *B. tectorum*, however, was already very abundant in the understory of *Tamarix* stands prior to control.

The cover of only three noxious species was consistently reduced in the *Tamarix* control sites: *Tamarix* spp. (tamarisks), *Elaeagnus angustifolia* (Russian olive) and *Alhagi maurorum* (camelthorn). Russian olive was the second most abundant invasive species in the undesirable reference sites (after *Tamarix*; Table B) and a frequent target of removal (e.g., Reynolds and Cooper, 2011). Another brome species, *Bromus rubens* (red brome), met the first four criteria but not the requisite of being widespread in the study region, as it was only found in the Grand Canyon of the Colorado and in streams draining into Lake Mead.

3.2. The method of Tamarix control affects the severity of secondary invasions

The responses of the secondary invasions to the *Tamarix* control methods were idiosyncratic. Overall, during the first three years since *Tamarix* control, two species: *B. scoparia* and *S. tragus* consistently exhibited higher abundance with the physical removal treatments (especially burning and heavy machinery for the former, and burning and cut for the latter species, Table 2; Fig. 2). Conversely, after at least five years since restoration, *A. repens* and *B. tectorum* tended to have higher abundance in the biocontrol sites. *B. scoparia* also progressively spread as the canopy layer opened following biocontrol, but never exceeding the cover found at the physical removal methods.

3.3. The severity of secondary invasions only changed slightly for the time period considered in this study

Change over time was not consistent between control methods or weed species. When we considered pattern of change over time as a trajectory for each species (diagonal arrows, Fig. 2), we found increasing abundance of *A. repens* and *B. tectorum* following biocontrol, decreasing abundance of *B. tectorum* following heavy machinery removal, and decreasing abundance of *B. tectorum*, *B. scoparia* and *S. tragus* following removal by cutting.

4. Discussion

4.1. Secondary invasions of noxious weeds following Tamarix control are frequent

Our results showed that secondary invasions of noxious weeds in the context of *Tamarix* control in southwestern U.S. rivers are frequent, which concurs with a recent review suggesting the commonness of this often-overlooked environmental problem across ecosystems (Pearson et al., 2016). In particular, the cases of *Bassia scoparia*, *Acroptilon repens* and, to a lesser extent, *Salsola tragus* should be of concern: these three species were present at very high frequencies and cover in the *Tamarix* control sites along most of the river reaches surveyed, at a significantly

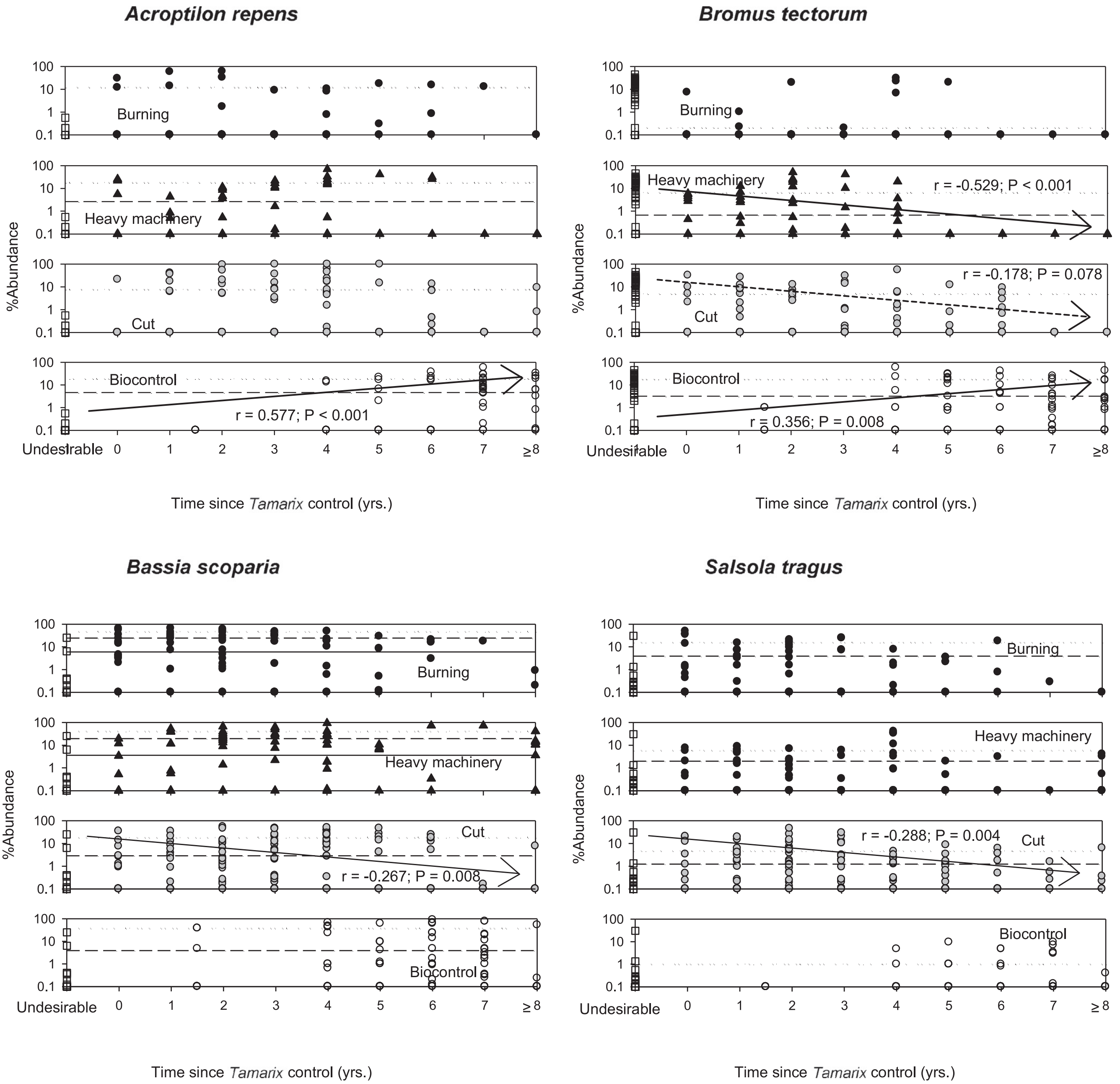

Fig. 2. Abundance over time of four noxious species after control of *Tamarix* in 244 sites classified by control method. Burning *Tamarix* stands (33 sites – black circles), mechanical removal using heavy machinery (57 sites – black triangles), mechanical removal using chain or hand saws (99 sites – gray circles) and defoliation of the biocontrol agent, the *Tamarix* beetle *Diorhabda* spp. (55 sites – open circles). For each species and control method, solid lines are the 50th percentile of all observations (median), dashed are the 75th and dotted the 90th. Line diagonal arrows indicate that species cover was increasing or decreasing over time (Spearman test, solid line: $P < 0.05$; dotted line: $P < 0.10$). Note that biocontrol sites of years 0, 1, 2 and 3 were merged into one only category denoted at the position 1.5 in the X axis, for their low number of replicates. Undesirable reference sites representing conditions prior to *Tamarix* control are illustrated with open squares. Note that year 0 represents a site monitored immediately after *Tamarix* physical removal in the same year or since beetle arrival (equating to the first defoliation event), not pre-treatment conditions. Pre-treatment conditions (43 sites) are pooled with theoretical undesirable reference sites (36 sites) as indicated in methods. No significant differences were found between the two types of reference sites for any of the four noxious species or total cover of all weeds (Mann-Whitney tests, $P > 0.05$, not shown).

higher cover than in undesirable reference conditions. *B. tectorum* also exhibited high frequencies and cover in the *Tamarix* control sites but this species was the second most abundant among all weeds in the undesirable reference conditions and its cover did not increase after control.

The emergence of these four weeds as secondary invasions in *Tamarix* treated sites was not surprising. *Bassia scoparia* tolerates drought and high salinity (Friesen et al., 2009) (both common conditions in the arid and semi-arid southwestern U.S., and particularly along *Tamarix*-infested rivers (Busch and Smith, 1995; McShane et al., 2015)), but also tolerates saturated soils that occur on floodplains (listed as a "Facultative" wetland species, it may "occur in wetlands", PLANTS Database of the U.S. Department of Agriculture, USDA-NRCS, 2014). *Acroptilon repens* has been reported to exploit shallow water tables and to be frequent on floodplains and along river corridors (Jacobs and Denny, 2006; Kennard et al., 2016). *Salsola tragus* may spread from adjacent xeric bottomland terraces where it commonly grows, and it also tolerates heat, drought and salinity (Beckie and Francis, 2009).

Table 2
Mean + 1 SE abundance over time of four noxious species after control of *Tamarix* in 244 sites classified by control method. Letters indicate homogeneous groups following Kruskal-Wallis ($P < 0.05$, not shown) and pairwise Mann-Whitney tests across treatments ($P < 0.05$). Number of sites used at year 0 = 53; year 1 = 75; year 2 = 82; year 3 = 62; year 4 = 70; year 5 = 56; year 6 = 54; year 7 = 38; year ≥ 8 = 37.

	Yr = 0	Yr = 1	Yr = 2	Yr = 3	Yr = 4	Yr = 5	Yr = 6	Yr = 7	Yr ≥ 8
Acroptilon repens									
Burning	2.8ab + 2.1	4.8a + 4.0	5.6ab + 4.0	0.9b + 0.9	1.9ab + 1.2	3.6b + 3.5	5.4 ac + 4.9	13.0a + 0.0	0.0ab + 0.0
Heavy	4.8a + 2.9	0.5a + 0.4	2.7a + 1.0	6.7a + 2.4	8.6ab + 3.8	8.3ab + 8.3	19.2a + 9.8	0.0ab + 0.0	0.0b + 0.0
Cut	1.2b + 1.2	2.7a + 1.4	4.9ab + 2.7	5.6b + 3.4	11.5a + 4.6	4.6a + 4.0	1.1b + 0.6	0.0b + 0.0	1.7a + 1.5
Biocontrol	0.0b + 0.0	0.0a + 0.0	0.0b + 0.0	0.0b + 0.0	2.2b + 1.5	2.3ab + 1.3	4.1bc + 2.1	9.1a + 2.7	7.8a + 3.0
Bromus tectorum									
Burning	0.5b + 0.5	0.1b + 0.1	1.2b + 1.2	0.0b + 0.0	6.0a + 3.5	4.0ab + 4.0	0.0a + 0.0	0.0ab + 0.0	0.0b + 0.0
Heavy	2.1a + 0.7	2.5a + 1.1	8.7a + 3.7	4.5a + 3.5	1.2a + 0.9	0.0b + 0.0	0.0a + 0.0	0.0ab + 0.0	0.0b + 0.0
Cut	2.7ab + 1.8	2.4ab + 0.9	1.1bc + 0.4	2.1ab + 1.2	2.8a + 2.1	0.5b + 0.5	0.8a + 0.4	0.0b + 0.0	0.0b + 0.0
Biocontrol	0.3ab + 0.2	0.3ab + 0.2	0.3c + 0.2	0.3ab + 0.2	7.0a + 4.8	6.6a + 2.3	4.3a + 2.0	3.6a + 1.4	5.8a + 3.0
Bassia scoparia									
Burning	15.3a + 5.4	24.5a + 5.6	17.4a + 5.2	13.0ab + 5.6	12.0a + 4.9	7.6 ac + 5.6	13.1a + 5.2	17.8a + 0.0	0.6b + 0.4
Heavy	3.2b + 1.9	13.2ab + 5.7	18.3ab + 4.5	24.9a + 6.5	13.2a + 4.9	6.3a + 1.7	24.2ab + 24.0	72.0a + 0.0	6.8ab + 3.0
Cut	3.6b + 2.0	2.4c + 1.1	4.6c + 1.8	8.3b + 2.6	11.3a + 2.8	4.4b + 2.2	3.8b + 1.5	0.0b + 0.0	1.3ab + 1.3
Biocontrol	9.0ab + 5.5	9.0bc + 5.5	9.0bc + 5.5	9.0b + 5.5	14.1a + 6.5	4.7bc + 3.0	12.6a + 5.3	8.9a + 4.2	3.6a + 3.6
Salsola tragus									
Burning	9.2a + 4.3	2.6ab + 1.1	5.0a + 1.7	6.4a + 3.2	1.1ab + 0.8	1.1a + 0.7	6.3a + 5.9	0.3a + 0.0	0.0a + 0.0
Heavy	1.5a + 0.8	2.4a + 0.9	1.1a + 0.4	0.8a + 0.5	7.7a + 3.1	0.5a + 0.4	1.0ab + 1.0	0.0a + 0.0	0.6a + 0.4
Cut	3.2a + 1.6	1.6b + 0.6	3.4a + 1.3	3.3a + 1.2	0.8a + 0.2	0.7a + 0.4	0.5b + 0.3	0.2a + 0.1	1.2a + 1.0
Biocontrol	0.0b + 0.0	0.0c + 0.0	0.0b + 0.0	0.0b + 0.0	0.4b + 0.4	0.6a + 0.5	0.5ab + 0.3	0.9a + 0.5	0.0a + 0.0

Bromus tectorum is a pest in North American rangelands and also common in riparian areas (Mack, 1981; Knapp, 1996; Sher et al., 2008).

Our study analyzed vegetation in "undesirable reference" sites compared to vegetation in *Tamarix* control sites in order to determine the presence and extent of secondary invasions. It would be preferable to use pre-treatment data at each removal site to compare to post-removal conditions; however, only a small minority of our sites had pre-treatment data. We selected our undesirable reference sites to pair with and represent as closely as possible the geomorphic, hydrologic and ecologic pre-treatment conditions of each of our *Tamarix* control sites. Since we relied upon reference sites instead of pre-treatment data we can only suggest general patterns and not cause-and-effect, in the strictest sense. However because our reference sites closely approximate general pre-treatment conditions at our control sites and are in the same geographic areas as those sites, our results remain compelling.

4.2. *Tamarix* control methods may contribute to produce secondary invasions but these differ between noxious weeds

Lacking pre-control data for most sites, our database was not suitable to discern whether the simple opening up of space following control of the target species rather than control method was the main driver of secondary invasions, as suggested by Pearson et al. (2016). If the first was true, a negative correlation between the absolute cover of *Tamarix* and the absolute cover of noxious weeds would be likely. However, this was not the case in our study: the Spearman rho correlation coefficient was 0.12 ($P = 0.07$), which suggests that non-target invasive species exploiting the space vacated by the first alien is not the only mechanism to explain the severity of secondary invasions in the case of *Tamarix* control. Our study did show that the method of *Tamarix* control was related to the severity of secondary invasions and that this relationship differed between species, but also was affected by time since *Tamarix* control.

The relationship between secondary invasion and control treatments was complex, however; the noxious species under study exhibited slightly different patterns, suggesting that the responses of secondary invaders to control method may be idiosyncratic, that is, species-specific. The tumbleweeds *B. scoparia* and *S. tragus* were slightly more favored by an initial peak of higher disturbance induced by the physical removal treatments, versus *A. repens* and *B. tectorum*, which were more favored by the cumulative effects over time of biocontrol. Removal of *Tamarix* by heavy machinery and burning might have induced a sudden release from competition due to a great pulse in resource availability with physical soil disturbance and removal of biomass, followed by a presumably progressive increase in competition with ecosystem recovery. This sudden release of resources differs from mechanical saw-cutting, where removal targets only *Tamarix* and other non-native woody species such as *E. angustifolia* but leaves other vegetation in place, and from biocontrol, where *Tamarix* is repeatedly but not uniformly defoliated over the years by beetles that exclusively feed on them (Hultine et al., 2015; Kennard et al., 2016). Surprisingly, cover of native species did not differ much between control treatments (Mean ± 1 SE: Undesirable = 53.3a ± 6.6, Biocontrol = 33.5ab ± 3.9, Cut = 37.2a ± 2.6, Heavy = 60.4a ± 8.0, Burning = 26.6b ± 4.4; González et al., 2017 with letters showing homogeneous groups after Mann-Whitney tests, $P < 0.05$). However, this does not exclude the possibility that there was also biotic resistance to invasion, that is, the resident community was reducing invasion success (Levine et al., 2004). Promoting native species establishment has been suggested as a primary mechanism to reduce secondary invasion after *Tamarix* control (Sher et al., 2010; Pearson et al., 2016). The recovery of native vegetation following *Tamarix* control was generally poor (González et al., 2017); therefore, we believe that biotic resistance is weak in this system, at least at the temporal scale considered. Another argument for biotic resistance not playing a major role in controlling secondary invasions in *Tamarix* control was that we did not find a negative correlation between the absolute cover of natives and the absolute cover of noxious weeds (Spearman rho correlation coefficient = 0.11; $P = 0.10$). Recent studies have suggested that functional (not taxonomical) diversity more strongly determines biotic resistance to invasion (Hooper and Dukes, 2010; Byun et al., 2013). Future research should explore interactions between local functional diversity and *Tamarix* removal to explore this possibility.

Life-history traits of the noxious weeds may help to explain differences in their responses to *Tamarix* control methods, particularly traits related to the propagule pressure exerted by invaders on the ecosystem. Propagule pressure also represents a key factor to explain invasion success (Catford et al., 2009; Thomsen et al., 2006; Byun et al., 2015). Both *B. scoparia* and *S. tragus* plants are tumbleweeds, annual forbs that reproduce only by seed (Friesen et al., 2009). The entire above-ground portions of tumbleweeds naturally break off at the base of the plant and tumble away in the wind, dropping seeds along the way (Baker et al., 2008). This mechanism of seed dispersal may be enhanced by the use of heavy machinery during *Tamarix* removal, which may break and spread mature individuals containing seeds (when present in the treated sites before intervention), ultimately increasing propagule pressure. *Tamarix* removal could have also simply opened the pathway for tumbleweed species to move longer distances. Being prolific seed producers and having efficient wind-mediated seed dispersal (Baker et al., 2008; Friesen et al., 2009), they may also be favored by the expanded availability of safe sites for recruitment that immediately follows soil disturbance and removal of competing vegetation caused by physical removal methods, even if not originally present in the site, as was the case for most of the sites. Without vegetative reproduction, they may be more negatively affected by presumably higher competition with natives (biotic resistance) and with *Tamarix* (Mean *Tamarix* cover ± 1 SE: Undesirable = 46.6a ± 3.8, Biocontrol = 20.6b ± 2.7, Cut = 4.5c ± 1.0, Heavy = 8.6c ± 2.1, Burning = 5.5c ± 1.6; González et al., 2017 with letters showing homogeneous groups after Mann-Whitney tests, $P < 0.05$), which may explain their relatively poor performance in the biocontrol sites.

Bromus tectorum is a winter annual frequently associated with *Tamarix*-infested areas (undesirable sites, Fig. 2, Table B), as it invades riparian areas from adjacent uplands where it thrives (Mack, 1981; Knapp, 1996). In a previous study implemented on the Arkansas River through southeastern Colorado, Sher et al. (2008) reported reduced cover of *B. tectorum* in mechanically removed *Tamarix* stands of three small drainages. Although *B. tectorum* is also a prolific seed producer and reproduces only from seed (Klemmedson and Smith, 1964), it did not respond to physical removal treatments, particularly to burning, as positively as the two tumbleweed species. *Tamarix* stem mulch left onsite after removal has been suggested to inhibit *B. tectorum* seedling establishment (Sher et al., 2008), and it could be affecting *B. tectorum* and the tumbleweeds differently. Dela Cruz et al. (2014) showed that burning effectively reduced invasive *Bromus* spp. in riparian zones along the Virgin River in Zion National Park (UT, USA). We did not find such a reduction in *B. tectorum* immediately after restoration, but our results are consistent with Sher et al. (2008) and Dela Cruz et al. (2014) in that burning did not increase its cover as much as removal by heavy machinery and saw-cutting. Moreover, we observed a progressive decrease of this species' cover, most notably after five years of monitoring, in the heavy machinery and cut sites. One possibility for this response is that, in the absence of further disturbance, it was progressively outcompeted by the tumbleweeds, and native grasses and forbs recovering from initial disturbance. A better performance of *B. tectorum* in biocontrol sites over time, particularly since the fifth year since beetle arrival, may be explained by the positive response of the species to an increase in light availability (Klemmedson and Smith, 1964) and better germination and growth over natives in response to *Tamarix* litter, litter leachates and other soil properties typical of defoliated sites (Sherry et al., 2016). The fact that *B. tectorum* and the two tumbleweed species share important life-history traits such as reproduction from seed but at the same time exhibit different responses to the control treatments reinforces the idea that the responses of noxious weeds to anthropogenic disturbance are mainly idiosyncratic.

In contrast, *A. repens* is a perennial, persistent forb that can reproduce by seed but is thought to expand largely by vigorously spreading rhizomes (Jacobs and Denny, 2006). In fact, targeting the belowground biomass of *A. repens* is recommended as the most effective practice to remove the weed (Jacobs and Denny, 2006). The physical removal methods used to remove *Tamarix* plants, although not targeting the understory vegetation layer where secondary invasions occur, are more likely to trample and uproot the pre-existing plants at a site and therefore make re-invasion from clonal growth more difficult. *A. repens* also has reduced growth and development under low light conditions (Jacobs and Denny, 2006). Therefore, openings in the mid- and over-story following defoliation by beetles, with no negative effect on the rhizome system, might provide ideal conditions for the spread of this species. Sherry et al. (2016) have also shown that *Tamarix* litter and litter leachate inputs following beetle defoliation may favor *A. repens* germination and growth over natives.

4.3. Persistence of noxious weeds

The cover of three out of the four secondary weeds analyzed (*B. tectorum*, *B. scoparia* and *S. tragus*) decreased over time in the cut treatment. Cutting was the most selective among the three physical removal treatment methods, and probably did not interfere with the resident plant community or disturbed the soil as much as the other two methods. Thus, the combination of less disturbance and more existing established plants may have facilitated the observed decline in abundance of annual secondary invaders over time in the cut treatment sites. In contrast, the noxious weeds (except *B. tectorum* in heavy machinery sites) did not significantly decline in abundance over time in the more heavily-disturbed heavy machinery and burning sites. Moreover, *A. repens* and *B. tectorum* increased over time at the biocontrol sites. This persistence was especially surprising for *B. tectorum* and the two tumbleweeds, which are annual species. Several factors may explain these results. Follow-up measures to control secondary invasions, which were frequent in our study sites (56 out of 244 sites), perhaps were not as effective as intended. The abundance of noxious weeds when herbicides were applied was in fact higher (27.5%) than in sites where they were not applied (16.4%, Mann-Whitney test $U = 2995$, $Z = -2.994$; $P = 0.003$). Although this difference could be due to the fact that herbicides were applied to the sites having a higher abundance of weeds, it is known that species such as *B. scoparia* and *S. tragus* have developed resistance to commonly used herbicides such as imazapyr and glyphosate, hampering their reduction and eradication (Primiani et al., 1990; Chodova and Mikulka, 2000; Shafroth et al., 2013). Alternative explanations for the ineffectiveness of herbicides is that these were applied directly on the weeds, leaving the seed bank intact, and that herbicides can negatively affect germination of competing natives (Dela Cruz et al., 2014; Douglass et al., 2016). Knowing which type of herbicides was used at each site could have helped to anticipate the response of different secondary invaders of different functional groups (e.g., broadleaf herbicides suppressing forbs but not grasses; Pearson et al., 2016). Unfortunately, we were unable to obtain such information for most of the sites. Also unfortunately, we only had eight sites where abundance of weeds was monitored before and after herbicide application, and 16 sites that were monitored multiple times following the application of herbicides (no decreasing pattern was observed either; data not shown), so we were unable to test the true effect of follow-up in controlling weed persistence.

Nevertheless, we suggest that the conditions that caused site degradation and *Tamarix* infestation may have persisted after removal and be continuously favoring weeds, which have functional traits typical of ruderal or stress-tolerant strategies, similarly to *Tamarix* (Glenn and Nagler, 2005). For example, *Tamarix* sites usually lack mycorrhizal fungi while ruderal weeds are typically non-mycorrhizal species (Shafroth et al., 2008; Beauchamp et al., 2009). Other legacies of *Tamarix* dominance, such as salt accumulation in the soils typical of some *Tamarix* stands (Merritt and Shafroth, 2012; Ohrtman et al., 2012), may be favoring more stress-tolerant noxious species as well. Rivers are inherently highly disturbed systems, so the persistence of opportunistic species is not surprising. In fact, riparian zones are known to be especially vulnerable to invasions (Planty-Tabacchi et al., 1996; Richardson et al., 2007). The unexpected persistence of noxious weeds in these systems warrants further studies that take into account longer temporal scales, as the average time since *Tamarix* control in our sites was only five years.

5. Conclusions

We found that control method of a target invasive species may help explain secondary invasions of non-target, noxious weeds in riparian zones, and that this relationship was species-specific and changed over time. Even though primary invasions of *Tamarix* spp. and *Elaeagnus angustifolia* were effectively controlled by several treatments, *Acroptilon repens*, *Bromus tectorum*, *Bassia scoparia* and *Salsola tragus* are relevant secondary invaders in the context of *Tamarix* control in southwestern U.S. rivers. When physical removal methods such as burning, heavy machinery and saw-cutting are used to remove *Tamarix*, attention needs to be paid to potential secondary invasions immediately following removal, especially by annual tumbleweeds (*B. scoparia* and *S. tragus*) that only reproduce from seed. If biocontrol is used, longer-term monitoring is necessary to control the spread of weeds with effective vegetative reproduction, notably *A. repens*. *B. tectorum* is an important secondary invader, but more because of its high abundance prior to removal of the primary invader than for its capacity to proliferate in the treated sites. The cover of *A. repens* increased over time in biocontrol sites and, with the exception of the cut treatment, the cover of weeds did not decrease in sites where physical removal methods were implemented, even with herbicide application. This finding suggests the need to implement long-term monitoring of these projects and explore additional measures to improve the ecological status of invasive species-infested riparian zones besides traditional physical removal followed by chemical treatment of noxious weeds, such as the reduction of negative side effects of control methods, the mitigation of legacy effects and the improvement of the techniques for active introduction of native vegetation (Shafroth et al., 2008; Pearson et al., 2016).

Acknowledgements

This research was supported by a Marie Curie International Outgoing Fellowship within the 7th European Community Framework Programme (ESFFORES project number 299044) and a National Science Foundation Dynamics of Coupled Natural and Human Systems award (project number 1617463). The authors also thank D. Merritt and C. Douglass for sharing their data. Jennifer Schuetz provided valuable help to interpret BEMP's project data (Table A). Tamara Naumann and her staff in Dinosaur National Monument provided invaluable help sampling sites and providing very fruitful discussions. The work of the field assistants Mike Nagy, Rick Kluiver and Stuart Coles was also very much appreciated. We appreciate the comments of Dr. Catherine Jarnevich, which improved an earlier version of the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.06.043.

References

Baker, D.V., Beck, G., Bienkiewicz, B.J., Bjostad, L.B., 2008. Forces necessary to initiate dispersal for three tumbleweeds. Invasive Plant Sci. Manage. 1, 59–65.

Bay, R.F., Sher, A.A., 2008. Success of active revegetation after *Tamarix* removal in riparian ecosystems of the Southwestern United States: a quantitative assessment of past restoration projects. Restor. Ecol. 16, 113–128.

Beauchamp, V.B., Walz, C., Shafroth, P.B., 2009. Salinity tolerance and mycorrhizal responsiveness of native xeroriparian plants in semi-arid western USA. Appl. Soil Ecol. 43, 175–184.

Beckie, H.J., Francis, A., 2009. The biology of Canadian weeds. 65. *Salsola tragus* (updated). Can. J. Plant Sci. 89, 775–789.

Belote, R.T., Makarick, L.J., Kearsley, M.J., Lauver, C.L., 2010. Tamarisk removal in Grand Canyon National Park: changing the native non-native relationship as a restoration goal. Ecol. Restor. 28, 449–459.

Birken, A.S., Cooper, D.J., 2006. Processes of *Tamarix* invasion and floodplain development along the Lower Green River, Utah. Ecol. Appl. 16, 1103–1120.

Busch, D.E., Smith, S.D., 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the Southwestern U.S. Ecol. Monogr. 65, 347–370.

Byun, C., de Blois, S., Brisson, J., 2013. Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. J. Ecol. 101, 128–139.

Byun, C., de Blois, S., Brisson, J., 2015. Interactions between abiotic constraint, propagule pressure, and biotic resistance regulate plant invasion. Oecologia 178, 285–296.

Catford, J.A., Jansson, R., Nilsson, C., 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Divers. Distrib. 15, 22–40.

Chodova, D., Mikulka, J., 2000. Identification of resistance to imazapyr and cross resistance to selected sulfonylurea herbicides in *Kochia scoparia*. Z. Pflanzenkrankh. Pflanzenschutz 17, 383–388.

Dela Cruz, M.P., Beauchamp, V.B., Shafroth, P.B., Decker, C., O'Neil, A., 2014. Adaptive restoration of river terrace vegetation through iterative experiments. Nat. Areas J. 34, 475–487.

Douglass, C., 2013. Ecosystem Impacts of Tamarisk (*Tamarix* spp.) Management in the Arkansas River Watershed, Colorado: Effects of Disturbance and Herbicide Residues on Passive Plant Community Restoration. Ph.D. dissertation Colorado State University.

Douglass, C.H., Nissen, S.J., Meiman, P.J., Kniss, A.R., 2016. Impacts of imazapyr and triclopyr soil residues on the growth of several restoration species. Rangel. Ecol. Manag. 69, 199–205.

Friedman, J.M., Auble, G.T., Shafroth, P.B., Scott, M.L., Merigliano, M.F., Freehling, M.D., Griffin, E.R., 2005. Dominance of non-native riparian trees in western USA. Biol. Invasions 7, 747–751.

Friesen, L.F., Beckie, H.J., Warwick, S.I., Van Acker, R.C., 2009. The biology of Canadian weeds. 138. *Kochia scoparia* (L.) Schrad. Can. J. Plant Sci. 89, 141–167.

Glenn, E.P., Nagler, P.L., 2005. Comparative ecophysiology of *Tamarix ramosissima* and native trees in western U.S. riparian zones. J. Arid Environ. 61, 419–446.

González, E., Sher, A.A., Anderson, R.M., Bay, R.F., Bean, D.W., Bissonnete, G.J., Bourgeois, B., Cooper, D.J., Dohrenwend, K., Eichhorst, K.D., El Waer, H., Kennard, D.K., Harms-Weissinger, R., Henry, A.L., Makarick, L.J., Ostoja, S.M., Reynolds, L.V., Robinson, W.W., Shafroth, P.B., 2017. Vegetation response to invasive *Tamarix* control in southwestern U.S. rivers: a collaborative study including 416 sites. Ecol. Appl.

Harms, R.S., Hiebert, R.D., 2006. Vegetation response following invasive tamarisk (*Tamarix* spp.) removal and implications for riparian restoration. Restor. Ecol. 14, 461–472.

Hooper, D.U., Dukes, J.S., 2010. Functional composition controls invasion success in a California serpentine grassland. J. Ecol. 98, 764–777.

Hulme, P.E., Bremner, E.T., 2006. Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. J. Appl. Ecol. 43, 43–50.

Hulme, P.E., Pysek, P., Jarosik, V., Pergl, J., Schaffner, U., Vila, M., 2013. Bias and error in understanding plant invasion impacts. Trends Ecol. Evol. 28, 212–218.

Hultine, K.R., Belnap, J., Van Riper III, C., Ehleringer, J.R., Dennison, P.E., Lee, M.E., Nagler, P.L., Snyder, K.A., Uselman, S.M., West, J.B., 2010. Tamarisk biocontrol in the western United States: ecological and societal implications. Front. Ecol. Environ. 8, 467–474.

Hultine, K.R., Dudley, T.L., Koepke, D.F., Bean, D.W., Glenn, E.P., Lambert, A.M., 2015. Patterns of herbivory-induced mortality of a dominant non-native tree/shrub (*Tamarix* spp.) in a southwestern US watershed. Biol. Invasions 17, 1729–1742.

Jacobs, J., Denny, K., 2006. Ecology and Management of Russian Knapweed (*Acroptilon repens* (L.) DC). US Department of Agriculture, Natural Resources Conservation Service.

Jarnevich, C.S., Evangelista, P., Graham, J., 2013. Predicting tamarisk current and future distribution. In: Sher, A.A., Quigley, M. (Eds.), Tamarix: A Case Study of Ecological Change in the American West. Oxford University Press, New York, NY, pp. 29–43.

Johnson, T.D., 2013. Tamarix: Passenger or driver of ecosystem change? In: Sher, A.A., Quigley, M. (Eds.), Tamarix: a case study of ecological change in the American West. Oxford University Press, New York, New York, USA, pp. 256–266.

Kennard, D., Louden, N., Gemoets, D., Ortega, S., González, E., Bean, D., Cunningham, P., Johnson, T., Rosen, K., Stahlke, A., 2016. Tamarix dieback and vegetation patterns following release of the northern tamarisk beetle (*Diorhabda carinulata*) in Western Colorado. Biol. Control 101, 114–122.

Klemmedson, J.O., Smith, J.G., 1964. Cheatgrass (*Bromus tectorum* L.). Bot. Rev. 30, 226–262.

Knapp, P.A., 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the great basin desert: history, persistence, and influences to human activities. Glob. Environ. Chang. 6, 37–52.

Kuebbing, S.E., Nuñez, M.A., Simberloff, D., 2013. Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. Biol. Conserv. 160, 121–129.

Levine, J.M., Adler, P.B., Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecol. Lett. 7, 975–989.

Loo, S.E., Mac Nally, R., O'Dowd, D.J., Lake, P.S., 2009. Secondary invasions: implications of riparian restoration for in-stream invasion by an aquatic grass. Restor. Ecol. 17, 378–385.

Mack, R.N., 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7, 145–165.

McShane, R.R., Auerbach, A.D., Friedman, J.M., Auble, G.T., Shafroth, P.B., Merigliano, M.F., Scott, M.L., Poff, N.L., 2015. Distribution of invasive and native riparian woody plants across the western USA in relation to climate, river flow, floodplain geometry and patterns of introduction. Ecography 38, 1254–1265.

Merritt, D.M., Poff, N.L., 2010. Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers. Ecol. Appl. 20, 135–152.

Merritt, D.M., Shafroth, P.B., 2012. Edaphic, salinity, and stand structural trends in chronosequences of native and non-native dominated riparian forests along the Colorado River, USA. Biol. Invasions 14, 2665–2685.

Nagler, P.L., Glenn, E.P., Jarnevich, C.S., Shafroth, P.B., 2011. Distribution and abundance of saltcedar and Russian olive in the Western United States. Crit. Rev. Plant Sci. 30, 508–523.

Ohrtman, M.K., Sher, A.A., Lair, K.D., 2012. Quantifying soil salinity in areas invaded by *Tamarix* spp. J. Arid Environ. 85, 114–121.

Ostoja, S., Brooks, M.L., Dudley, T., Lee, S.R., 2014. Short-term vegetation response following mechanical control of saltcedar (*Tamarix* spp.) on the Virgin River, Nevada, USA. Invasive Plant Sci. Manage. 7, 310–319.

Pearson, D.E., Ortega, Y.K., Runyon, J.B., Butler, J.L., 2016. Secondary invasion: the bane of weed management. Biol. Conserv. 197, 8–17.

Perkins, D.W., Scott, M.L., Naumann, T., 2015. Abundance of invasive, non-native riparian herbs in relation to river regulation. River Res. Appl. 32, 1279–1288.

Planty-Tabacchi, A.M., Tabacchi, E., Naiman, R.J., Deferrari, C., Décamps, H., 1996. Invasibility of species-rich communities in riparian zones. Conserv. Biol. 10, 598–607.

Primiani, M.M., Cotterman, J.C., Saari, L.L., 1990. Resistance of kochia (*Kochia scoparia*) to sulfonylurea and imidazolinone herbicides. Weed Technol. 4, 169–172.

Ransom, C.V., Christensen, S.D., Edvarchuk, K.A., Naumann, T., 2012. A reinventory of invasive weed species in Dinosaur National Monument to determine management effectiveness. Invasive Plant Sci. Manage. 5, 300–309.

Reynolds, L.V., Cooper, D.J., 2011. Ecosystem response to removal of exotic riparian shrubs and a transition to upland vegetation. Plant Ecol. 212, 1243–1261.

Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P., Pysek, P., Hobbs, R.J., 2007. Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Divers. Distrib. 13, 126–139.

Shafroth, P.B., Beauchamp, V.B., Briggs, M.K., Lair, K., Scott, M.L., Sher, A.A., 2008. Planning riparian restoration in the context of *Tamarix* control in Western North America. Restor. Ecol. 16, 97–112.

Shafroth, P.B., Merritt, D.M., Briggs, M.K., Beauchamp, V.B., Lair, K.D., Scott, M.L., Sher, A.A., 2013. Riparian restoration in the context of *Tamarix* control. In: Sher, A.A., Quigley, M. (Eds.), Tamarix: A Case Study of Ecological Change in the American West. Oxford University Press, New York, NY, pp. 404–425.

Sher, A.A., Hyatt, L.A., 1999. The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. Biol. Invasions 1, 107–114.

Sher, A.A., Gieck, S., Brown, C.S., Nissen, S.J., 2008. First-year responses of cheatgrass following *Tamarix* spp. control and restoration-related disturbances. Restor. Ecol. 16, 129–135.

Sher, A.A., Lair, K., DePrenger-Levin, M., Dohrenwend, K., 2010. Best Management Practices for Revegetation in the Upper Colorado River Basin. Denver Botanic Gardens, Denver, CO, pp. 56.

Sherry, R.A., Shafroth, P.B., Belnap, J., Ostoja, S., Reed, S.C., 2016. Germination and growth of native and invasive plans on soil associated with biological control of tamarisk (*Tamarix* spp.). Invasive Plant Sci. Manage. 9, 290–307.

Stromberg, J.C., Lite, S.J., Marler, R., Paradzick, C., Shafroth, P.B., Shorrock, D., White, J.M., White, M.S., 2007. Altered stream-flow regimes and invasive plant species: the *Tamarix* case. Glob. Ecol. Biogeogr. 16, 381–393.

Thomsen, M.A., D'Antonio, C.M., Suttle, K.B., Sousa, W.P., 2006. Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. Ecol. Lett. 9, 160–170.

U.S. Dept of Agriculture-Natural Resources Conservation Service (USDA-NRCS), 2014. The PLANTS Database. http://plants.usda.gov.