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Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe

Janet S. Prevéy · Matthew J. Germino · Nancy J. Huntly · Richard S. Inouye

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Abstract Dominant plant species, or foundation species, are recognized to have a disproportionate control over resources in ecosystems, but few studies have evaluated their relationship to exotic invasions. Loss of foundation species could increase resource availability to the benefit of exotic plants, and could thereby facilitate invasion. The success of exotic plant invasions in sagebrush steppe was hypothesized to benefit from increased available soil water following removal of sagebrush (*Artemisia tridentata*), a foundation species. We examined the effects of sagebrush removal, with and without the extra soil water made available by exclusion of sagebrush, on abundance of exotic and native plants in the shrub steppe of southern Idaho, USA. We compared plant responses in three treatments: undisturbed sagebrush steppe; sagebrush removed; and sagebrush removed plus plots covered with "rainout" shelters that blocked winter-spring recharge of soil water. The third treatment allowed us to examine effects of sagebrush removal alone, without the associated increase in deep-soil water that is expected to accompany removal of sagebrush. Overall, exotic herbs (the grass *Bromus tectorum* and four forbs) were 3–4 times more abundant in shrub-removal and 2 times more abundant in shrub-removal + rainout-shelter treatments than in the control treatment, where sagebrush was undisturbed. Conversely, native forbs were only about half as abundant in shrub removal compared to control plots. These results indicate that removal of sagebrush facilitates invasion of exotic plants, and that increased soil water is one of the causes. Our findings suggest that sagebrush plays an important role in reducing invasions by exotic plants and maintaining native plant communities, in the cold desert we evaluated.

Keywords Shrub steppe · Cold desert · Soil water · Exotic forbs · Foundation species · Invasion · *Bromus tectorum*

Introduction

In many plant communities, one or a few species have disproportionate control of hydrology, nutrient cycling, or other ecosystem processes and thus are referred to as "foundation" species (Jones et al. 1994; reviewed in Ellison et al. 2005). Disturbances that result in the loss of foundation species can alter the stability of ecosystems (Ellison et al. 2005). However,

J. S. Prevéy · M. J. Germino (✉) · N. J. Huntly ·
R. S. Inouye
Department of Biological Sciences, Idaho State
University, Mail Stop 8007, Pocatello, ID 83209, USA
e-mail: germmatt@isu.edu

Present Address:
N. J. Huntly · R. S. Inouye
National Science Foundation, 4201 Wilson Blvd.,
Arlington, VA 22201, USA

few studies have evaluated how foundation species affect other native species or community invasibility. The removal of foundation plant species from an ecosystem may increase the availability of limiting resources, and increased resource availability has been implicated as a mechanism for invasion and persistence of exotic species (Davis et al. 2000; Davis and Pelsor 2001; Shea and Chesson 2002; Daehler 2003).

The perennial shrub *Artemisia tridentata* (big sagebrush) could be considered a foundation species in shrub-steppe, cold-desert ecosystems of the Great Basin, USA, where it is both locally abundant and widespread (Dobrowolski et al. 1990; Smith et al. 1997). Land disturbances, such as fire and conversion to cropland, have eliminated sagebrush and other dominant shrubs and increased exotic herbs in areas of historic sagebrush steppe (Piemeisel 1951; Noss et al. 1995; Knick and Rotenberry 1997; Kulmatiski 2006). Indirect evidence suggests that large fires occurred at 30 to longer than 200 year intervals in sagebrush steppe before the arrival of European settlers (Houston 1973; Baker 2006), but current fire-return intervals have become as frequent as every 5 years in large areas of the Great Basin (Whisenant 1990). Sagebrush is fire-intolerant and herbs dominate community cover while sagebrush populations slowly re-establish after fire (Young and Evans 1978).

Sagebrush and herb abundances can be inversely related, and the assumption that sagebrush generally has negative, competitive effects on herbs has contributed to the purposeful removal of sagebrush to increase forage for cattle or wildlife (e.g., Mueggler and Blaisdell 1958; Cook and Lewis 1963; Sturges 1973; Van Dyke and Darragh 2006). However, Welch's (2005) review did not support the generalization that sagebrush competitively excludes herbs, and instead he highlighted evidence for positive effects of sagebrush on other species. Positive or facilitative effects of sagebrush might be particularly evident for native herbs that have long been part of the same community (Bruno et al. 2003). Specifically, sagebrush may facilitate the growth of other native plants through influences on nutrients in resource islands, temperature extremes, or herbivory (Charley and West 1975; Callaway 1997; Bechtold and Inouye 2007, Karban 2007). Karban (2007) observed that the native species *Wyethis mollis* (mule's ears) experienced less insect herbivory when growing near sagebrush, indicating associational resistance.

A number of annual grasses and tap-rooted forbs that were originally from Europe or Eurasia are now invaders of sagebrush steppe (Whitson 2000), particularly in the herb-dominated communities that colonize disturbed sites. The exotic annual grass *Bromus tectorum* (cheatgrass) is near ubiquitous in disturbed sagebrush-steppe ecosystems (Pickford 1932; Mack 1981). *Bromus tectorum* does particularly well in recently burned areas and also tends to increase fire frequencies (D'Antonio and Vitousek 1992). The vigorous growth of *B. tectorum* after fire has been linked to the availability of soil resources, such as water, resulting from the removal of competitors (Melgoza et al. 1990; Chambers et al. 2007). Sagebrush can use both shallow- and deep-soil water (Dobrowolski et al. 1990), and removal of sagebrush could facilitate invasion of *B. tectorum* by increasing available shallow-soil water.

Compared to most native herbs, sagebrush and other cold-desert shrubs tend to use more deep-soil water, which is a water source that results from infiltration of winter and spring precipitation (Caldwell 1985). Ecophysiological and isotopic evidence suggests that exotic tap-rooted forbs, such as *Centaurea maculosa* and *Centaurea diffusa* (knapweeds), are similar to sagebrush in their ability to use water from deeper in the soil profile than native herbs and especially grasses (Hill et al. 2006; Kulmatiski et al. 2006). Another key trait shared between exotic forbs and sagebrush is persistent water use for photosynthesis during summer drought (Hill et al. 2006). Loss of sagebrush can lead to local increases in available soil moisture, particularly below the rooting depths of grasses (Cook and Lewis 1963; Sturges 1973; Inouye 2006). Use of deep-soil water made available by removal of sagebrush could contribute to successful establishment of exotic forbs in disturbed steppe ecosystems.

We experimentally removed sagebrush to examine its effects on herb community cover and composition in a sagebrush-steppe ecosystem. To separate other effects of sagebrush from the increases in deep-soil water that normally accompany loss of sagebrush, we also removed sagebrush and covered plots with "rainout" shelters that blocked winter and spring recharge of deep-soil water. We then compared the plant communities in these treatments to those of unaltered sagebrush steppe. We expected differences in the responses of native versus exotic forbs to removal of sagebrush, based on greater functional similarities of exotic forbs and sagebrush and on the hypothesized potential for positive interactions of sagebrush with native forbs. We had three main hypotheses: (1) cover of *B. tectorum* would be greater following removal of sagebrush, (2) density of tap-rooted exotic forbs would be greater following removal of sagebrush, but not when additional deep-soil water was blocked by rain-out shelters, and (3) native forbs would increase less than exotics, or even decrease following removal of sagebrush.

Methods

Study site

Our study was conducted at the Idaho State University (ISU) Barton Road Ecological Research Area in Pocatello, Idaho, USA, located east of the ISU campus along Barton Road, Bannock County (42.853°N, 112.402°W; ~1460 m elevation). All plots were located within a 3 ha area with a west-facing aspect and an average slope of 10°. Soils in the area are fine-grained calcareous silt loams (McGrath 1987).

The area was grazed by livestock before 1990 and was designated as a research area in 1996 (Inouye 2006). The area is in a sagebrush-steppe ecosystem dominated by the shrub *Artemisa tridentata* (sagebrush), with lesser amounts of the shrubs *Chrysothamnus nauseosus* (rubber rabbitbrush), *C. viscidiflorus* (yellow rabbitbrush), *Atriplex canescens* (fourwing saltbrush), and *Eurotia lanata* (winterfat). Grasses common to the site are *Bromus tectorum* (cheatgrass), *Agropyron cristatum* (crested wheatgrass), *Stipa comata* (needle-and-thread grass), and *Elymus elymoides* (squirreltail). Native forbs include *Erigeron* spp. (fleabane), *Phlox hoodii* (Hood's phlox), *Calochortus nuttallii* (sego lily), *Zigadenus venenosus* (meadow death camas), *Plantago patagonica* (woolly plantain), *Crepis occidentalis* (hawk's beard), *Sphaeralcea munroana* (orange globe mallow), and *Castilleja* spp. (Indian paintbrush). Exotic forbs include *Tragopogon dubius* (false salsify), *Lactuca serriola* (prickly lettuce), *Melilotus officinalis* (yellow sweet clover), *Sisymbrium altissimum* (tumble mustard), and *Alyssum desertorum* (desert alyssum). Plant taxonomy follows Hitchcock and Cronquist (1973).

Treatment manipulation

We allocated three treatments (control, shrub-removal, and shrub-removal + rainout-shelter) to each of six blocks in a randomized complete-block design during October–November 2006. Each treatment was applied to a 9 × 11.5 m^2 plot within each block, for a total of 18 plots dispersed over several hectares. The "control" treatment was undisturbed. We removed all shrubs from the plots assigned to the "shrub-removal" treatment. The majority of the shrubs on plots were *Artemisia tridentata* (98%), but small amounts of *Chrysothamnus* spp. were also present (2%). Shrubs were removed with saws at the base of the stem and plots were otherwise undisturbed. Plots assigned to the "shrub-removal + rain-out-shelter" treatment had all shrubs removed and were covered with clear polyethylene roof shelters from November through April to exclude deep-soil water recharge. The shelters covered the entire plot and selectively blocked the winter and early spring precipitation that contributes to deep-soil water. The clear plastic was suspended on tubular steel rafters (5 cm diameter) separated by 1.22 m, and additionally supported by three horizontal purlins made of narrower tubing. Shelters had an open-ended "quonset"-style roof, with the center ridge height between 3.5 and 5 m above ground and the lower edges (sides of shelters) of plastic between 1 and 2 m height above ground, to allow ventilation and minimize unwanted warming artifacts.

Because shelters covered plots during the cold season (November–April), they blocked precipitation when it would have exceeded potential evapotranspiration (Fig. 1). Mean annual precipitation for the Pocatello, ID, is ca. ~320 mm, with most occurring in the winter and spring (National Climatic Data Center). However, during the study period, yearly precipitation averaged 254 mm (October 2006–September 2008). Shelters blocked 94 mm precipitation in 2006–2007, and 139 mm precipitation in 2007–2008.

Rainout shelters often impart other climatic effects. Our shelter design was intended to minimize such effects, and shelters were present only when plants were mostly dormant. Nevertheless, to test for differences in temperature between rainout-shelter and shrub-removal treatments, temperature was recorded with Campbell CR10 dataloggers (Campbell

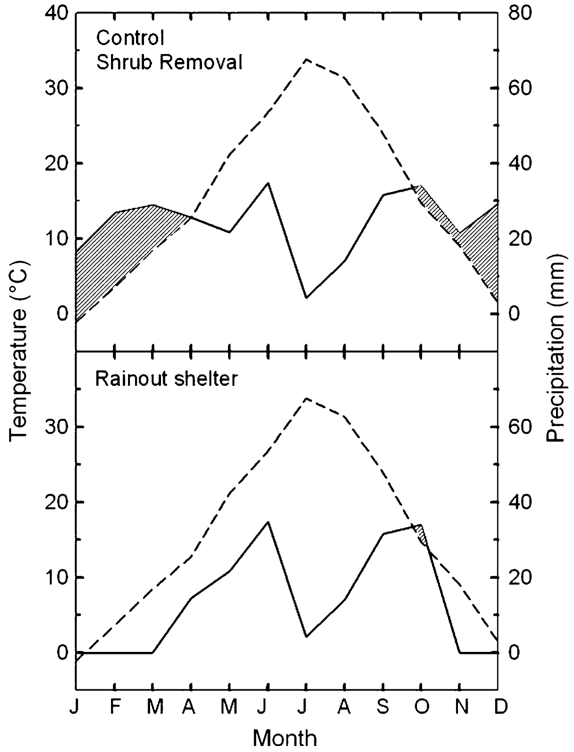


Fig. 1 Climate diagrams for control, shrub-removal (*top panel*), and rainout-shelter treatments (*bottom panel*) averaged over the duration of the study, 1 November 2006–31 August 2008. *Solid lines* depict precipitation and *dashed lines* depict temperature. *Stippling* indicates periods when precipitation exceeded potential evapotranspiration. Weather data was collected from Pocatello 2 NE reporting station, located ~6 km from the ISU ecological research area, Pocatello, ID, USA

Scientific Inc., Logan, UT, USA) and thermocouples positioned at 10 cm underground, at the soil surface, and at 1 m aboveground under radiation shields during the winter and early spring of 2007 and 2008. Each plot had one underground temperature sensor, two soil surface sensors, and one air sensor. Simultaneous measurements were made on shrub-removal and rainout-shelter treatments within each block, and dataloggers and thermocouples were rotated among blocks approximately biweekly in March and April 2007, and December, March, and April 2008. We compared average temperatures between shrub-removal and rainout-shelter plots for all biweekly measurement intervals (2 per block) with one-way analysis of variance (PROC GLM, SAS 9.1.3, SAS Institute, Cary, NC, USA). We adopted an $\alpha = 0.05$ for all analyses.

Soil water

We used a neutron probe (CPN 503DR Hydroprobe, Martinez, CA, USA) to measure soil-water content in each plot throughout the summer. We inserted two 2-m-long aluminum access tubes vertically into core holes located centrally within each plot. The tubes were ~4 m from either edge of the plot and 2 m from each other. Soil moisture was measured at 20-cm intervals from 20 to 180 cm below the soil surface. We could not measure soil water shallower than 20 cm because neutron probe measurements at shallow depths are often unreliable (Bell 1987). Soil-moisture was measured at 2-week intervals during the growing seasons (27 April–20 August) of 2007 and 2008. Count data from the neutron probe were converted to gravimetric soil-water content using calibration data from soils in the same research area (Inouye 2006). We converted gravimetric water content to volumetric water content (VWC) using the average bulk density of the soil in the study area ($1.39\ \mathrm{g/cm^3} \pm 0.01$ SE). We estimated bulk density from nine soil cores taken at 20, 40, and 60 cm depths near the study plots on 28 May 2007. Bulk density did not differ between depths, so the same bulk density value was used for all VWC calculations. Water retention curves ($n = 6$) were constructed using a WP4T WaterpotentiaMeter (Decagon, WA, USA) to determine the volumetric water content that corresponded with −1.5 MPa.

We used a mixed-model ANOVA with repeated measures and Tukey's 'Honestly Significant Difference' (HSD) tests to assess differences in shallow- and deep-soil water between treatments over the course of the growing season (PROC MIXED, SAS 9.1.3, SAS Institute). Treatment and sampling date (time) were fixed effects, and block was a random effect. Soil moisture deeper than 80 cm was similar for all treatments (all $F_{2,10} < 1$, $P > 0.9$), and soil-water recharge or depletion was not observed below 80 cm in 2007 or 2008 (Fig. 2). Thus, we analyzed volumetric water content to 80 cm depth. We analyzed "shallow-soil water" at a depth of 20 cm and "deep-soil water" averaged over depths from 40 to 80 cm. We analyzed data from 2007 and 2008 separately due to large differences in winter precipitation (National Climatic Data Center).

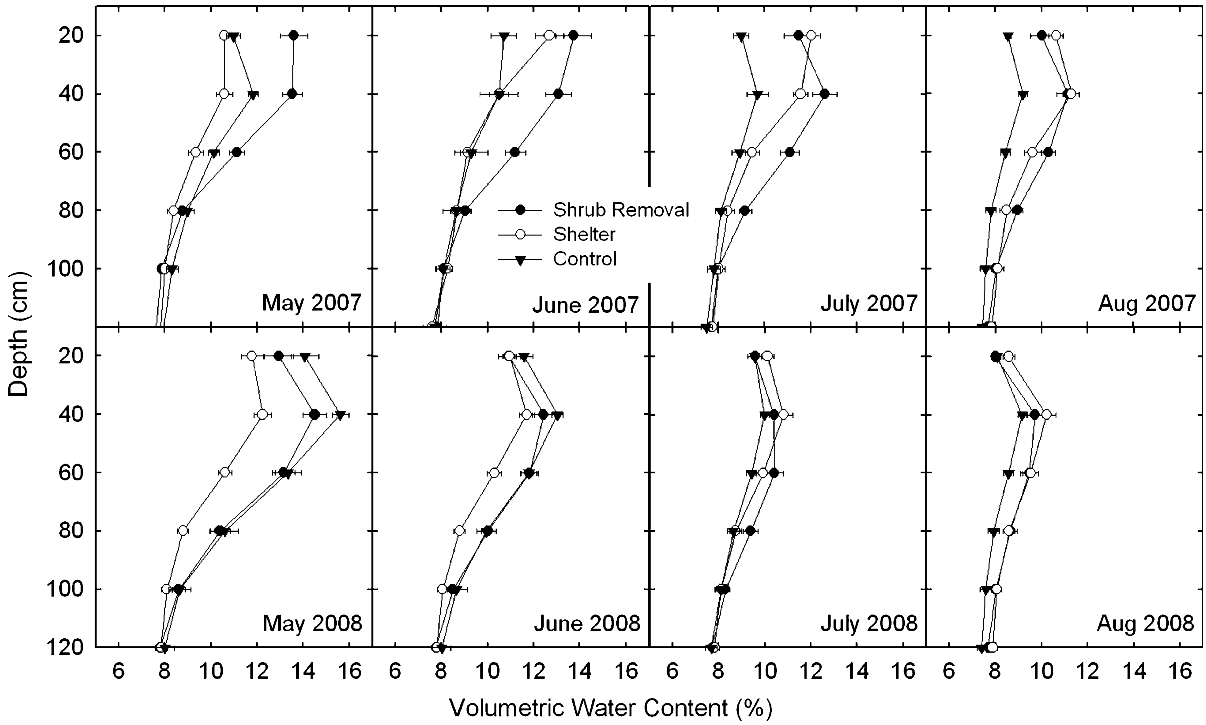


Fig. 2 Average monthly volumetric soil water content (%) from 20 to 120 cm depth, in shrub-removal, rainout-shelter, and control treatments, ±1 standard error, during the summers of 2007 and 2008

Vegetation cover and density

We measured vegetation cover with the line–point intercept method on 31 July 2006 (pre-treatment), 11–13 July 2007, 5–12 June 2008, and 11–15 July 2008. The measurements in July reflect peak summer biomass and the measurements in June 2008 revealed density of native forbs before they senesced. We surveyed plants along transects located at 1 m intervals across the 9 m side of each plot. At 0.5 m intervals along each transect, a thin metal rod was positioned vertically and all living plants touching the rod were recorded. To avoid edge effects, no measurements were taken in the outer 1 m of each plot. The number of points intercepting a plant species was divided by the total number of points sampled in a plot (160) to calculate percent cover of each species. To obtain more detailed data on exotic forbs, density (# individuals/m^2) was also determined by counting all exotic forbs within 1 × 9.5 m^2 belt transects across each plot on the same sampling dates as the line–point intercept surveys. In November 2007, an additional survey was conducted to reveal late fall differences in density of exotic forbs, however, only shrub-removal and rainout-shelter treatments were surveyed due to time limitations and the scarcity of exotic forbs in the control treatment. In June 2008, density of native forbs was measured using the same belt transects.

We used multivariate analyses to determine how community composition differed among treatments. In July 2006, before treatment manipulation, percent covers of shrubs, bunchgrasses, annual exotic grass (*B. tectorum*), exotic forbs, and native forbs were analyzed with a non-parametric multivariate analysis of variance (PERMANOVA) using the vegan library (10,000 random permutations; Anderson 2001; McArdle and Anderson 2001; Oksanen et al. 2008) in R (R Development Core team 2007) to ensure that there were no pre-treatment differences in vegetation cover. After treatments were implemented, percent covers of bunchgrasses, annual exotic grass (*B. tectorum*), exotic forbs, and native forbs in July 2007, June 2008, and July 2008 were analyzed with separate PERMANOVAs to test the hypothesis that community composition of herbaceous species differed between treatments. Cover of shrubs was not included in post-treatment PERMANOVAs because shrub removal was part of treatment manipulation, and our focus was changes in the herbaceous community. Pairwise comparisons among treatments were adjusted using Benjamini and Hochberg's method (Benjamini and Hochberg 1995, BH). Results were graphed with non-metric multidimensional scaling (nMDS) plots based on the matrix of Bray-Curtis coefficients.

To address our hypotheses that cover of *B. tectorum* would be greater following removal of sagebrush, we compared *B. tectorum* cover in June 2008 among treatments using blocked-ANOVA (PROC GLM) and Tukey's HSD tests. Cover of *B. tectorum* was not analyzed for July sampling dates because it had already mostly senesced. To address our hypothesis that density of exotic forbs would be greater following removal of sagebrush, except when additional deep-soil water was blocked by rain-out shelters, we compared densities of exotic forbs among treatments on July 2006, June 2008, and July 2008 using a mixed-model ANOVA with repeated measures (PROC MIXED) and Tukey's HSD tests. Treatment and sampling date (time) were fixed effects, and block was a random effect. Because control plots were not sampled in November 2007, data from this date were not included in the mixed-model ANOVA. Excluding the control treatment and including November 2007 in the model did not change our findings on how the densities of exotic forbs differed between the shrub-removal and rainout-shelter plots. To further help separate effects of soil water from sagebrush presence on exotic forb abundances, we correlated density of exotic forbs in July 2007 with average volumetric water content at 20–80 cm depths between 10 May and 11 July 2007 in each plot (PROC REG). We correlated exotic forb densities with soil water averaged between 20 and 80 cm depths to relate the total amount of soil water available (both shallow and deep) with the abundance of exotic forbs.

To address our hypothesis that density of native forbs would be lower following removal of sagebrush, we compared densities of native forbs in June 2008 using a blocked-ANOVA (PROC GLM) and Tukey's HSD tests. The densities of *L. serriola*, *M. officinalis*, and total exotic forbs in 2007 and 2008 and of total native forbs in June 2008 had unequally distributed errors and were $\log_{10}$-transformed to meet assumptions of normality. Zero entries were replaced with the smallest non-zero value recorded for any species in a model before $\log_{10}$-transformation.

Results

Temperature comparison

Average air temperatures 1 m aboveground and temperatures at the soil surface did not differ appreciably between sheltered and un-sheltered plots over winter and early spring in 2007 and 2008 (air temperature: $F_{1,11} = 4.22$, $P = 0.10$, soil temperature: $F_{1,11} = 2.48$, $P = 0.17$, Table 1). Average temperatures 10 cm underground were 1.5°C greater in rain-shelter plots than shrub removal plots ($F_{1,11} = 7.97$, $P = 0.04$, Table 1). Temperatures were recorded while rainout shelters covered the plots in the winter and early spring, when plants were largely dormant. Rainout shelters were removed from plots in early April, before most plants were physiologically active.

Soil water

Soils with a volumetric water content of approximately 8.43% corresponded to water potentials of -1.5 MPa. Overall, shallow-soil water content (20 cm depth) was greater in shrub-removal and rainout-shelter plots than control plots in 2007 (RM ANOVA, Tukey's, $P < 0.04$ for both tests, Table 2, Fig. 2), but differences between treatments diminished as the summer progressed (date × treatment interaction, Table 2, Fig. 2). There was also more deep-soil water (40–80 cm depth) in shrub-removal plots than rainout-shelter and especially control plots until August 2007 (Tukey's, $P < 0.05$ for both tests, Fig. 2). Over the summer of 2008, neither shallow- nor deep-soil water differed significantly among treatments (Tukey's, $P > 0.1$ for all tests, Table 2, Fig. 2), however, from 20 April 2008 through 15 June 2008, deep-soil water was $\sim$2% greater in shrub-removal and control treatments than in the rainout-shelter treatment (Fig. 2).

Vegetation cover and density

Pre-treatment cover of shrubs, bunchgrasses, *B. tectorum*, exotic forbs, and native forbs was similar among

Table 1 Comparison of air temperature (1 m above ground), soil surface temperature, and underground temperature (10 cm below surface) in shrub-removal and rainout-shelter plots

Treatment	Air temperature (°C)			Soil surface temperature (°C)			Underground temperature (°C)		
	Average	Max	Min	Average	Max	Min	Average	Max	Min
Shrub removal	5.89 ± 1.19	22.47	−8.47	8.23 ± 1.45	44.03	−8.91	7.84 ± 1.52*	26.67	-4.46
Rainout shelter	5.66 ± 1.20	22.69	−7.94	8.88 ± 1.59	40.47	−9.86	9.34 ± 1.58	25.11	-4.82

Temperatures were recorded during March and April 2007, and December, March, and April 2008

* Significant differences between averages (ANOVA, $P < 0.05$)

treatments (PERMANOVA, $F_{2,17} = 0.54$, and $P = 0.61$). After treatments were imposed, the herbaceous community differed between control and shrub-removal or rainout-shelter plots (all $F_{2,17} > 3.15$, $P < 0.04$, comparison between control and shrub-removal or rainout-shelter plots, all $P < 0.05$ with BH correction, Fig. 3). In contrast, the communities of shrub-removal and rainout-shelter plots did not differ (all $P > 0.32$ with BH correction, Fig. 3).

Cover of *B. tectorum* was 30% greater in shrub-removal than control plots in June 2008 and similar among shrub-removal and rainout-shelter plots (Table 4, Fig. 4). The mean density of exotic forbs (# individuals/m^2) was 4–6 times greater in shrub-removal and 2 times greater in rainout-shelter treatments than controls, over the course of the study (RM ANOVA, Tukey's, $P < 0.0004$, Table 3, Fig. 5). Total density of exotic forbs was similar in shrub-removal and rainout-shelter plots (Tukey's, $P = 0.46$). However, individual species responded differently to treatments. The exotic forb *Tragopogon dubius* was up to twice as abundant in shrub-removal plots compared with rainout-shelter and control plots over all sample dates (Tukey's, $P < 0.006$, Fig. 5). The densities of the exotic species *Lactuca serriola* and *Melilotus officinalis* were 2–4 times greater in shrub-removal and rainout-shelter plots than in control plots (Tukey's, $P < 0.05$, Fig. 5), but did not differ between shrub-removal and rainout-shelter treatments (Tukey's, $P > 0.09$, Fig. 5).

Table 2 Mixed-model ANOVA with repeated measures for the comparison of average volumetric water content between shallow (20 cm depth) and deep (40–80 cm depth) soil water for treatment, block, and time over the summers of 2007 and 2008

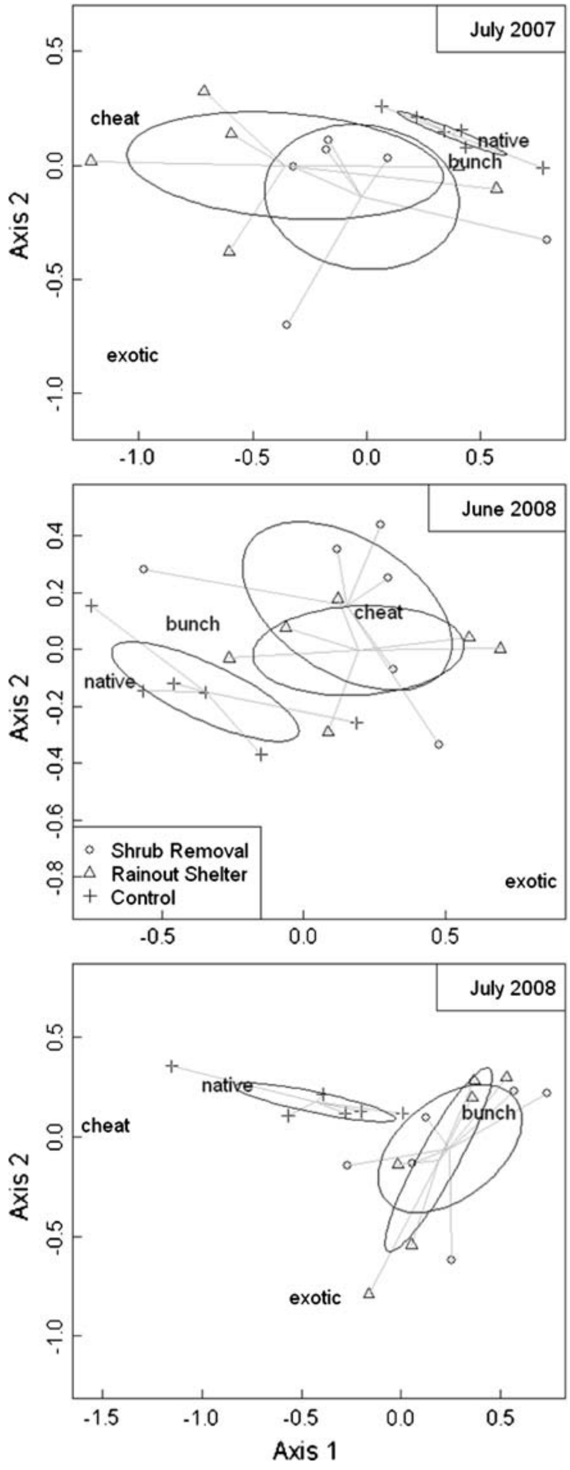
Effect	df	*F*	*P*
2007			
Shallow (20 cm depth)			
Treatment	2,15	11.16	0.001
Date	7,105	37.63	<0.0001
Date × treatment	14,105	7.40	<0.0001
Deep (40–80 cm depth)			
Treatment	2,15	5.27	0.02
Date	7,105	2.97	<0.0001
Date × treatment	14,105	3.38	<0.0001
2008			
Shallow (20 cm depth)			
Treatment	2,15	1.15	0.34
Date	8,120	166.82	<0.0001
Date × treatment	16,120	7.94	<0.0001
Deep (40–80 cm depth)			
Treatment	2,15	2.88	0.09
Time	8,120	74.13	<0.0001
Time × treatment	16,120	8.71	<0.0001

There was a significant correlation between the densities of *T. dubius*, *L. serriola*, and total exotic forbs in July 2007 and the average volumetric water content from 20 to 80 cm during the preceding month (Fig. 6). Density of *M. officinalis* was not significantly correlated with soil water ($P = 0.22$).

The density of native forbs was twofold greater in control than shrub-removal plots in June 2008 (Table 4, Fig. 7). Two of the most abundant native forbs at the study site, *Zigadenus venenosus* and *Calochortus nuttallii*, were more numerous in control than shrub-removal or rainout-shelter plots (Tukey's, $P < 0.02$, Table 4, Fig. 7).

Discussion

Increased resource availability has been implicated as a cause of increased invasibility of ecosystems (Davis et al. 2000) and foundation species modulate resource



◀**Fig. 3** Non-metric multidimensional scaling (nMDS) plots of plant community cover in plots with 95% confidence intervals around treatment centroids. The nMDS plots show the relative differences in community composition of bunchgrasses (*bunch*), cheatgrass (*cheat*), exotic forbs (*exotic*), and native forbs (*native*). Stress < 7 for all plots

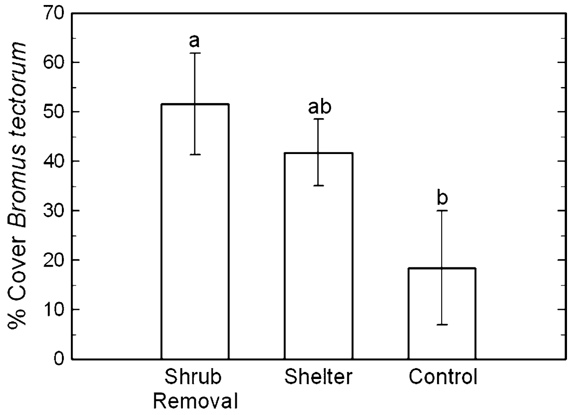


Fig. 4 Average % cover of *Bromus tectorum* in shrub-removal, rainout-shelter, and control treatments on 8 June 2008, ±1 standard error. Means with *different letters* are significantly different (Tukey's HSD < 0.05)

Table 3 Mixed-model ANOVA with repeated measures for the comparison of exotic forb densities over the summers of 2007 and 2008

Effect	df	*F*	*P*
Total exotic forb density			
Treatment	2,15	23.93	<0.0001
Date	2,30	46.44	<0.0001
Date × treatment	4,30	1.95	0.13
Tragopogon dubius density			
Treatment	2,15	14.74	0.0003
Date	2,30	7.23	0.003
Date × treatment	4,30	3.14	0.03
Lactuca serriola density			
Treatment	2,15	17.02	0.0001
Date	2,30	7.23	<0.0001
Date × treatment	4,30	3.14	<0.0001
Melilotus officinalis density			
Treatment	2,15	4.10	0.03
Date	2,30	0.01	0.99
Date × treatment	4,30	0.96	0.44

levels in ecosystems (Ellison et al. 2005). Removal of foundation species could increase resource availabilities to the benefit of other species, particularly

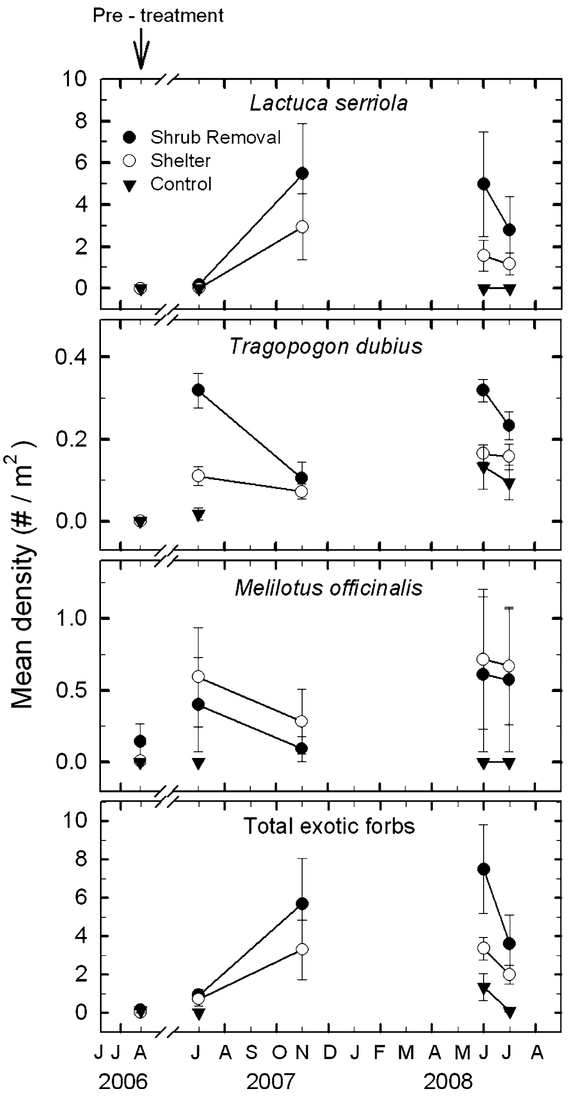


Fig. 5 Average densities of exotic forbs per m^2 in shrub-removal, rainout-shelter, and control treatments, ±1 standard error. The numbers of *Lactuca serriola*, *Melilotus officinalis*, and total exotics were $\log_{10}$-transformed prior to analysis

Table 4 Blocked-ANOVA for the comparison of *Bromus tectorum* cover and native forb densities in June 2008

Effect	df	*F*	*P*
Bromus tectorum			
Treatment	2,10	4.77	0.04
Block	5,10	0.58	0.72
Total native forb density			
Treatment	2,10	4.01	0.05
Block	5,10	3.11	0.06
Calochortus nuttallii density			
Treatment	2,10	8.52	0.007
Block	5,10	1.19	0.38
Zigadenus venenosus density			
Treatment	2,10	4.46	0.04
Block	5,10	1.82	0.20

invading exotic plants, which also may quickly establish due to higher dispersal and growth rates than typical native forbs. While studies have shown that resource levels (Davis and Pelsor 2001) and species composition (Fargione and Tilman 2005; Emery and Gross 2007) can affect invasibility, few studies have experimentally assessed loss of dominant plant species without the corresponding increases in resource availability attributed to the species. We aimed to assess the effects of a foundation species, and its associated use of a limiting growth resource, on community composition and invasibility. Sagebrush removal changed the composition of the herbaceous community substantially. Increased soil water after removal of sagebrush was important for some exotic invaders, but other factors associated with sagebrush removal also contributed to establishment of exotic plants.

Sagebrush removals that were intended to promote forage have, in cases, led to persistent invasions of *B. tectorum* (Hedrick et al. 1966; Blumenthal et al. 2006), and cover of native plants was negatively correlated with *B. tectorum* in sagebrush steppe (Anderson and Inouye 2001). Similarly, shrub removal in the current study led to loss of native forbs and increased cover of *B. tectorum* (Fig. 4). Sagebrush, in particular, has been shown to reduce seed production of nearby *B. tectorum* due to belowground competition (Reichenberger and Pyke 1990), and seedling emergence and survival of *B. tectorum* are lower under sagebrush canopies than in interspaces (Chambers et al. 2007). Our findings, combined with those of previous studies, suggest that cold desert plant communities with sagebrush are more resistant to invasion by *B. tectorum* than communities without sagebrush.

Exotic forbs also responded strongly to removal of sagebrush. *Tragopogon dubius* became more abundant in shrub-removal plots than rainout-shelter or control plots, as predicted (Fig. 5). Furthermore, exotic forbs, especially *T. dubius*, were more abundant where and when there was more available soil

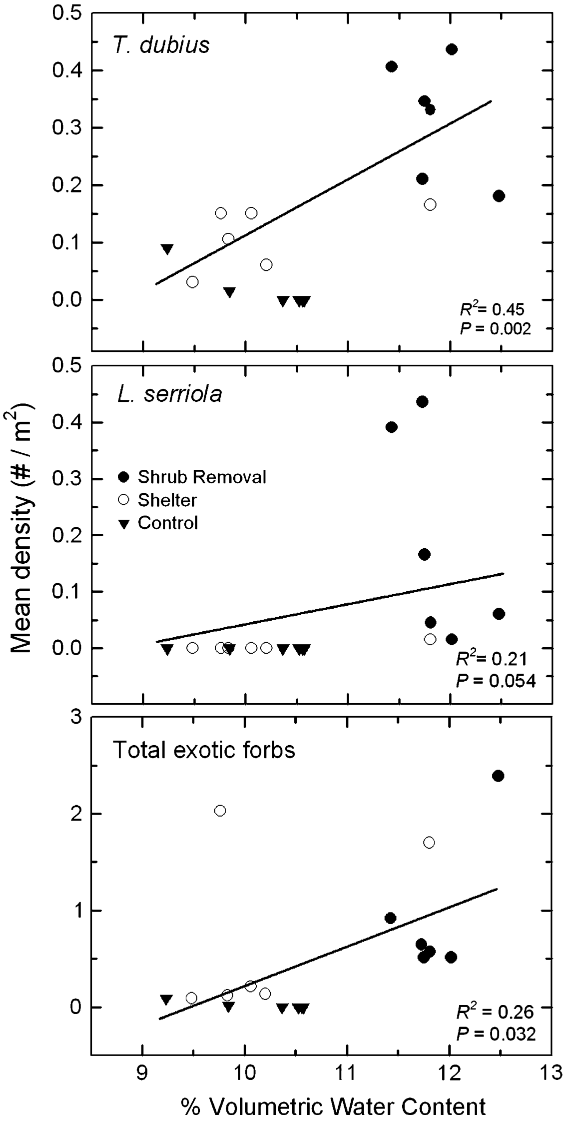


Fig. 6 Correlation between densities of *Tragopogon dubius* (*top panel*), *Lactuca serriola* (*middle panel*), and total exotic forbs (*bottom panel*) in July 2007 and volumetric water content (20–80 cm depth) averaged from 10 May through 11 June 2007 for shrub-removal, rainout-shelter, and control treatments ($n = 18$)

water (Fig. 6). *Tragopogon dubius* appeared to benefit from the increase in deep-soil water that followed removal of sagebrush.

In contrast, *Melilotus officinalis* and *Lactuca serriola* were similarly abundant in rainout-shelter and shrub-removal plots in July 2008, despite lower amounts of soil water in rainout-shelter plots in the preceding spring. These two species may have benefited from other conditions associated with removal of sagebrush not evaluated in the present study. Additionally, physiological adaptations of *L. serriola* may allow it to reduce its water use (Hill and Germino unpublished data; Werk and Ehleringer 1985) and thrive in low moisture conditions. The scarcity of exotic forbs in control plots strongly contrasted with the higher densities observed in the other treatments (Fig. 5). Our experiment suggests that water is an important part of the mechanism for invasion of some exotic forb species, yet during June 2008, when soil water was similar in control and shrub-removal plots (Fig. 2), controls still had fewer exotic forbs (Fig. 5). Competition for other resources, such as nutrients, light availability, fewer establishment sites, or other factors we did not evaluate also could play a role in limiting exotic plant invasions in intact sagebrush steppe.

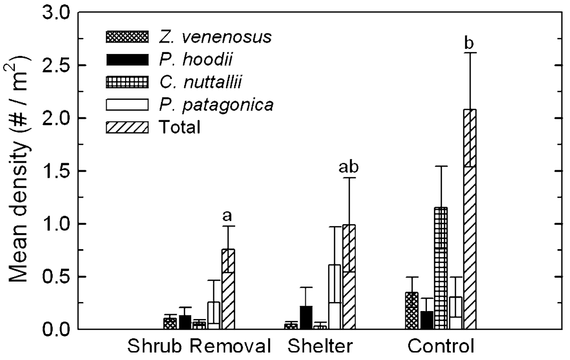


Fig. 7 Average densities of native forbs per m^2 in shrub-removal, rainout-shelter, and control treatments on 8 June 2008, ±1 standard error. The numbers of all native forbs were $\log_{10}$-transformed prior to analysis. Means with different letters are significantly different (Tukey's HSD < 0.05)

Whereas herbs have traditionally been expected to increase upon shrub removal, we found that native forbs were most abundant in undisturbed sagebrush plots (Fig. 7). Native forb responses to sagebrush removal ranged among species from no change to several-fold decreases in the most abundant forbs. This provides preliminary evidence that sagebrush presence could have a net benefit to the growth of native forbs directly or indirectly, and supports findings that foundation species can serve an important role in maintaining native communities (Bruno et al. 2003; Ellison et al. 2005).

The greater increase of exotic compared to native forbs to sagebrush removal could result from (1) direct or indirect positive effects of sagebrush on native forbs, or (2) greater phenological differences between sagebrush and native forbs than sagebrush and exotic forbs and (3) from greater seed output, dispersal and growth rates of exotic forbs that could lead to more rapid establishment where shrubs once existed. Native forbs may benefit from reduced herbivory near sagebrush (Karban 2007). 'Resource islands' of increased C and N often form beneath the canopies sagebrush and could benefit herbs (Bechtold and Inouye 2007), both native and exotic alike. Moreover, these resource islands have been observed to persist 6 years after sagebrush removal (Bechtold and Inouye 2007), so our shrub-removal treatment may have not had substantial changes in nutrient conditions over the 2 years of our observations following shrub removal. A key phenological distinction between the native and exotic forbs is the tendency for exotic forbs to extend their growth period into the later and drier periods of the growth season, when many native herbs have senesced (e.g., Hill et al. 2006) but when exotic forbs might interact more intensely with sagebrush. In particular, the late-season phenology and deeper rooting patterns of exotic forbs would seem to make them most likely of all herbs in this community to compete with established sagebrush for soil water.

The scarcity of native forbs in shrub-removal plots could have resulted from competition for resources with the more abundant *B. tectorum*, though our data cannot test this. Establishment and cover of cheatgrass have been associated with reduced native plant cover (Young and Evans 1973; Anderson and Inouye 2001). The shallow-water content of *B. tectorum*-dominated communities can be lower than intact sagebrush communities in early summer (Prater et al. 2006). We also found the high percentage cover of *B. tectorum* in shrub-removal and rainout-shelter plots in June 2008 corresponded with a reduction in shallow-soil moisture in late May and early June 2008 (Fig. 2). By pre-empting soil water and other resources in spring and early summer, *B. tectorum* can negatively impact the growth of native plants (Harris 1967; Melgoza et al. 1990) and lead to shifts in plant community composition in sagebrush steppe (Young and Evans 1978).

Depletion of deep-soil water over the summer also differed between treatments in a pattern that implicates water in mediating interactions of native and exotic plants. As expected, deep-soil water was depleted more over the course of the growing season in plots with sagebrush than in those from which sagebrush was removed (Fig. 2). Surprisingly, deep-soil water was depleted more in shrub-removal plots than rain-out-shelter plots (Fig. 2). This depletion could have resulted from the increased abundance of invasive forbs in shrub-removal plots in 2007. Exotic forbs may use more deep-soil water than native forbs and grasses late in the growing season (Hill et al. 2006; Kulmatiski et al. 2006), and such use of deep-soil water by established non-native forbs can interfere with the re-establishment of native shrubs (DiCristina and Germino 2006). Reduction of deep-soil water in shrub-removal plots over summer 2008 was comparable to that observed in undisturbed plots, indicating that within 2 years following sagebrush removal, water-use in plots dominated by bunchgrasses and exotic forbs was as great as that of intact sagebrush communities.

In summary, we found that the removal of sagebrush from a shrub-steppe ecosystem altered the herb community. Abundance of exotic forbs increased and that of native forbs decreased. Ecosystems with greater native plant cover or diversity often have been identified as more resistant to invasion (Elton 1958; Naeem et al. 2000; Anderson and Inouye 2001), but certain species may be more important than overall diversity in preventing invasions (Emery and Gross 2007; Thomsen and D'Antonio 2007). Our results illustrate the strong effects of a specific 'foundation' species, sagebrush, on the hydrology and plant community composition of an ecosystem. Our study clearly showed that exotic plants were less abundant and native forbs were more abundant in undisturbed sagebrush steppe than in areas where sagebrush had been removed. The re-establishment of sagebrush in disturbed areas should be a priority for effective reduction of exotic plant invasions and restoration of functional native plant communities.

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