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Ecosystem response to removal of exotic riparian shrubs and a transition to upland vegetation

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Abstract Understanding plant community change over time is essential for managing important ecosystems such as riparian areas. This study analyzed historic vegetation using soil seed banks and the effects of riparian shrub removal treatments and channel incision on ecosystem and plant community dynamics in Canyon de Chelly National Monument, Arizona. We focused on how seeds, nutrients, and ground water influence the floristic composition of post-treatment vegetation and addressed three questions: (1) How does pre-treatment soil seed bank composition reflect post-treatment vegetation composition? (2) How does shrub removal affect post-treatment riparian vegetation composition, seed rain inputs, and ground water dynamics? and (3) Is available soil nitrogen increased near dead Russian olive plants following removal and does this influence post-treatment vegetation? We analyzed seed bank composition across the study area, analyzed differences in vegetation, ground water levels, and seed rain between control, cut-stump and whole-plant removal areas, and compared soil nitrogen and vegetation near removed Russian olive to areas lacking Russian olive. The soil seed bank contained more riparian plants, more native and fewer exotic plants than the extant vegetation. Both shrub removal methods decreased exotic plant cover, decreased tamarisk and Russian olive seed inputs, and increased native plant cover after 2 years. Neither method increased ground water levels. Soil near dead Russian olive trees indicated a short-term increase in soil nitrogen following plant removal but did not influence vegetation composition compared to areas without Russian olive. Following tamarisk and Russian olive removal, our study sites were colonized by upland plant species. Many western North American rivers have tamarisk and Russian olive on floodplains abandoned by channel incision, river regulation or both. Our results are widely applicable to sites where drying has occurred and vegetation establishment following shrub removal is likely to be by upland species.

Keywords *Tamarix* spp. · *Elaeagnus angustifolia* · Seed inputs · Riparian ground water · Soil seed banks · Soil nitrogen

Introduction

Understanding shifts in plant community composition due to the impacts of changing abiotic conditions, human land management, and exotic species invasions is a critical challenge for scientists and land managers (Simberloff 2005; Jackson and Hobbs 2009). In many cases, plant communities have changed dramatically from their historic conditions

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and formed novel ecosystems (Cooper and Andersen 2010; Johnson 2002). These ecosystems present unique challenges to scientists who seek to understand future trajectories of vegetation composition and land managers who facilitate the development of plant and animal habitat (Hobbs et al. 2009). Riparian areas are of particular concern because they enhance regional biodiversity despite covering a small percentage of the landscape (Sabo et al. 2005). They also have been invaded by exotic species disproportionately more than other habitats worldwide (Stohlgren et al. 1998). Effectively analyzing change over time is essential for managing important ecosystems such as riparian areas (Harms and Hiebert 2006).

Impacts from land use, river regulation, climate changes and exotic species invasions on riparian areas in the southwestern US have led to significant changes in floodplain landforms and plant community composition over the last century (Stromberg 2001; Webb and Leake 2006). Many streams have incised due to river regulation and climatic variability that has disconnected streams from their floodplains (Birken and Cooper 2006; Graf 1983; Johnson 2002). Also, southwestern floodplains have been invaded by the exotic riparian shrubs tamarisk (*Tamarix ramosissima* Ledebour, *T. chinensis* Loureiro, and their hybrids) and Russian olive (*Elaeagnus angustifolia* L.) (Friedman et al. 2005) that form dense stands in many areas. Historically they had less vegetation cover and were characterized by stands of native cottonwood (*Populus deltoides* Marshall subsp. *wislizeni* (Watson) Eckenwalder) and willows (*Salix* spp.) (Webb and Leake 2006).

To restore southwestern riparian areas, many land managers are removing stands of exotic riparian shrubs. Common goals of riparian shrub removal programs include restoring native vegetation, increasing water availability, and improving wildlife habitat (Shafroth et al. 2005). Tamarisk and Russian olive were thought to deplete scarce water supplies in arid regions (Stromberg et al. 2009; Cleverly et al. 2006), however, recent research indicates that tamarisk water use is nearly equivalent to native riparian trees on a leaf area basis (Nagler et al. 2009; Sala et al. 1996). Nevertheless, increasing water availability continues to be a principal goal of riparian shrub eradication efforts (Shafroth et al. 2005).

Despite these control efforts (Bay and Sher 2008; Tiedemann and Klemmedson 2004), little is known about vegetation history prior to invasion or vegetation response to the removal treatments (Shafroth et al. 2008). The removal of shrubs and trees in other ecosystems has produced increases in understory cover and richness (Martin and Morton 1993; Herbel et al. 1983; Brudvig and Asbjornsen 2007). However, because southwestern rivers are largely controlled by dams and water diversions, and have floodplains that are drier than historic conditions, the plant communities that establish following exotic shrub removal may be distinct from historic plant communities (Seastedt et al. 2008; Johnson 2002). Environmental shifts away from historic conditions are an essential consideration when planning restoration and understanding potential outcomes (Hobbs et al. 2010; Hobbs et al. 2009). Key ecosystem factors that will influence the future community composition include water, seed, and nutrient availability (Richter and Stromberg 2005; Berlow et al. 2003).

Seed availability, from aerial seed rain inputs and soil seed banks, can influence vegetation composition following disturbances such as plant removal (Gurevitch et al. 2002; Vosse et al. 2008). Riparian soil seed banks include seeds that have arrived in river-deposited sediment, or by wind and animal dispersal. Species present in the seed bank may reflect past and present vegetation and can be useful in restoration (Goodson et al. 2001; Richter and Stromberg 2005; Holmes and Cowling 1997).

Nutrient availability may also influence vegetation establishment after woody plant removal especially in arid region ecosystems where shrubs may concentrate nutrients and moisture around them (Schade and Hobbie 2005; Klemmedson and Tiedemann 1986). Russian olive in particular may have a lasting impact on floodplain soils since it forms a symbiosis with nitrogen fixing bacteria (Bertrand and Lalonde 1985; DeCant 2008). In addition, Russian olive leaf litter is higher in nitrogen than native cottonwood (Harner et al. 2009; Shah et al. 2010) and may alter vegetation composition by increasing available soil nitrogen while it is alive and after it has been removed (Hughes and Denslow 2005; Marchante et al. 2009).

In this study, our goals were to analyze historic vegetation using soil seed banks and to analyze the effects of riparian shrub removal treatments on ecosystem and plant community dynamics in Canyon de Chelly National Monument (Canyon de Chelly), Arizona. We focused on how seeds, nutrients, and ground water influence the floristic composition of post-treatment vegetation and addressed three questions: (1) How does pre-treatment soil seed bank composition reflect post-treatment vegetation composition? (2) How does shrub removal affect post-treatment riparian vegetation composition, seed rain inputs, and ground water dynamics? and (3) Is available soil nitrogen increased near dead Russian olive plants following removal and does this influence post-treatment vegetation?

Methods

Study area

Our study was conducted in Canyon de Chelly National Monument, within the Navajo Nation near Chinle, AZ (Fig. 1). Two main canyons, Canyon de Chelly and Canyon del Muerto drain the western side of the Chuska Mountains and join to form Chinle Wash. Our study area included the lower 25 km of Canyon de Chelly, the lower 17 km of Canyon del Muerto, and the first 10 km of Chinle Wash. The town of Chinle receives an annual average of 23.3 cm of precipitation, with >50% falling during the mid to late summer due to strong monsoon-driven precipitation events. Chinle Wash is an intermittent stream with a bimodal flow pattern: discharge peaks occur due to both spring snowmelt runoff and late-summer monsoon rains. During 1934–1937 the U.S. Soil Conservation Service planted tamarisk and Russian olive in Canyon de Chelly in an effort to protect ancient Pueblo ruins and modern farms from river bank erosion (SCS 1934). Tamarisk and Russian olive subsequently spread throughout Canyon de Chelly and now dominate the riparian vegetation. The historic streambeds in Canyon de Chelly, Canyon del Muerto, and Chinle Wash were wide, shallow, and braided, and Chinle Wash remains wide today. However, upstream of Chinle Wash the current stream channel bed is now 1–4 m below terraces that support dense tamarisk, Russian olive, and cottonwood stands (Rink 2003; Cadol et al. 2010).

Study design

Plant removals occurred within six 1.1-km-long study reaches which were the width of the riparian plant community. The upstream 300 m of each reach was the untreated control, and directly downstream was a 300 m long cut-stump treatment, where plants were cut by chainsaw and stumps treated with Garlon 4® herbicide by National Park Service Exotic Plant Management staff. Downstream of the cut-stump treatment was a 200 m buffer zone, and a 300-m-long whole-plant removal treatment reach where tamarisk and Russian olive stems and the largest roots were removed by Canyon de Chelly staff using a backhoe. This configuration was necessary to limit the downstream effects of treatments on each other or the control. Exotic plant removals were started in the winter of 2005 and continued through fall of 2006. Wood produced by the treatments was piled and burned. All data were collected in these six study areas except soil seed bank samples that were collected outside the removal study areas due to the effect that sampling might have on the vegetation in the removal study areas. See "Soil seed bank" section below for details on site selection.

Soil seed bank

The riparian soil seed bank was analyzed using samples collected in June 2007 from 12 randomly selected points in Canyon de Chelly. The riparian zone was stratified by plant patch type (Russian olive, tamarisk, cottonwood/willow, and meadows lacking woody cover) and floodplain terrace (active channel, young terrace, and old terrace). Floodplain terraces were identified from aerial photographs of Canyon de Chelly from 1935, 1965, 1974, 1981, and 2004. Little vegetation occurred along the stream between 1935 and 1981, thus "old" terraces were stabilized by vegetation prior to the 1981 aerial photographs and "young" terraces were those terraces stabilized between 1981 and the 2004 photographs (Cadol et al. 2010). Soil samples were collected at one random location within each patch type and terrace age combination in each site. A 30 cm × 30 cm × 5 cm square of top soil was extracted at each sample location. Samples were spread onto individual 25 cm × 20 cm trays in a greenhouse and watered twice daily with 1 cm of water through the entire growing season. The seed bank study was designed to determine which species could emerge during 1 year. Almost all germinants emerged from the seed bank during the first 1–2 months of the study. Germinating

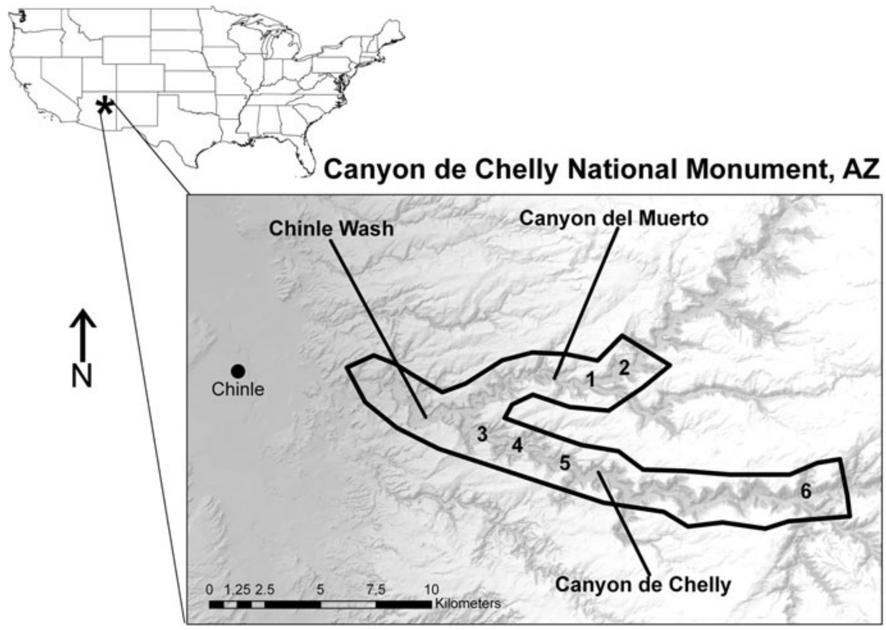

Fig. 1 Map of Canyon de Chelly National Monument, Arizona, United States. The *star* on the map of the United States indicates the location of Canyon de Chelly and the enlarged area. Exotic plant extraction study site locations are indicated by numbers: *1* Navajo Fortress, *2* Standing Cow, *3* Lower White House, *4* Upper White House, *5* Sliding Rock, and *6* Spider Rock

seedlings were identified and removed. Plants that did not flower were brought to Colorado State University in November 2007 and placed in a heated greenhouse until they could be identified. Nomenclature follows the USDA PLANTS Database (USDA 2010). Species were identified as "riparian" if their wetland indicator status was "Obligate" or "Facultative wetland" for Region 7, Arizona, and wetland indicator scores (WISs) were assigned according to the USDA PLANTS database and Reed (USDA 2010; Reed 1997). WISs included obligate wetland (1), facultative wetland (2), facultative (3), facultative upland (4), and upland (5) (Reed 1997). An analysis of variance model was used to test the effect of plant patch type and terrace age on relative abundance of exotic species, native species, and riparian species (a subset of native species) in the soil seed bank.

Vegetation

Vegetation was analyzed in plots along regularly spaced transects in the six study areas. Three transects were aligned perpendicular to the canyon wash in each control and treatment, spaced 100 m apart, yielding nine transects in each study site, and 54 total transects. Each transect spanned the riparian area width. Plots were placed continuously along the transect length. Each plot was three m in radius with a 0.5 m radius plot nested inside. Percent canopy cover of woody species was visually estimated to the nearest percent within the 3 m radius plot and percent cover of herbaceous plants was estimated within 0.5 m radius plots. Species were identified and characterized as native or exotic and assigned WISs. Weighted-average WISs were calculated for extant vegetation and soil seed bank vegetation by multiplying the relative cover of plants (extant vegetation) or the relative density of plants (soil seed bank) within each wetland indicator class by class scores (Wentworth et al. 1988). Lower weighted-average WISs indicate more mesic plants and higher weighted-average WISs indicate more xeric plants. For statistical analyses, cover estimates by species within plots were summed across each transect because plots within transect were not independent, and divided by area (m^2) sampled in each transect. Transects were treated as the sampling unit.

Non-metric multidimensional scaling (NMDS) was used to analyze herbaceous community composition between transects among treatments in 2005 (pre-treatment) and in 2008 (post-treatment). NMDS grouped transects with similar herbaceous composition and is considered a robust unconstrained ordination analysis (Minchin 1987). The "vegan" package in the program R version 2.8.1 was used to conduct Wisconsin double standardization of the data. Bray–Curtis dissimilarities were calculated for the standardized data and the ordination performed from several random starts until a convergent solution was found (R Development Core Team 2010). We used PRIMER v.6 software to conduct Analysis of Similarity (ANOSIM) on the dissimilarity matrix and to calculate species contribution to dissimilarity percentages (simper analysis) between treatments controlling for site differences in 2005 and in 2008 (Clarke and Gorley 2006). ANOSIM tested for differences between treatments and sites by calculating an R statistic: R values of 1 indicate complete difference in species composition and an R of 0 indicates no difference in species composition.

We used a univariate approach to analyze the effect of treatment and years (pretreatment: 2005, and post-treatment years: 2007 and 2008) on native and exotic species cover of herbaceous and woody vegetation using a mixed-effects model where "treatment nested within site" is a random effect, allowing inference to the landscape from which sites were selected (Bolker et al. 2009).

Wind-born seed rain

Wind-dispersed tamarisk, cottonwood, and willow seed densities were measured using sticky traps. Traps were 30 cm × 30 cm plywood slabs oriented horizontal to and 1 m above the ground, attached to a fence post and installed in May 2005. Tanglefoot©, a sticky substance was applied to traps weekly. One transect of three seed traps was established perpendicular to the channel in each treatment and control, yielding nine seed traps per study site and 54 traps total. Caught seeds were counted and removed from traps weekly from late-May through mid-August each summer: 2005–2007. Data were log-transformed to correct for over-dispersion and mixed-effects Poisson regression was used to analyze the effect of treatment and date on tamarisk seed rain. We assumed a Poisson error structure because our data were counts including zeros (Crawley 2007). We analyzed one pre-treatment (2005) and one post-treatment year (2007). For both 2005 and 2007 models, the random effects "site", "trap within site", "site and treatment interaction", and "site and date interaction" and the fixed effects "treatment", "date" and "tamarisk canopy" were included in the mixed-effects model.

Ground seed rain

Seed abundance on the soil surface was assessed during May and June 2007. 25 cm × 25 cm plots were established 6 m in each cardinal direction from each seed rain trap. We collected, counted, and identified all mature seeds on plants within the plot and on the ground. Seed abundances were summed across plots within each trap site and data were log-transformed to correct for over-dispersion. Mixed-effects regression was used to analyze the effect of treatment on richness and the abundance of native and exotic species seeds. The random effects "site" and "trap within site" and the fixed effect "treatment" were included in each mixed-effects model.

Ground water

Depth to the water table was measured weekly during the summers of 2005–2007 using slotted, hand-installed ground water monitoring wells. Each study site had three well transects perpendicular to the channel, one transect in each treatment and control. Within each 1100 m long stream reach site (see "Study design" section), treatments and controls experienced the same stream flow due to close proximity. Two to four wells were evenly spaced along each transect and at least one well on each channel bank. Ground water variation among years is non-linear, therefore pre- and post-treatment years 2005 and 2007 were modeled separately. In 2007, only pre-monsoon season data were analyzed (May–July 15) to assess dry season ground water decline. We employed a mixed-effects model for both pre- and post-treatment years and included the random effects "site" and "treatment within site" and the fixed effects treatment, "date", and "distance (distance from the stream channel)."

Soil nitrogen and vegetation

Soil nitrogen (N) availability was analyzed using ion exchange resin bags that absorb available nitrate and ammonium from the soil and provide an estimate of plant available soil N (Binkley and Matson 1983). Following removal treatments, soil N was analyzed near cut-stump Russian olives and in adjacent meadows that lacked Russian olives in 2006 and 2007. Three vegetation sampling plots (see "Vegetation" section) were randomly chosen in each cut-stump treatment at sites 3–6 (Fig. 1). The Russian olive bole closest to each randomly chosen plot was found and five resin bags were placed 40 cm deep, within the root zone where we found root nodules, around the cut Russian olive bole. Resin bags were installed in September of 2006 and collected in March of 2007 to exploit the winter period of high soil moisture and the spring pulse of nutrient availability. More resin bags were installed in September 2007 and collected in March 2008. For reference, five control resin bags were placed in an X pattern, 75 cm from each other and at least 10 m from the closest Russian olive bole. Mixed-effects models were used to determine the effect of Russian olive cut-stump presence on available soil nitrogen in 2006 and 2007. “Plot within site” was included as a random effect. All soil nitrogen data were log-transformed to meet normality assumptions. Mixed-effects models were also used to determine the post-treatment effect of Russian olive cut-stump presence (vegetation plots with greater than 30% Russian olive canopy cover in the 2005) on percent exotic species cover and percent native species cover within cut-stump treatment sites. “Site” was included as a random effect.

All statistical analyses, except ANOSIM and Simper as indicated above, were conducted in the R program version 2.8.1 (R Development Core Team 2010).

Results

Soil seed bank

The soil seed bank had lower relative abundance of exotic species and higher relative abundance of native species than the extant treatment plot vegetation relative cover in 2008 (Fig. 2). Weighted-average WIS for the soil seed bank was 2.82 ± 0.10 (mean $\pm$ SE) and ranged between 3.60 ± 0.10 and 3.80 ± 0.06 for extant vegetation in treatment plots (Fig. 2). Thirteen riparian species were found in the soil seed bank across all sites compared with only six in the extant vegetation (Appendix). Patch type did not affect seed bank composition of native, exotic, or riparian species, but terrace age did with more exotic and fewer native and riparian species in the active channel compared to older terraces (Fig. 3).

The average percent exotic species did not vary across patch types ($F = 1.63$, $P = 0.16$), or between floodplain terraces of different ages ($F = 2.00$, $P = 0.14$) and the percent of exotic species in a given patch type did not depend on terrace age ($F = 0.47$, $P = 0.75$, Fig. 3). The highest percentages of native species occurred on the terraces and the lowest in the channel ($F = 2.50$, $P = 0.04$, Fig. 3). Average percent of native species varied across terrace age with increasing native species with increasing terrace age ($F = 6.61$, $P = 0.01$, Fig. 3). Percent native species by patch type did not depend on terrace age ($F = 0.81$, $P = 0.52$). The average percent of germinating riparian species did not vary across patch types and increased slightly with increasing terrace age ($F = 1.15$, $P = 0.34$ and $F = 3.75$, $P = 0.06$) and the percent of riparian species in a given patch type did not depend on terrace age ($F = 0.23$, $P = 0.92$).

Vegetation

Herbaceous plant species cover

105 herbaceous plant species were identified in the vegetation plots (Appendix). Species with the highest cover were both exotic and native and mostly upland species (WIS = 4–5) (Table 1). NMDS indicated that in 2005 there was little differentiation between sites prior to the implementation of treatments. However, the differentiation of transects between treatment types was apparent in the 2008 data (Fig. 4). A two-way analysis of similarity (ANOSIM) in 2005 indicated no difference between treatments, controlling site-effects (Global $R = 0.043$, $P = 0.26$) but showed significant differences among sites (Global $R = 0.27$, $P < 0.001$). A two-way ANOSIM of 2008 data indicated significant differences between treatments, controlling for site (Global $R = 0.48$, $P < 0.001$) and significant differences between sites (Global $R = 0.43$, $P < 0.001$).

Simper analysis of vegetation in 2008 indicated that differences in community composition between controls and treatments were due primarily to the abundance of *Bromus tectorum* and *Bromus rigidus* in controls and *Sporobolus cryptandrus* in treatment plots (Fig. 4; Table 1). Several other species also contributed to differences between control and treatment sites (Fig. 4; Table 1). Control sites and cut-

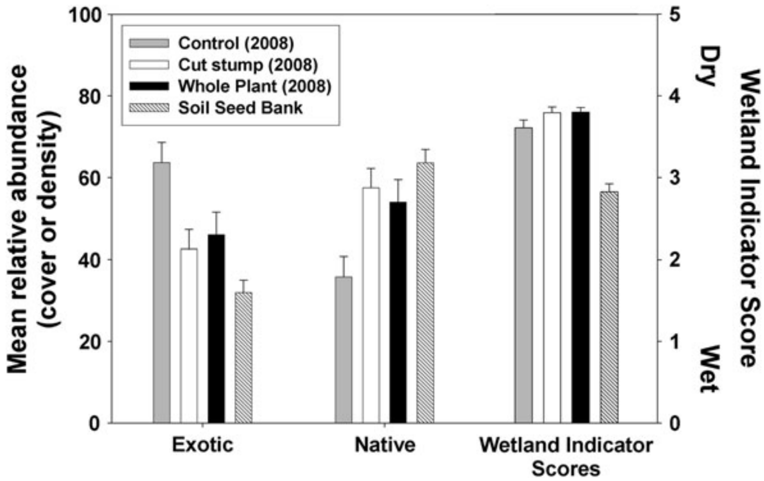

Fig. 2 Mean ± SE relative abundance (cover for treatments and density for seed bank on the *left axis*) of exotic and native species and mean ± SE weighted-average wetland indicator scores per m^2 (*right axis*) for herbaceous vegetation in 2008 in removal treatments and soil seed bank: control (*gray*), cut-stump (*white*), whole-plant removal (*black*), and soil seed bank (*hatched*)

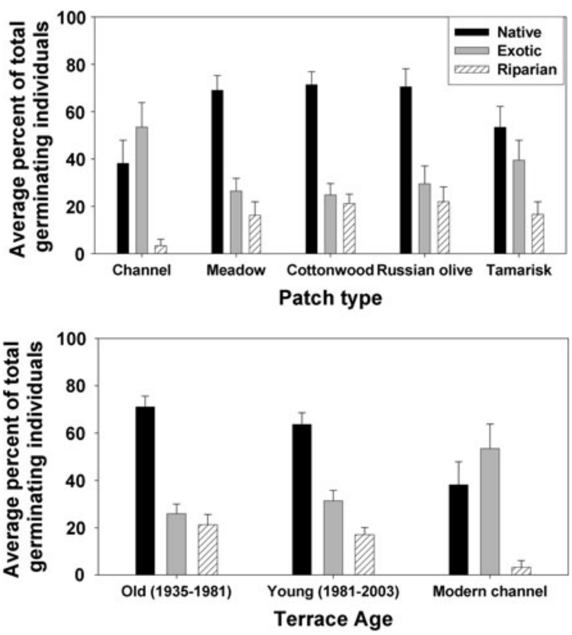

Fig. 3 Average percent of the total number of germinating individuals that were native (*black*), exotic (*gray*), and riparian species (*hatched*, a subset of native) in soil seed bank samples from different patch types (*top panel*) and on terraces of different ages (*bottom panel*)

stump treatment sites were less different (average dissimilarity = 68.56) than controls and whole-plant removal sites (average dissimilarity = 84.07, Fig. 4). Herbaceous composition across years and treatments was predominantly of upland species with WISs of 3 or greater (Table 1; Fig. 4).

Transects within both the cut-stump and the whole-plant removal treatments had fewer exotic herbaceous species and higher native herbaceous species cover (Fig. 5) than control sites. A random effects model of percent exotic herbaceous species cover indicated that the effect of treatment depended on year, confirming that there was no effect of treatment in 2005, but a treatment effect appeared in 2007–2008. Both the cut-stump and whole-plant treatments had a lower percent of exotic herbaceous species compared to the control after 2005 (estimate = −7.43, $t = -2.86$, $P < 0.001$, and estimate = −10.54, $t = -3.95$, $P < 0.001$). Both the cut-stump and whole-plant treatment plots had higher percent native herbaceous species compared to controls after 2005 (estimate = 7.55, $t = 2.92$, $P = 0.004$; and estimate = 10.64, $t = 4.01$, $P < 0.001$). There was no effect of cut-stump or whole-plant removal treatment on species richness across years ($t = 0.37$, $P = 0.72$ and $t = -0.24$, $P = 0.81$) but richness increased with year across treatments (estimate = 1.26, $t = 4.88$, $P < 0.001$).

Woody plant species cover

A total of 14 woody plant species were found in the plots (Appendix). Russian olive had the greatest cover across all sites followed by cottonwood and tamarisk. The cut-stump and whole-plant removal treatments reduced exotic woody plant canopy cover (predominantly tamarisk and Russian olive) nearly to zero from 2005 through 2008 (Cut-stump: estimate = −16.67, $t = -5.02$, $P < 0.001$; Whole-plant: estimate = −24.26, $t = -7.05$, $P < 0.001$). Native canopy cover remained constant across treatments and years, neither cut-stump nor whole-plant treatment had an effect on the percent of native woody species compared to the

Table 1 Average abundances (Ave. abund.), average dissimilarities (Ave. dissim.), and dissimilarity percentage contributions of the ten species that most influenced differences in vegetation composition between (A) control and cut-stump treatments and between (B) control and whole-plant treatments (lower table) in 2008 vegetation plots

Species	Control Ave. abund.	Treatment Ave. abund.	Ave. dissim.	Dissim. contribution %	Cumulative contribution %
(A) Control vs. cut-stump treatment					
Bromus tectorum (E,3)	38.88	19.27	15.53	22.66	22.66
Sporobolus cryptandrus (N,4)	2.83	8.11	8.28	12.07	34.73
Bromus rigidus (E,4)	16.55	4.36	7.30	10.65	45.38
Heterotheca villosa (N,5)	8.02	6.74	3.71	5.41	50.79
Salsola iberica (E,4)	0.31	6.28	3.12	4.55	55.35
Hordeum murinum (E,4)	1.95	3.98	2.37	3.46	58.81
Croton texansis (N,4)	0.13	4.47	2.20	3.20	62.01
Senecio spartioides (N,4)	2.22	4.23	1.65	2.40	64.42
Ambrosia acanthacarpa (N,4)	1.37	3.38	1.65	2.40	66.82
Artemisia ludoviciana (N,5)	1.66	3.29	1.61	2.35	69.17
(B) Control vs. whole-plant treatment					
Bromus tectorum (E,3)	38.88	6.54	17.59	20.92	20.92
Bromus rigidus (E,4)	16.55	1.30	9.41	11.19	32.11
Sporobolus cryptandrus (N,4)	2.83	17.16	7.87	9.36	41.48
Ambrosia acanthacarpa (N,4)	1.37	15.68	7.56	8.99	50.47
Salsoa iberica (E,4)	0.31	13.78	6.75	8.03	58.49
Heterotheca villosa (N,5)	8.02	1.08	4.41	5.24	63.74
Hordeum murinum (E,4)	1.95	9.40	4.02	4.78	68.52
Croton texansis (N,4)	0.13	5.51	2.71	3.23	71.74
Tribulus terrestris (E,4)	0.00	4.79	2.39	2.85	74.59
Polygonum aviculare (E,2)	0.82	3.74	1.76	2.09	76.69

Species that have higher abundances in treatments than in controls appear in bold print. Status as exotic (E) or native (N) and wetland indicator scores are in parentheses next to species names

control, from 2005 through 2008 (Estimate $= -1.12$, $t = -0.45$, $P = 0.66$ and estimate $= -2.22$, $t = -0.85$, $P = 0.40$, Fig. 5).

Wind-born Seed rain

Native cottonwood and willow aerial seed rain peaked earlier than tamarisk seed rain across sites between years, and occurred during May and June. Tamarisk seed rain peaked during May through July, and occurred for longer duration than cottonwood and willow every year, and continued until late August in all years (Fig. 6). Average peak seed rain for tamarisk, cottonwood and willow 2005–2007 in control sites was 3020 ± 723 (mean ± SE), 325 ± 253, and 213 ± 164 seeds/m^2/day. A mixed-effects Poisson regression model for 2005 tamarisk seed rain indicated that, prior to removal, daily seed rain density was not different between treatment sites ($Z = -0.14$, $P = 0.89$ and $Z = 1.08$, $P = 0.28$) but date and percent tamarisk cover around each trap were significant predictors of seed rain density ($Z = 5.75$, $P < 0.001$ and $Z = 2.95$, $P = 0.003$). A mixed-effects Poisson regression model for 2007 tamarisk seed rain indicated that treatment effected seed rain, with both the cut-stump and the whole-plant treatments significantly reducing seed rain when compared to the control ($Z = -5.90$, $P < 0.001$ and $Z = -4.56$, $P < 0.001$). Date was also a significant factor ($Z = 3.79$, $P < 0.001$), but tamarisk cover at the traps was not a significant factor ($Z = -0.37$, $P = 0.71$).

Ground seed rain

Ground seed rain species richness was highest in the whole-plant removal sites ($t = 3.35$, $P = 0.002$)

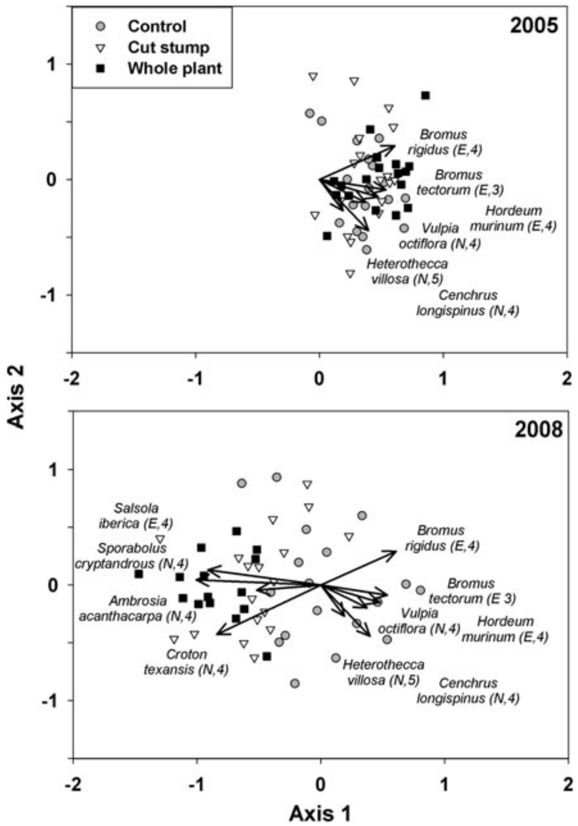

Fig. 4 Results of a Non-metric multidimensional scaling (NMDS) analysis of plant community composition in 2005 (pre-treatment, *top panel*) and 2008 (post-treatment, *bottom panel*) along transects in control (*gray circle*), cut-stump (*inverted triangle*), and whole-plant (*square*) treatments. Species ordination is overlaid on the plot ordination with *arrows* indicating the direction of influence of various species. The ten most abundant species across all plots are shown. Status as exotic (E) or native (N) and wetland indicator scores are shown in *parentheses* next to species names

compared to the cut-stump and control sites where richness was not significantly different ($t = -0.33$, $P = 0.74$). Native species seed rain was significantly greater in the whole-plant removal than control sites ($Z = 4.96$, $P < 0.001$), but not different between cut-stump removal sites and controls ($Z = 0.42$, $P = 0.68$). Exotic species seed rain was high in both the control and the whole-plant treatments which were not significantly different from each other ($Z = -0.04$, $P = 0.78$), and the cut-stump had marginally lower ground seed rain than the control sites ($Z = -0.25$, $P = 0.08$). Russian olive seed rain was reduced from 27.8 ± 11.3 seeds/m^2 (mean ± SE) in control sites to 0.5 ± 0.3 and 0.3 ± 0.2 seeds/m^2 in cut-stump and whole-plant removal sites.

Ground water

A perennial water table occurred beneath all floodplain areas, and all monitored stream reaches were hydrologically losing, with ground water elevation decreasing in elevation with distance from the channel relative to stream bed elevation. Water table was most shallow during the winter and spring (1–4 m deep), decreased during the summer (2 to >6 m deep) and increased again in fall. A mixed-effect regression model for ground water depth in 2005 (pre-treatment) showed that neither treatment accounted for any variation in ground water depth compared to controls (−39.18 ± 32.40 (estimate ± SE), $P = 0.10$ and −26.44 ± 26.35, $P = 0.35$). However, "date" and "distance from the streambed" were significant predictors with positive relationships between increasing water table depth and increasing time during the summer and distance from the streambed (7.62 ± 2.40, $P = 0.002$ and 1.43 ± 0.23, $P < 0.0001$). A model for ground water in 2007, prior to the monsoon season, showed no effect of either treatment (17.38 ± 48.59, $P = 0.73$ and −20.49 ± 51.51, $P = 0.70$), but the effect of the treatment depended on distance from the streambed (−0.66 ± 0.66, $P = 0.32$ and −1.51 ± 0.56, $P = 0.0072$). Again, the predictors "date" and "distance" were significant with increasing time during the summer and increasing distance from the streambed accounting for increasing depth to water table (8.69 ± 1.44, $P < 0.0001$ and 2.59 ± 0.42, $P < 0.0001$).

Soil nitrogen and vegetation

In 2006, available soil nitrate and ammonium concentrations within a 2 m radius of killed Russian olive boles were higher than reference areas that lacked Russian olive (nitrate: $t = 3.08$, $P = 0.003$; ammonium: $t = 4.77$, $P < 0.001$; Fig. 7). Available soil nitrate and ammonium concentrations remained higher in 2007 within a 2 m radius of dead Russian olive boles than reference areas (nitrate: $t = 4.26$, $P = 0.0001$; ammonium: $t = 2.75$, $P = 0.01$; Fig. 7).

In 2005 the presence of Russian olive boles had no effect on percent exotic species cover (t = 0.70, $P = 0.49$) or native species cover ($t = -0.78$,

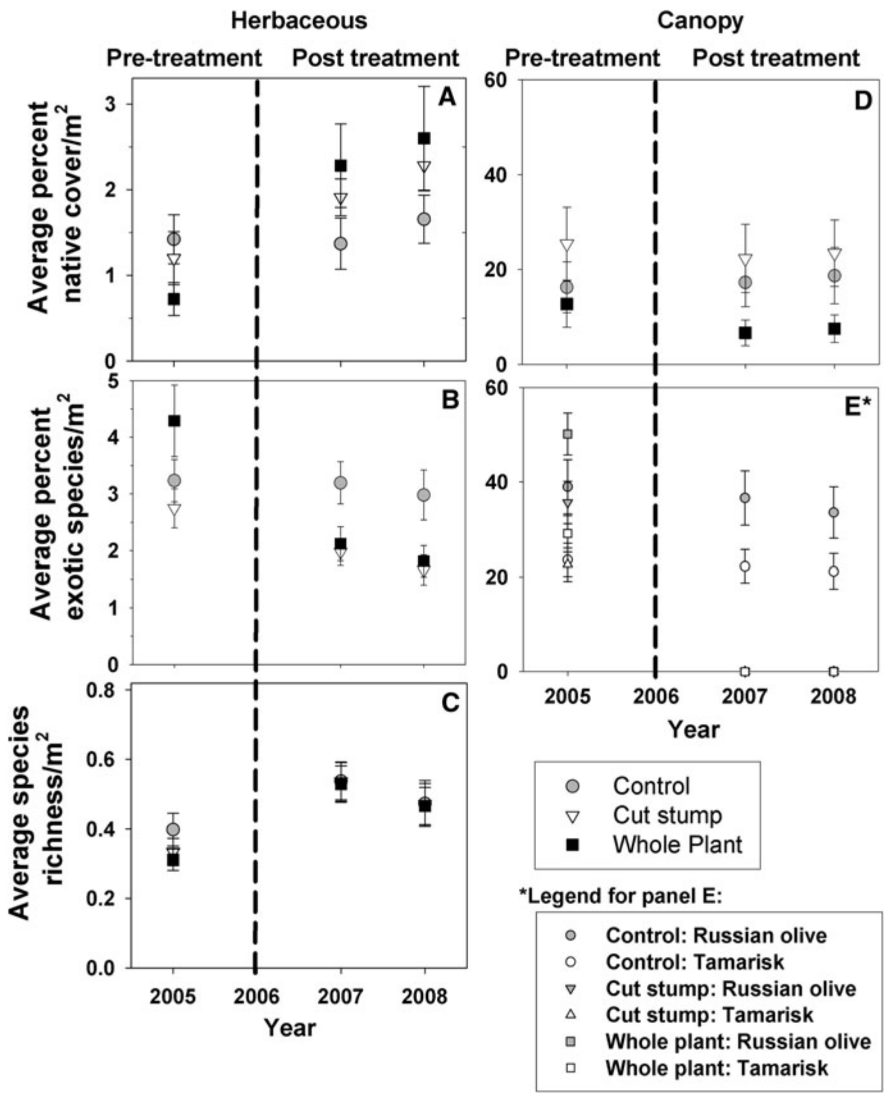

Fig. 5 Average ± SE percent cover per area (m^2) of herbaceous (**A**–**C**) and canopy (**D**, **E**), native species (**A**, **D**), exotic species (**B**, **E**), and total species richness (**C**) in each treatment in years 2005, 2007, and 2008. Treatments are indicated by symbols: control (*gray circles*), cut-stump (*white triangles*), and whole-plant removal (*black squares*). **E** shows cover of exotic species Russian olive (*gray*) and tamarisk (*white*) with the same shapes for treatments. Sampling in year 2005 occurred before treatments were implemented (pre-treatment), treatments were completed in 2006, and post-treatment sampling occurred in 2007 and 2008

$P = 0.44$). In post-treatment years 2007 and 2008 the presence of dead Russian olive boles also had no effect on percent exotic cover (2007: $t = -1.87$, $P = 0.07$, 2008: $t = -1.16$, $P = 0.26$) or native cover (2007: $t = 0.92$, $P = 0.36$, 2008: $t = 1.32$, $P = 0.20$).

Discussion

A shift occurred in our study sites toward a novel floodplain ecosystem that is drier and supports more upland species than occurred in the past. This shift began with a dramatic reduction in over-bank flooding and lowering of the ground water table concurrent with down-cutting (incision) of the stream channel over the last 30 years (Cadol et al. 2010). Stream incision was then followed by a transition to vegetation dominated by more upland plant species. Historic vegetation, as reflected by the soil seed bank, contained lower WISs, more native species, and fewer exotic species than the extant vegetation in 2008 (Fig. 2). A viable soil seed bank dominated by native species has persisted for many decades, including twice as many riparian species as the extant vegetation. Terraces that were abandoned due to channel incision prior to 1981, and likely have been unflooded since then, had more native and riparian species than terraces of younger age. The

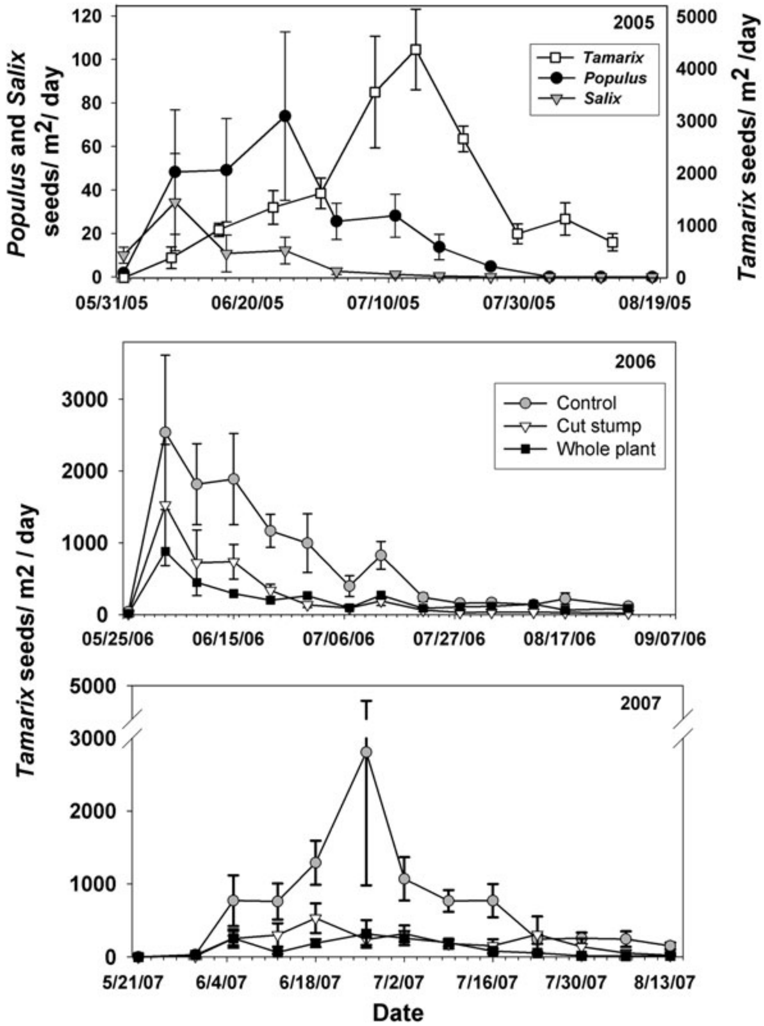

Fig. 6 *Top panel*: the average number of aerially dispersed *Tamarix* (*open squares*), *Populus* (*circles*), and *Salix* (*inverted triangles*) seeds per m^2 per day (±SE) across all pre-treatment sites in Canyon de Chelly during summer of 2005. *Middle* and *lower panels*: average number of aerially dispersed *Tamarix* seeds per m^2 per day (±SE) in 2006 (*middle panel*) and in 2007 (*lower panel*) in whole-plant removal treatments (*solid circles*), cut-stump removal treatments (*open circles*), and control treatments (*inverted triangles*)

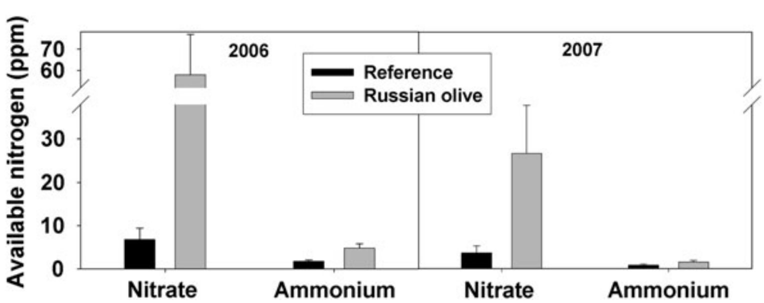

Fig. 7 Available nitrate and ammonium (ppm) ± SE next to Russian olive stumps (*gray bars*) and in reference soils without Russian olive roots (*black bars*) in 2006 (*left panel*) and 2007 (*right panel*)

oldest terraces had been seasonally inundated floodplains that supported riparian plants including *Eleocharis palustris, Juncus bufonius,* and *Veronica anagallis-aquatica*, whose viable seeds are still present in the soil. Many of these surfaces support sparse stands of *Phragmites communis* that likely was a riparian dominant prior to channel incision.

Riparian seed banks have been shown to contain more riparian plants than extant vegetation where stream flow regimes have been altered and the frequency of flooding has been reduced compared to historic conditions (Stromberg et al. 2008; Boudell and Stromberg 2008). More native and fewer exotic species in older terrace seed banks could indicate that fewer exotic species or exotic species cover occurred in the past contributing to the seed bank. Or it could indicate greater longevity of native compared with exotic species seeds (Williams et al. 2008). Recently, greater flood scour in the channel and lower surfaces has produced younger seed banks that support fewer native and wetland species and more exotic species.

Whole-plant removal of exotic shrubs provided a complete removal of target shrubs, yet was costly, labor-intensive, and provided little if any increased benefit to native vegetation establishment over the cut-stump method. Both shrub removal methods resulted in decreased exotic herbaceous species cover, increased native cover, and had little effect on species richness or WISs. There was some inter-annual variation in native and exotic species composition and species richness independent of treatment that was most likely attributable to variation in precipitation.

Shrub removal impacted seed dispersal processes by reducing seed rain inputs of both tamarisk and Russian olive into treatment plots and lowering the likelihood of reinvasion (Fig. 6). With respect to ground-level seed rain, whole-plant treatments had greater input from both native and exotic species than the control and cut-stump sites. This may be due to the greater disturbance in the whole-plant removal treatments compared to cut-stump and control sites. Other restoration studies have shown that initial decreases in seed availability after disturbances are followed by an increase in seed inputs (Heleno et al. 2010; Dolle and Schmidt 2009). Unexpectedly, the cut-stump removal treatment had lower ground seed rain from both exotic and native species than the control and whole-plant removal sites. However, seed dispersal can also be affected by birds and mammals, which we did not analyze (Katz et al. 2001).

Tamarisk and Russian olive removal did not affect the riparian ground water dynamics. The water table at our sites was quite deep, varying from 1 to 6 m below the floodplain, but did provide perennially available water to woody phreatophytes (Reynolds and Cooper 2010). Our removal sites may have been too small to affect the riparian water table, although Cleverly et al. (2006) indicated that tamarisk and Russian olive removal can result in modest increases in water availability. It is likely that woody plant removal had little influence on local water table depths because tamarisk stand evapotranspiration is relatively low (Nagler et al. 2009; Shafroth et al. 2010).

Ecosystem nutrient levels were impacted by shrub removal, but the change had no effect on the plant community. The decomposing roots of Russian olive trees killed by the cut-stump method provided a short-term increase in available soil nitrogen, especially nitrate (Fig. 7). However, increased nitrogen near Russian olive stumps did not influence the cover of exotic or native species in our herbaceous vegetation plots. Although high soil nitrogen concentrations provided by exotic species have been shown to facilitate plant invasions, this is did not occur in the Russian olive stands we analyzed (Hughes and Denslow 2005).

There is great potential for native riparian species colonization of treatment sites from the soil seed bank. However, shifts in abiotic ecosystem characteristics appear to have crossed a water availability threshold, making the establishment of riparian plants a rare phenomenon: flooding rarely occurs due to stream channel incision which has left the former floodplain hydrologically disconnected from the stream channel (Cadol et al. 2010). Following the removal of tamarisk and Russian olive, our study sites are transitioning to dry grasslands, as indicated by an increasing abundance of native upland species such as sand drop seed grass (*Sporobolus cryptandrus*) and hairy golden aster (*Heterotheca villosa*) (Table 1). These processes are in contrast to previous studies of riparian exotic plant removal sites in the western US where greater native species cover was correlated with greater water availability, precipitation, and flooding frequency (Bay and Sher 2008).

Many rivers in western North America have experienced floodplain abandonment due to channel incision, river regulation by dams or both (Stromberg et al. 2007; Friedman et al. 1998). Our results are applicable to sites across western North America where tamarisk and Russian olive stands rarely or infrequently flood and where establishment following exotic plant removal is of mostly upland, not riparian species (Johnson 2002). Restoration of historic riparian communities along rivers that have incised may not be possible (Seastedt et al. 2008). Therefore, land managers must consider strategies for managing viable native upland communities in exotic riparian removal sites.

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Appendix: species lists for vegetation and soil seed bank surveys in Canyon de Chelly National Monument

See Tables 2, 3, and 4.

Table 2 Herbaceous plant species in vegetation survey plots 2005–2008

Species	Native status	Wetland indicator score
Achillea millefolium L., common yarrow	N	4
Acroptilon repens L., hardheads	E	3
Agropyron smithii (Rydb.), western wheatgrass	N	3
Agropyron trachycaulum (Link), slender wheatgrass	N	3
Alyssum simplex Rudolphi, alyssum	E	4
Amaranthus blitoides S. Watson, mat amaranth	E	4
Amaranthus retroflexus L., redroot amaranth	N	4
Ambrosia acanthicarpa Hook, flatspine burr ragweed	N	4
Ambrosia artemisiifolia L., annual ragweed	N	4
Artemisia dracunculoides(DC.) Nutt, tarragon	N	4
Artemisia filifolia Torr., sand sagebrush	N	4
Artemisia ludoviciana Nutt., white sagebrush	N	5
Artemisia tridentata Nutt., big sagebrush	N	5
Bouteloua barbata Lag., sixweeks grama	N	5
Bouteloua gracilis (Willd. Ex Kunth) Lag. ex Griffiths, blue grama	N	4
Brickellia californica (Torr. & A. Gray) A. Gray, california brickellbush	N	4
Brickellia grandiflora (Hook.) Nutt., tasselflower brickellbush	N	4
Bromus racemosus L., bald brome	E	4
Bromus rigidus Roth, ripgut brome	E	4
Bromus tectorum L., cheatgrass	E	3
Capsella bursa-pastoris (L.) Medik., shepherd's purse	E	3
Carduus nutans L., musk thistle, nodding plumeless thistle	E	3
Carex spp.	N	1
Cenchrus longispinus (Hack.) Fernald, mat sandbur	N	4
Centaurea diffusa Lam., white knapweed	E	4
Chamaesyce maculata L. Small, spotted sandmat	N	4
Chenopodium album L., lambsquarters	N	3
Chrysothamnus viscidiflorus (Hook.) Nutt., yellow rabbitbrush	N	5
Clematis ligusticifolia Nutt., western white clematis	N	3
Cleome serrulata Pursh, rocky mountain beeplant	N	3
Convolvulus arvensis L., field bindweed	E	4
Conyza canadensis (L.) Cronquist, Canadian horseweed	N	4
Croton texensis (Klotzsch) Müll. Arg., Texas croton	N	4
Dalea candida Michx. ex Willd., white prairie clover	N	4

Table 2 continued

Species	Native status	Wetland indicator score
Datura wrightii Regel, sacred thorn-apple	N	4
Descurainia pinnata (Walter) Britton, western tansymustard	N	4
Distichlis spicata (L.) Greene, inland saltgrass	N	2
Draba cuneifolia Nutt. ex Torr. & A. Gray, wedgeleaf draba	N	3
Eleocharis palustris (L.) Roem. & Schult., common spikerush	N	1
Elymus canadensis L., Canada wildrye	N	3
Equisetum laevigatum A. Braun, smooth horsetail	N	2
Erigeron speciosus (Lindl.) DC., aspen fleabane	N	3
Erodium cicutarium (L.) L'Hér. ex Aiton, redstem stork's bill	E	4
Galium wrightii A. Gray, wright's bedstraw	N	3
Gutierrezia sarothrae (Pursh) Britton & Rusby, broom snakeweed	N	5
Halogeton glomeratus (M. Bieb.) C.A. Mey., saltlover	E	4
Helianthus annuus L., common sunflower	N	4
Heterotheca villosa (Pursh) Shinners, hairy false goldenaster	N	5
Hordeum murinum L., mouse barley	E	4
Ipomopsis aggregata (Pursh) V.E. Grant, scarlet gilia	N	5
Ipomopsis longiflora (Torr.) V.E. Grant, flaxflowered ipomopsis	N	4
Juncus articulatus Willd., jointleaf rush	N	1
Juncus bufonius L., toad rush	N	1
Kochia scoparia (L.) A.J. Scott, Mexican-fireweed	E	3
Lactuca serriola L., prickly lettuce	E	3
Marrubium vulgare L., horehound	E	3
Medicago lupulina L., black medick	E	3
Medicago sativa L., alfalfa	E	3
Melilotus albus Medik., white sweetclover	E	4
Melilotus officinalis (L.) Lam., yellow sweetclover	E	4
Mirabilis multiflora (Torr.) A. Gray, Colorado four o'clock	N	4
Monroa squarrosa (Nutt.) Torr., false buffalograss	N	3
Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi, scratchgrass	N	2
Oenothera albicaulis Pursh, whitest evening-primrose	N	4
Opuntia polyacantha Haw., plains pricklypear	N	5
Opuntia whipplei (Engelm. & Bigelow) F.M. Knuth, whipple cholla	N	5
Oryzopsis hymenoides (Roem. & Schult.) Barkworth, indian ricegrass	N	4
Panicum dichotomiflorum Michx., fall panicgrass	N	3
Phalaris arundinacea L., reed canarygrass	N	1
Phragmites australis (Cav.) Trin. ex Steud., common reed	N	2
Physalis hederifolia A. Gray, ivyleaf groundcherry	N	4
Physalis longifolia Nutt., longleaf groundcherry	N	4
Plantago major L., common plantain	E	2
Plantago patagonica Jacq., woolly plantain	N	5
Pleuraphis jamesii Torr., James' galleta	N	4
Poa pratensis L., kentucky bluegrass	N	4
Polygonum aviculare L., prostrate knotweed	E	2
Portulaca oleracea L., little hogweed	E	3

Table 2 continued

Species	Native status	Wetland indicator score
Ranunculus cymbalaria Pursh, alkali buttercup	N	1
Salsola iberica L., prickly Russian thistle	E	4
Senecio douglasii (Hook. & Grev.) Spring, douglas' ragwort	N	4
Senecio flaccidus Less., threadleaf ragwort	N	4
Senecio spartioides Torr. & A. Gray, broomlike ragwort	N	4
Sisymbrium altissimum L., tall tumblemustard	E	3
Solanum elaeagnifolium Cav., silverleaf nightshade	N	4
Solidago velutina DC., threenerve goldenrod	N	3
Sphaeralcea coccinea (Nutt.) Rydb., scarlet globemallow	N	4
Sporobolus airoides (Torr.) Torr., alkali sacaton	N	3
Sporobolus cryptandrus (Torr.) A. Gray, sand dropseed	N	4
Taraxacum officinale F.H. Wigg., common dandelion	N	4
Thelesperma megapotamicum (Spreng.) Kuntze, Hopi tea greenthread	N	5
Thlaspi arvense L., field pennycress	E	5
Townsendia incana Nutt., hoary townsend daisy	N	5
Tradescantia occidentalis (Britton) Smyth, prairie spiderwort	N	4
Tragopogon dubius Scop., yellow salsify	E	5
Tribulus terrestris L., puncturevine	E	4
Urtica dioica L., stinging nettle	N	2
Verbena bracteata Cav. ex Lag. & Rodr., bigbract verbena	N	3
Vulpia octoflora (Walter) Rydb., sixweeks fescue	N	4
Xanthium strumarium L., rough cockleburr	N	3

Native status is indicated by an E (exotic) or N (native). Wetland indicator scores are indicated by 1–5 as defined by USDA PLANTS Database in Region 7 (USDA 2010)

Table 3 Woody plant species in vegetation survey plots 2005–2008

Species	Native status	Wetland indicator score
Acer negundo L., boxelder	N	2
Elaeagnus angustifolia L., Russian olive	E	2
Forestiera neomexicana A. Gray, stretchberry	N	4
Juglans major (Torr.) A. Heller, Arizona walnut	N	2
Juniperus utahensis (Torr.) Little, Utah juniper	N	5
Pinus edulis Engelm., two needle pinyon	N	4
Populus x acuminata Rydb. (pro sp.) [*angustifolia* × *deltoides*], lanceleaf cottonwood	N	2
Populus fremontii S. Watson, Fremont cottonwood	N	2
Salix amygdaloides Andersson, peachleaf willow	N	2
Salix exigua Nutt., narrowleaf willow	N	1
Salix gooddingii C.R. Ball, Goodding's willow	N	1
Salix lucida Muhl., shining willow	N	2
Tamarix ramosissima Ledebour, *T. chinensis* Loureiro, and hybrids, saltcedar	E	2
Ulmus pumila L., Siberian elm	E	3

Native status is indicated by an E (exotic) or N (native). Wetland indicator scores are indicated by 1–5 as defined by USDA PLANTS Database in Region 7 (USDA 2010)

Table 4 Species list from soil seed bank study 2007

Species	Native status	Wetland indicator score
Acer negundo L., boxelder	N	2
Agrostis scabra Willd., rough bentgrass	N	3
Amaranthus blitoides S. Watson, mat amaranth	E	4
Amaranthus retroflexus L., redroot amaranth	N	4
Ambrosia acanthacarpa Hook, flatspine burr ragweed	N	4
Anaphalis margaritacea (L.) Benth., western pearly everlasting	N	3
Anemopsis californica (Nutt.) Hook. & Arn., yerba mansa	N	1
Artemisia ludoviciana Nutt., white sagebrush	N	5
Astragalus nuttallianus DC., smallflowered milkvetch	N	4
Bouteloua barbata Lag., sixweeks grama	N	5
Bromus rigidus Roth, ripgut brome	E	4
Bromus tectorum L., cheatgrass	E	3
Carduus nutans L., musk thistle, nodding plumeless thistle	E	3
Celtis laevigata Willd., sugarberry	N	5
Cenchrus longispinus (Hack.) Fernald, mat sandbur	N	4
Chamaesyce maculata (L.) Small, spotted sandmat	N	4
Clematis ligusticifolia Nutt., western white clematis	N	3
Conyza canadensis (L.) Cronquist, Canadian horseweed	N	4
Descurainia pinnata (Walter) Britton, western tansymustard	N	4
Draba cuneifolia Nutt. ex Torr. & A. Gray, wedgeleaf draba	N	3
Elaeagnus angustifolia L., Russian olive	E	2
Eleocharis palustris (L.) Roem. & Schult., common spikerush	N	1
Elymus trachycaulus (Link), slender wheatgrass	N	3
Epilobium ciliatum Raf., fringed willowherb	N	2
Eragrostis cilianensis (All.) Vign. ex Janchen, stinkgrass	E	4
Eragrostis pectinacea (Michx.) Nees ex Steud., tufted lovegrass	N	3
Eragrostis pilosa (L.) P. Beauv., Indian lovegrass	N	4
Erigeron colomexicanus A. Nelson, running fleabane	N	4
Erigeron pumilus Nutt., shaggy fleabane	N	4
Erigeron speciosus (Lindl.) DC., aspen fleabane	N	3
Erodium cicutarium (L.) L'Hér. ex Aiton, redstem stork's bill	E	4
Gutierrezia sarothrae (Pursh) Britton & Rusby, broom snakeweed	N	5
Halogeton glomeratus (M. Bieb.) C.A. Mey., saltlover	E	4
Helianthus annuus L., common sunflower	N	4
Heterotheca villosa (Pursh) Shinners, hairy false goldenaster	N	5
Hordium murinum L., mouse barley	E	4
Ipomopsis aggregata (Pursh) V.E. Grant, scarlet gilia	N	5
Ipomopsis longiflora (Torr.) V.E. Grant, flaxflowered ipomopsis	N	4
Juncus articulatus Willd., jointleaf rush	N	1
Juncus bufonius L., toad rush	N	1
Juncus confusus Coville, Colorado rush	N	1
Juncus ensifolius Wikstr. var. *montanus* (Engelm.) C.L. Hitchc., Rocky mountain rush	N	1
Juncus mexicanus Willd. ex Schult. & Schult. f., Mexican rush	N	1
Juncus saximontanus A. Nelson, Rocky Mountain rush	N	1

Table 4 continued

Species	Native status	Wetland indicator score
Kochia scoparia (L.) A.J. Scott, Mexican-fireweed	E	3
Lepidium densiflorum Schrad., common pepperweed	N	3
Lupinus brevicaulis S. Watson, shortstem lupine	N	4
Medicago lupulina L., black medick	E	3
Monroa squarrosa (Nutt.) Torr., false buffalograss	N	3
Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi, scratchgrass	N	2
Muhlenbergia richardsonis (Trin.) Rydb., mat muhly	N	4
Oenothera albicaulis Pursh, whitest evening-primrose	N	4
Opuntia whipplei (Engelm. & Bigelow) F.M. Knuth, whipple cholla	N	5
Panicum capillare L., witchgrass	N	3
Phalaris arundinacea L., reed canarygrass	N	1
Physalis crassifolia Benth., yellow nightshade groundcherry	N	4
Physalis hederifolia A. Gray, ivyleaf groundcherry	N	4
Plantago major L., common plantain	E	2
Plantago patagonica Jacq., woolly plantain	N	5
Poa annua L., annual bluegrass	E	3
Poa canbyi (Scribn.) Howell	N	4
Poa compressa L., Canada bluegrass	E	4
Polypogon monspeliensis (L.) Desf., annual rabbits foot grass	E	2
Populus fremontii S. Watson, Fremont cottonwood	N	2
Portulaca oleracea L., little hogweed	E	3
Ranunculus cymbalaria Pursh, alkali buttercup	N	1
Salix spp.	N	2
Salsola collina Pall., slender Russian thistle	E	4
Salsola iberica L., prickly Russian thistle	E	4
Scirpus spp.	N	1
Senecio douglasii (Hook. & Grev.) Spring, Douglas' ragwort	N	4
Senecio spartioides Torr. & A. Gray, broomlike ragwort	N	4
Spergularia salina J. Presl & C. Presl, salt sandspurry	N	1
Sporobolus cryptandrus (Torr.) A. Gray, sand dropseed	N	4
Tamarix ramosissima Ledebour, *T. chinensis* Loureiro, and hybrids, saltcedar	E	2
Taraxacum officinale F.H. Wigg., common dandelion	N	4
Tribulus terrestris L., puncturevine	E	4
Verbena bracteata Cav. ex Lag. & Rodr., bigbract verbena	N	3
Veronica anagallis-aquatica L., water speedwell	N	1
Vulpia octiflora (Walter) Rydb., sixweeks fescue	N	4

Native status is indicated by an E (exotic) or N (native). Wetland indicator scores are indicated by 1–5 as defined by USDA PLANTS Database in Region 7 (USDA 2010)

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