

## RESPONSE OF HERBS TO SHRUB REMOVAL ACROSS NATURAL AND EXPERIMENTAL VARIATION IN SOIL MOISTURE

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**Abstract.** Like many semiarid grasslands, large montane meadows of the Sierra Nevada Mountains, California (USA) have experienced widespread expansion of woody plants (here Rothrock sagebrush, or *Artemisia rothrockii*), a reduction in herbaceous species cover, and apparent aridification over the past century. Because soil moisture is an important limiting resource in this system, we investigated the interactive effects of shrub removal and soil moisture on herbaceous species recovery. We conducted replicated shrub removal experiments across four sagebrush habitats that differed in soil moisture, water table depth, and related characteristics (e.g., soil texture, initial total herbaceous cover, and initial shrub biomass). Changes in herb cover after shrub removal were monitored over four years that differed in spring snow pack, a critical source of water in this system. To more directly quantify the effects of soil moisture on shrub–herb competition, shrub removal was combined with experimental water addition in the most xeric habitat and monitored for two years. Total herb cover increased significantly with shrub removal, but the magnitude of this effect varied among years and habitats, and with experimental watering. Regardless of the source of soil moisture variation (i.e., experimental, spatial, or temporal variation), the absolute change in herb cover with shrub removal increased linearly with moisture at the dry end of the gradient (<15% gravimetric soil moisture). An apparent reversal of this trend under wetter conditions was not possible to evaluate due to few data points above 15% soil moisture. Sagebrush growth rates increased with surface soil moisture, suggesting that this woody species can use water sources similar to those used by herbaceous species. In xeric sites dominated by sagebrush, increasing water availability alone is unlikely to increase herb biomass because suppression by shrubs negates the positive effect of watering. Shrub removal alone has the potential to increase herb biomass at mesic sites or during wet years at xeric sites.

**Key words:** desertification; environmental stress; grasslands; interaction strength; interspecific competition; meadows; rangeland; restoration; riparian; sagebrush; shrub invasion and control; Sierra Nevada, California.

### INTRODUCTION

Over the past century, many arid and semiarid grass-dominated habitats throughout the world have experienced increases in shrub or tree cover and reduced cover of native graminoids (Vavra et al. 1994, Archer et al. 1995, Arnalds and Archer 1999, Van Auken 2000). Conceptual models and observations suggest that expansion of woody plants is not easily reversible (West 1983, Archer 1989, Westoby et al. 1989, Schlesinger et al. 1990, Friedel 1991, Laycock 1991, Vavra et al. 1994). Various forms of shrub control (e.g., clearing, herbicide spraying, burning) have been used since 1950 to restore native herbaceous species, with the stat-

ed intention to release them from competition with shrubs (e.g., reviewed in Hedrick et al. 1966, Sturges 1993, Olson and Whitson 2002). The success of these efforts, however, has been variable both among sites and within a site over time (e.g., Hessary and Gifford 1979, Johnson and Strang 1983, Gibbens et al. 1993, Giorgetti et al. 1997, Havstad et al. 1999). Understanding what regulates variation in the outcome of shrub control is essential to predict the site-specific effectiveness of this restoration tool (e.g., McDaniel and Balliet 1986, Page et al. 2000, Chambers and Linnerooth 2001, Olson and Whitson 2002, Wright and Chambers 2002).

The rich history of basic research on the relationship between competition intensity and productivity or environmental stress (e.g., Grime 1979, Tilman 1982, Menge and Sutherland 1987, Goldberg and Barton 1992) can potentially contribute to understanding variation in the outcome of shrub control efforts. Despite considerable debate (Thompson 1987, Tilman 1987, Thompson and Grime 1988, Goldberg and Novoplan-

Manuscript received 22 March 2002; revised 7 January 2003; accepted 13 January 2003; final version received 10 February 2003. Corresponding Editor: D. Peters.

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PLATE 1. View of the middle section Mulkey Meadow facing north. Mulkey is one of a series of large montane meadows on the Kern Plateau of the southern Sierra Nevada in Kern County, California, USA. The shrubs visible are native Rothrock sagebrush (*Artemisia rothrockii*) individuals which have been invading these herbaceous meadows from surrounding meadow edge over the past century. The small shrubs in the foreground have invaded this particular meadow site within the past 15 years. The sandy unvegetated soil between the meadow and the semiarid lodgepole pine (*Pinus contorta*) forest on the surrounding hillsides is typical of many meadows in this region of the Sierra Nevada. Person for scale: Eric L. Berlow; photo by Anthony Darrouzet-Nardi.

sky 1997), one consistent result has been that the absolute increase in abundance of a target species in response to removal of a competitor tends to increase in magnitude with increased productivity, often measured as standing herbaceous biomass (e.g., Gurevitch 1986, Reader et al. 1994, Kadmon 1995). In arid and semiarid grasslands, soil moisture is a critical limiting resource that is characteristically variable and can drive strong spatial and temporal variation in standing herbaceous biomass (Noy-Mier 1973, Lauenroth et al. 1978, Clary and Jameson 1981, Giorgetti et al. 1997, Burke et al. 1998). We applied this basic understanding of competition to predict variation in the outcome of shrub removal as a restoration tool in a semiarid, montane meadow system where shrub invasion has occurred in multiple micro-habitats with contrasting soil moisture regimes. In this system, soil moisture is a strong predictor of live herbaceous standing biomass, which in turn is strongly related to annual herbaceous production because all species die back each winter.

Large montane meadows of the southern Sierra Nevada, California, USA (see Plate 1), have experienced expansion of Rothrock sagebrush (*Artemisia rothrockii*), reduction in herbaceous species cover, and aridification of the habitat over the last century. *A. rothrockii* (hereafter "sagebrush") is native to this region, but was historically restricted to the dry soils between the meadow edge and the lodgepole pine (*Pinus contorta*) forest on adjacent hill slopes. Shrub invasion into the meadows began in the mid 1800s after the onset of livestock grazing (Ratliff 1985, Odion et al. 1988,

Menke et al. 1996, USDA Forest Service 1998, Dull 1999) and continues today (Bauer et al. 2002, Berlow et al. 2002). Sagebrush has expanded into areas that range from now xeric terraces with low herbaceous cover where stream channel incision has lowered the water table (Kattelman and Embury 1996, Knapp and Mathews 1996, Kirchner et al. 1998, USDA Forest Service 2000) to mesic expanses with a shallow water table, moist surface soil, and high herbaceous cover (Bauer et al. 2002, Berlow et al. 2002).

These patterns of sagebrush expansion raise two related questions about restoration options in this system: First, is soil moisture a good predictor of when and where herbs will exhibit the strongest response to shrub removal? Second, in the most xeric habitat, where it is commonly assumed that low soil moisture alone precludes herb growth, will proposed efforts to increase water availability (USDA Forest Service 1998) successfully facilitate herbs, or have no effect because of increased suppression by shrubs or low herb propagule supply?

To address these questions, we conducted replicated shrub removal experiments across four sagebrush habitats that varied naturally in soil moisture, water table depth, and other related characteristics (Table 1). Changes in herb cover were monitored over four years that differed in spring snow pack, the primary source of water in this system. We also combined shrub removal with experimental addition of water in the most xeric sagebrush habitat (i.e., deep water table, dry surface soil, and low herbaceous cover). This approach

TABLE 1. Mean biotic and abiotic characteristics (1 SE in parentheses) of the different sagebrush vegetation types.

Sagebrush vegetation type	Meadow	July water		Soil texture (sand/silt/ clay) (%)§	Soil total C/N (mg/g)	Total herb cover (%)†	Bare soil cover (%)†	Shrub biomass (kg/m <sup>2</sup> )¶
		July soil moisture (g/g soil)†	table depth (m)‡					
Low-terrace Sage	Mulkey	6.8 (0.8)	0.67 (0.04)	87.4/12.3/0.4 (1.6/1.6/0.2)	0.92/0.07 (0.21/0.02)	28 (4)	55 (5)	0.57 (0.07)
Low-terrace Sage–Herb	Mulkey	17.1 (3.6)	0.63 (0.03)	85.8/14.4/0.1 (0.8/0.8/0.1)	1.93/0.14 (0.13/0.01)	75 (5)	11 (5)	1.01 (0.12)
High-terrace Sage	Mulkey	3.7 (0.2)	1.44 (0.07)	84.6/14.8/0.6 (0.5/0.4/0.2)	no data	21 (5)	53 (3)	0.44 (0.10)
High-terrace Sage–Herb	Ramshaw	10.0 (1.9)	1.07 (0.1)	72.6/26.9/0.5 (3.7/3.9/0.2)	no data	40 (4)	16 (3)	no data

† Averaged within each sampling site over all years for which data were available from 1998–2001; then averaged over sites;  $n = 5$  sites for Low-terrace Sage, Low-terrace Sage–Herb, High-terrace Sage–Herb, and  $n = 9$  sites for High-terrace Sage.

‡ Measured with observation wells, and averaged within each well over all years for which data were available from 1998–2001;  $n = 5$  wells for Low-terrace Sage, Low-terrace Sage–Herb, High-terrace Sage–Herb;  $n = 4$  wells for High-terrace Sage, because the water table dropped below some wells on this terrace level.

§ Soil texture of the top 10 cm was analyzed for cores taken in two paired under-shrub and inter-shrub locations in each experimental plot from which shrubs were not removed. Under- and inter-shrub locations were pooled here to characterize each vegetation type;  $n = 5$  sites for each vegetation type. Soil was sieved with a 2-mm mesh prior to analysis. Following dispersion with sodium hexametaphosphate, texture was analyzed with a standard hydrometer approach (Klute 1986).

|| Carbon and nitrogen were analyzed on pooled samples of soil from each Low-terrace Sage and Low-terrace Sage–Herb plot (four cores per vegetation type per block were pooled into one mean per block). After drying at 55°C for 3 d, samples were sieved through 2-mm mesh, ground with a mortar and pestle, and a 30-mg subsample was combusted on a Fison's Carlo Erba CHN analyzer (Carlo Erba, Beverly, Massachusetts, USA). Data are mg/g soil. Samples from under-shrub and inter-shrub spaces were pooled within each sampling site;  $n = 5$  sites for each vegetation type.

¶ Shrub biomass estimates pooled within a sampling site;  $n = 5$  sampling sites for Low-terrace Sage, Low-terrace Sage–Herb, High-terrace Sage–Herb, and  $n = 4$  for sampling sites for High-terrace Sage.

allowed us to compare the effects of spatial, temporal, and experimental variation in soil moisture on herb growth with and without shrubs removed.

#### STUDY SYSTEM

This study was conducted in two large (5–7 km long) montane meadows of the Golden Trout Wilderness in the Inyo National Forest of the southern Sierra Nevada, California, USA. Mulkey Meadow (36°24' N, 118°12' W, 2750 m; see Plate 1) and Ramshaw Meadow (36°15' N, 118°15' W, 2550 m) are part of the largest meadow complex in the Sierra Nevada and occur in depositional basins along the South Fork Kern River. These meadows are in wilderness areas accessible only by foot or horseback and are several hours from the nearest trailhead, hence restoration options are limited. Both meadows are grazed by cattle under regulation by the U.S. Forest Service (USFS). In order to examine factors that suppress herbaceous species independent of livestock grazing, the experiments reported were conducted within livestock enclosures installed in Ramshaw (1983) and Mulkey (1991) Meadows. Each enclosure is ~2 km in length and extends 50–150 m to include upland meadow vegetation on either side of the stream. The herbaceous meadow vegetation is almost entirely native with the only common exotic species, *Taraxicum officinale*, occupying <1% cover. The meadows are generally covered with snow from November to May, and the summer growing season lasts from approximately late May to August, depending on the timing of snow melt. The meadows occur in a semiarid region

where annual precipitation is ~50–70 cm (USDA Forest Service 1998). Most precipitation is in the form of snow; for the past 14 years, the mean cumulative rainfall during the growing season was only 7 cm (California Department of Water Resources [CADWR] 2001, *available online*).<sup>5</sup>

Most meadows of the Kern Plateau have at least three terrace levels, including one created by stream channel incision that likely occurred in the past century (Collins 1995). Water table depth generally increases with vertical distance from the stream that bisects the meadows (Sarr 1995). Sagebrush occurs in a number of distinct habitat types (Table 1). It is abundant on the highest terrace level where the water table is consistently >1 m, hereafter referred to as "High-terrace Sage." These xeric sagebrush-dominated areas typically have <25% herbaceous cover. Sagebrush patches co-occur with mesic herbaceous meadow on lower terraces and the active floodplain, where the mean water table soon after snowmelt is typically <50 cm (Berlow et al. 2002). In these low terrace patches, sagebrush can be found either with a significant herbaceous understory ("Low-terrace Sage–Herb"), or with a sparse herb cover and abundant exposed soil ("Low-terrace Sage"). High-terrace Sage and Low-terrace Sage are similar in herb cover and exposed soil, but the latter has a consistently shallower water table (Table 1). A fourth sagebrush habitat abundant in Ramshaw Meadow was used as an independent test of predictions derived from the ex-

<sup>5</sup> URL: <http://cdec.water.ca.gov>

periments in Mulkey Meadow. This High-terrace Sage–Herb habitat, like High-terrace Sage has a deep water table, but has at least 35–40% herbaceous cover. In all study plots, sagebrush was the only woody species present. These different sagebrush habitats represent complex natural gradients of soil moisture, water table depth, soil texture, soil total nitrogen and carbon, initial herb cover, and initial shrub biomass (Table 1). We focused, however, on midsummer soil moisture in the top 30 cm because it was a strong predictor of initial total herbaceous cover ( $R^2 = 0.76$ ,  $P < 0.001$ ), and because it was the most significant explanatory variable in a multiple regression describing variation in herb cover response to shrub removal (results not shown). Most of these habitat attributes were significantly correlated with one another ( $P < 0.01$  for 80% of all pairwise correlations); thus, we considered soil moisture a surrogate for this complex physical gradient.

## METHODS

### *Comparative sagebrush removal experiments*

We combined the results of three separate experiments to investigate how the effects of sagebrush removal varied with soil moisture. The first experiment, hereafter called the “Mulkey removal experiment,” is described in detail in Berlow et al. (2002). Briefly, in late August 1996 and June 1997, sagebrush was either removed (by cutting at the base of the stem) or left intact within each of the Low-terrace Sage–Herb, Low-terrace Sage, and High-terrace Sage vegetation types in Mulkey Meadow. To minimize soil disturbance, we did not extract sagebrush root systems, but instead trimmed re-sprouting stumps throughout the experiment.

Paired sagebrush removal and control plots were replicated in five blocks located along stream reaches where all three vegetation types occurred in close proximity, giving a total of 10 plots for each vegetation type. The livestock enclosure in Mulkey was large enough that all five blocks were separated by at least 100 m. Experimental plots were limited to 4 m<sup>2</sup> because low-terrace sagebrush patches were rarely larger than 15–20 m<sup>2</sup>. When the experiment was initiated, we observed significantly more pocket gopher disturbance in the low-terrace vs. high-terrace sagebrush habitats (Berlow et al. 2002). To control for this among-habitat variation in disturbance, we excluded gophers from the low-terrace plots by burying 0.6-cm mesh aviary netting 40 cm deep, leaving a 5-cm extension above ground. While gophers were present in the High-terrace Sage, their activity only occasionally created disturbances within the experimental plots over the entire course of the study (E. L. Berlow, *unpublished data*).

A second experiment (the “Mulkey watering experiment”) was initiated in an extensive High-terrace Sage stand in Mulkey Meadow in 1999. In this xeric habitat, shrub removal was crossed with the experimental ad-

dition of water. To minimize potential edge effects of watering small plots, we used a split-plot design where sagebrush removal and control treatments (25 m<sup>2</sup>) were paired within a larger area (50 m<sup>2</sup>) that was watered or not. All four treatments were replicated in four separate blocks separated by at least 50 m. Plots were watered with a drip irrigation system that drew water from the stream using pumps (6.8 L/min, 7 amps 12 VDC [volts direct current]; Shurflo Pump Manufacturing, Cypress, California, USA) powered by 60-W solar panels. The plots were <100 m horizontal and <3 m vertical distance from the stream. The pumps ran only with sunlight, and on several occasions the irrigation system stopped due to overnight freezing or chewing of lines by black bears and marmots.

In a third experiment (the “Ramshaw removal experiment”), we took advantage of extensive stands of High-terrace Sage–Herb in Ramshaw Meadow, a vegetation type uncommon in Mulkey Meadow. Paired shrub removal and control plots (25 m<sup>2</sup>) were established in July 1998 in five blocks separated by at least 100 m within the Ramshaw livestock enclosure. Shrub removal plots were initiated in July 1998. The Ramshaw enclosure is eight years older than that in Mulkey, and the meadow is ~200 m lower. The lower elevation resulted in a generally earlier onset of the summer growing season as well as warmer temperatures. Given these differences between Ramshaw and Mulkey, we used results of the Ramshaw experiment as an independent test of predictions generated from results of the Mulkey Meadow experiments.

All experimental plots were located within one livestock enclosure in each meadow because we were interested in understanding the processes that inhibit meadow restoration in the absence of livestock grazing. We purposefully did not examine the effects of the livestock enclosures themselves because only one existed per meadow, and their locations were not randomly determined. The enclosures were large enough to include multiple sagebrush habitat types and associated physical gradients of water table depth and soil moisture.

### *Herb and shrub responses*

In all three experiments, we monitored percentage of herbaceous species cover in July of each year, the time of peak flowering, and biomass. We used this measure because it was nondestructive, and total herbaceous canopy cover was strongly correlated with standing herbaceous biomass ( $R^2 = 0.78$ ,  $P < 0.001$ ). In the Mulkey removal experiment, herbaceous species cover for each 4-m<sup>2</sup> plot was estimated in July 1998, 1999, 2000, and 2001. In 1998, canopy cover of each species in the Low-terrace Sage–Herb was estimated visually in one 0.09-m<sup>2</sup> quadrat in an inter-shrub location near the center of each plot. In the more xeric Low- and High-terrace Sage, where herbaceous cover was sparse, we estimated cover over a larger area using two 0.25-

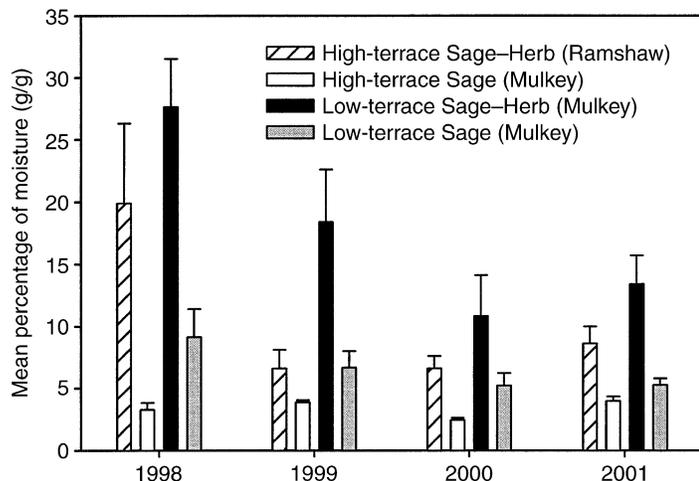


FIG. 1. Mean (+1 SE) midsummer moisture over time for the four sagebrush vegetation types in this study.

m<sup>2</sup> point-intercept quadrats on the center diagonal of each plot. Cover for each species was estimated from the proportion of intersections with a grid of 81 points, spaced 5 cm apart, in each quadrat. Because the canopies of different species often overlapped, total herbaceous cover could exceed 100%. Data from the two quadrats in each plot were pooled. In subsequent years, the two 0.25-m<sup>2</sup> quadrats were also used in the Low-terrace Sage-Herb. Field observations suggest that the small area sampled in 1998 was representative of the area sampled in later years, but we do not have the data to directly compare the two sampling methods. Thus, differences in cover in the Low-terrace Sage-Herb between 1998 and the later years should be interpreted with the caveat the 1998 data came from less intensive sampling. In the larger (25-m<sup>2</sup>) plots of the Ramshaw removal and Mulkey watering experiments, species cover was estimated in three 0.25-m<sup>2</sup> point-intercept quadrats spaced 1 m apart along two transects within each plot. Cover was averaged across all six quadrats within each experimental plot so that replication was at the scale of the blocks ( $n = 5$ ).

To quantify the effects of watering and among-habitat and among-year variation in water availability on sagebrush growth, we measured branch elongation rates over each growing season (~May–August) for 1998–2000 in each of the sage-present treatments. In the Mulkey removal experiment, within each 4-m<sup>2</sup> sage-present plot we marked 5 live branches on each of 3 individual sagebrush in early spring before sagebrush began active growth. In the Ramshaw removal experiment and the Mulkey watering experiment, since the plots were larger, we allocated the branch sampling among more individuals. In each 25-m<sup>2</sup> sage-present plot, we marked 4 branches on each of 6 randomly selected individuals. Branch length from the label to the end of the longest vegetative stem was recorded once at the start of each growing season (soon after snow melt), and again at the end (late August/early

September). New branches were labeled at the start of each growing season.

#### *Soil moisture variation among habitats and years and with watering*

To explore how the magnitude of herb response to shrub removal varied with natural and manipulated variation in water availability, we measured soil moisture, integrated over the top 30 cm, with Time Domain Reflectometry (TDR) probes (Environmental Sensors, Victoria, British Columbia, Canada) in all experimental plots concurrent with the July monitoring of species cover. The only exception was for the 2001 growing season, when we used moisture measurements from early August because of unusually intense rainstorms just prior to the July species cover monitoring. In the 4-m<sup>2</sup> plots of the Mulkey removal experiment, soil moisture was measured in one inter-shrub location near the center of each unmanipulated plot. In the 25-m<sup>2</sup> plots of the Mulkey watering and Ramshaw removal experiments, two TDR readings were taken at random inter-shrub locations in each plot where sagebrush was not removed. More intensive sampling early in the experiment suggested that more measurements per plot were not necessary to characterize among-habitat variation in plot-level soil moisture (E. L. Berlow, unpublished data). TDR values of volumetric moisture were converted to gravimetric moisture using bulk density measurements of soil from each vegetation type (Berlow et al. 2002). In the watering experiment, we conservatively estimated moisture in the watered treatments by using the mean TDR data from two dates in July: one after the irrigation system had been off for about one week, and the other four days after it was repaired. There were no differences in surface gravimetric percentage of soil moisture among watered and un-watered plots before irrigation was initiated in July 1999 ( $F = 3.71$ ,  $df = 1, 3$ ,  $P = 0.15$ ). In the two subsequent years, the irrigated plots were on average

significantly wetter than the un-watered plots (Wilks' Lambda = 0.026,  $df = 1, 3$ ,  $P = 0.002$ ). Since these mean moisture values for each year included time periods when the irrigation system was not functioning properly, they are a conservative estimate of the time-averaged increase in soil moisture due to irrigation. Spring snowpack in the southern Sierra Nevada was highly variable among years. During our study, 1998 May snow pack depth was greater than 200% of the 30-yr mean, and the meadows were not snow-free until early June. 1999 and 2000 were both drought years with spring snowpack <50% of the 30-yr mean (CADWR 2001, *available online*<sup>5</sup>). 2001 was closer to average with regard to spring snowpack, but midsummer rain was >200% of the mean for the past 13 years. Annual variation in midsummer moisture differed among vegetation types (rm-ANOVA, within-subject interaction of VegType  $\times$  Year, Wilks' Lambda = 0.29,  $df = 9, 22$ ,  $P = 0.002$ ; Fig. 1). The sagebrush types with an herbaceous understory (Low- and High-terrace Sage-Herb) exhibited greater variation in soil moisture among years, a pattern that mirrored annual variation in spring snowpack. By contrast, the sagebrush types without a dense understory (Low- and High-terrace Sage) had consistently low moisture. Overall, midsummer soil moisture varied significantly among vegetation types (rm-ANOVA,  $F = 8.71$ ,  $df = 3, 10$ ,  $P = 0.004$ ; Fig. 1). The Low-terrace Sage-Herb was consistently wettest, and the High-terrace Sage was the driest. Controlling for among-vegetation type differences in moisture, the percentage of change in moisture (relative to 1998) over time also varied significantly among vegetation types (rm-ANOVA, within-subject VegType  $\times$  Year interaction, Wilks' Lambda = 0.17,  $df = 6, 20$ ,  $P = 0.004$ ). These patterns of natural variation allowed us to compare the effects of both temporal (i.e., annual) and spatial (i.e., among-vegetation type) variation in soil moisture on the response of herbs to shrub removal.

#### Data analysis

*a) Does the effect of shrub removal on herbaceous cover vary over time, among vegetation types, and with watering?*—The effect of sagebrush removal on total herbaceous cover over time was evaluated with a randomized-block, repeated-measures analysis of variance (rm-ANOVA). Each shrub removal experiment was analyzed separately because they were initiated in different years. In the Ramshaw removal experiment, since there was only one vegetation type (High-terrace Sage-Herb), a blocked one-way rm-ANOVA was used to evaluate sagebrush effects for 1999–2001. In the Mulkey removal experiment, sagebrush treatments were nested within vegetation type, so a two-way, split-plot rm-ANOVA was used to analyze the effects of sagebrush and vegetation type for 1998–2001. The Block  $\times$  VegType interaction was used to test for differences in herb response among vegetation types, and the residual error was used to test for effects of “Sage”

(sagebrush removal) and the Sage  $\times$  VegType interaction. In the Mulkey watering experiment, sagebrush treatments were nested within watering treatments, and a two-way, split-plot rm-ANOVA was used to analyze the effects of water and sagebrush for 1999–2001. Here, the Block  $\times$  Water interaction term was used to test for the main effect of watering, and the residual error was used to test of Sage and Sage  $\times$  Water effects. Where the variances in percentage of cover were heterogeneous, arcsine square-root transformation increased variance homogeneity. In general, the results were similar whether or not the data were transformed. In 2001, two outliers (one Low-terrace Sage and one Low-terrace Sage-Herb replicate) were omitted from the analysis due to data collection error in estimating species cover.

*b) How does the magnitude of competitive suppression vary with soil moisture?*—We considered the difference in herb cover between paired sagebrush removal and control treatments to be a measure of the absolute magnitude of competitive suppression by sagebrush. Thus, a greater response of herbs to shrub removal was interpreted as more intense competition. Hereafter, this measure of the magnitude shrub removal effects is referred to as “absolute competition intensity.” To standardize herb response magnitude by total herb cover in each block, we calculated the “log response ratio” for each pair of shrub removal and control plots as:  $\ln(\text{HerbCover}_{-\text{shrubs}}/\text{HerbCover}_{+\text{shrubs}})$ . Compared to other relative measures of response magnitude, the log response ratio is symmetric about zero and is interpretable under some conditions as the coefficient of competition intensity in simple Lotka-Volterra competition models (Laska and Wootton 1998, Berlow et al. 1999, Goldberg et al. 1999, Hedges et al. 1999).

Results of all three shrub removal experiments were used to compare the magnitude of shrub removal effects across all four vegetation types, all years, and between the +Water and -Water treatments in the High-terrace Sage watering experiment. Visual inspection of the results suggested a strong linear relationship between absolute competition intensity and midsummer soil moisture at the dry to mesic end of the moisture gradient (gravimetric soil moisture <15%). Above 15% moisture there were only two data points to evaluate changes in this trend, thus, we focused our analysis on the drier moisture range.

Since annual variation in herb cover was measured within the same plots each year, we used Pearson product-moment pairwise correlation coefficients to evaluate when the response of herbs among years were independent (Sall et al. 2000). Herb response magnitude was significantly correlated between years only for 2000 and 2001 (correlation coefficient = 0.7,  $P = 0.0003$ ). Thus, with a coin toss we selected one of these years (2000) to exclude from the regression analysis

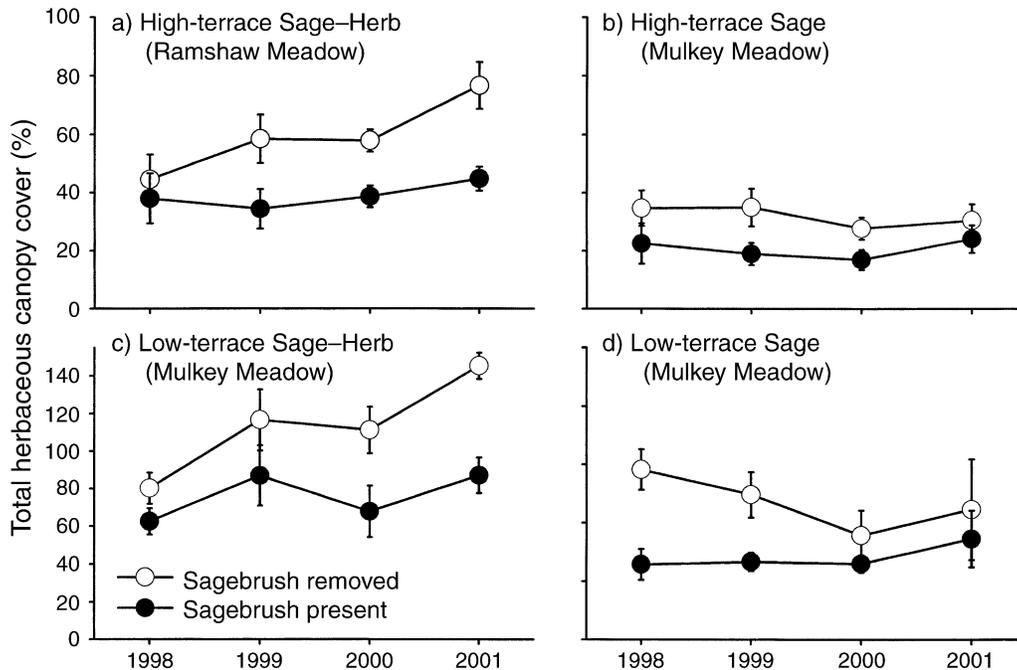


FIG. 2. Mean ( $\pm 1$  SE) total herbaceous canopy cover over time in (a) High-terrace Sage-Herb (Ramshaw Meadow), (b) High-terrace Sage (Mulkey Meadow), (c) Low-terrace Sage-Herb (Mulkey Meadow), and (d) Low-terrace Sage (Mulkey Meadow). In each panel, the first year shown is one year after sagebrush was removed. Because cover estimates included multiple canopy layers, total cover sometimes exceeded 100%, especially in the Low-terrace Sage-Herb. Note the different y-axis scaling for this vegetation type.

and considered data from 1998, 1999, and 2001, to be statistically independent. Additionally, since the Ramshaw removal experiment was conducted in a different meadow that varied in attributes not included in the regression (e.g., different elevation, older livestock exclusion, longer growing season, etc.), we used only Mulkey data for this regression analysis. We then used results of the Ramshaw experiment to test predictions from the relationship generated using Mulkey data. Linear regression was used to examine the relationship between herb response magnitude and midsummer soil moisture for each vegetation type, year, and irrigation treatment (watered or not). Initially, we included other explanatory variables: water table depth for each vegetation type and year, spring snow pack (percentage of the 40-yr mean), initial shrub biomass, initial total herb cover, and soil percentage of sand; however, only midsummer soil moisture was significant (results not shown).

*c) Does sagebrush growth differ among habitats, years, and with watering?*—In the Ramshaw removal experiment and the Mulkey watering experiment, differences in branch elongation rates (millimeters per month) among years or with experimental watering were analyzed with randomized block ANOVA. In the Mulkey removal experiment, a split-plot ANOVA was used to test whether differences among vegetation types varied among years (vegetation type was nested within year). Repeated-measures ANOVA was not used

because different branches were measured each year. Some marked branches developed into long flowering stalks by the end of the summer growing season and were not included in the analysis. When a marked branch died over the course of the summer, growth of that branch was recorded as zero. Visual inspection of residual plots and normal probability plots suggested that data transformation was not necessary to meet the assumptions of ANOVA.

## RESULTS

*a) Does the effect of shrub removal on herbaceous cover vary over time, among vegetation types, and with watering?*—Total herbaceous cover was generally higher in sagebrush removals compared to control plots, but the magnitude of the effect varied among vegetation types (rm-ANOVA Sage  $\times$  VegType interaction:  $F = 6.2$ ,  $df = 2, 9$ ,  $P = 0.02$ ; Fig. 2). Variation among years in the effect of sagebrush also differed among vegetation types (rm-ANOVA Sage  $\times$  VegType  $\times$  Year interaction: Wilks' Lambda = 0.07,  $df = 6, 14$ ,  $P = 0.002$ ; Fig. 2). For example, in the mesic, Low-terrace and High-terrace Sage-Herb (Fig. 2c), the effect of sage removal was greatest in 2000 and 2001. By contrast, in the Low-terrace Sage, herbaceous cover was higher in the absence of sagebrush in 1998, but not in 2000 or 2001 (Fig. 2d).

In the Mulkey watering experiment, adding water alone (i.e., with sagebrush present) had little effect on

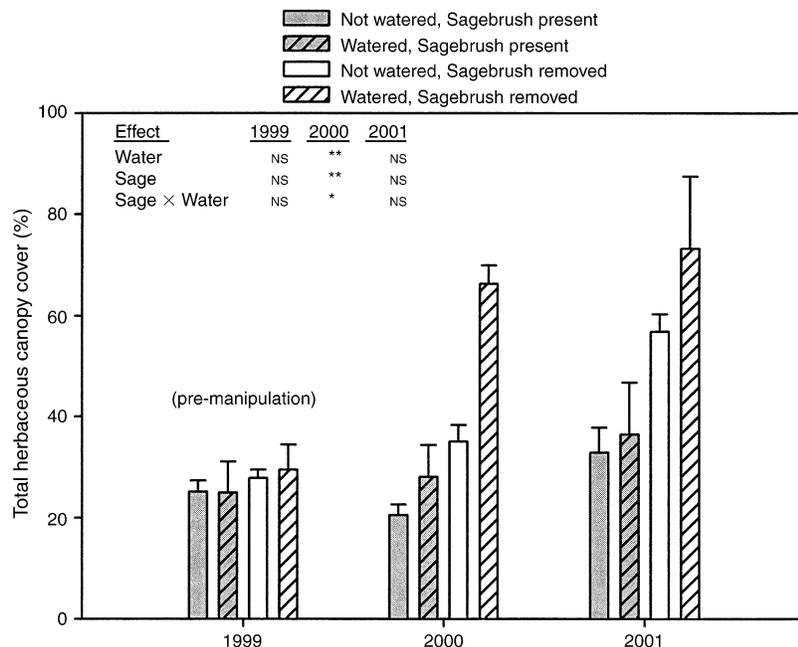


FIG. 3. Mean (+1 SE) total herbaceous canopy cover for each year in the Mulkey watering experiment; 1999 was the pre-manipulation cover. Univariate statistics for the effects of Watering, Sagebrush removal, and the Watering  $\times$  Sagebrush interaction for each separate year are shown: \* $P < 0.05$ ; \*\* $P < 0.01$ ; NS, not significant ( $P > 0.05$ ).

total herbaceous cover in either year (rm-ANOVA  $F = 2.54$ ,  $df = 1, 3$ ,  $P = 0.21$ ; Fig. 3): As long as sagebrush was present, herbaceous cover was low. Removal of sagebrush had a significant effect on herb cover overall, although the effect varied between years (rm-ANOVA Sage  $\times$  Year interaction: Wilks' Lambda = 0.1,  $df = 2, 5$ ,  $P = 0.003$ ). In 2000, the effect of removing sagebrush on total herbaceous cover increased significantly with water addition (Fig. 3). This pattern was less apparent in 2001, the summer that experienced substantial midsummer rains. Hence, in the absence of added water, removing sagebrush alone had a weaker effect in the drier (2000) compared to the wetter summer (2001). In the presence of added water, removal of sagebrush resulted in a consistent, strong increase in herb cover.

While mean total herbaceous cover consistently increased with sagebrush removal, the identity of species responding most strongly to removal varied both among vegetation types. The primary species contributing to increases in herb cover in each habitat respectively were as follows: (1) Low-terrace Sage; *Poa secunda* var. *juncifolia*, *Koeleria macrantha*, *Antennaria rosea*, *Eriogonum umbellatum*, and *Ivesia campestris*; (2) Low-terrace Sage-Herb; *Agrostis idahoensis*, *Deschampsia cespitosa*, *Ivesia campestris*, *Trifolium monanthum*, *Potentilla gracilis*, and *Carex* spp.; (3) High-terrace Sage-Herb, *Elymus elymoides*, *Muhlenbergia richardsonis*, *Eriogonum umbellatum*; and (4) High-terrace Sage-Herb: *Muhlenbergia richardsonis*, *Poa secunda* var. *juncifolia*, *Gayophytum decipiens*,

*Lupinus* spp., and *Carex* spp. Within each vegetation type, the species that dominated the herbaceous response also varied among blocks. For example, in the Mulkey watering experiment, in blocks one and two, the annual forb, *Gayophytum decipiens*, increased dramatically with shrub removal in watered plots. By contrast, in blocks three and four, the response was dominated by vegetative growth of the perennial rush, *Juncus balticus*. While total herb cover generally increased with shrub removal, a few species had lower cover in sagebrush removal plots. However, there was no consistent pattern of facilitation across species, vegetation types, or experimental block. Summed across all species, facilitation of herbs by shrubs was rarely observed. For example, in 2000 only 2 of 28 species exhibited lower total herb cover in shrub removal plots than in paired control plots.

b) *How does the magnitude of competitive suppression vary with soil moisture?*—When all experiments are combined, the absolute change in herb cover with shrub removal, or absolute competition intensity, increased linearly with mean soil moisture under xeric (soil moisture  $< 15\%$ ) conditions ( $R^2 = 0.71$ ,  $P < 0.0001$ ; Fig. 4a). The results of the Ramshaw removal experiment fit well with the relationship predicted from this regression, which was fit to Mulkey removal and watering experiments (Fig. 4a, open symbols). This pattern was consistent regardless of whether differences in moisture were due to spatial variation, annual variation in precipitation, or experimental irrigation. In the more mesic Low-terrace Sage-Herb (Fig. 4a, closed

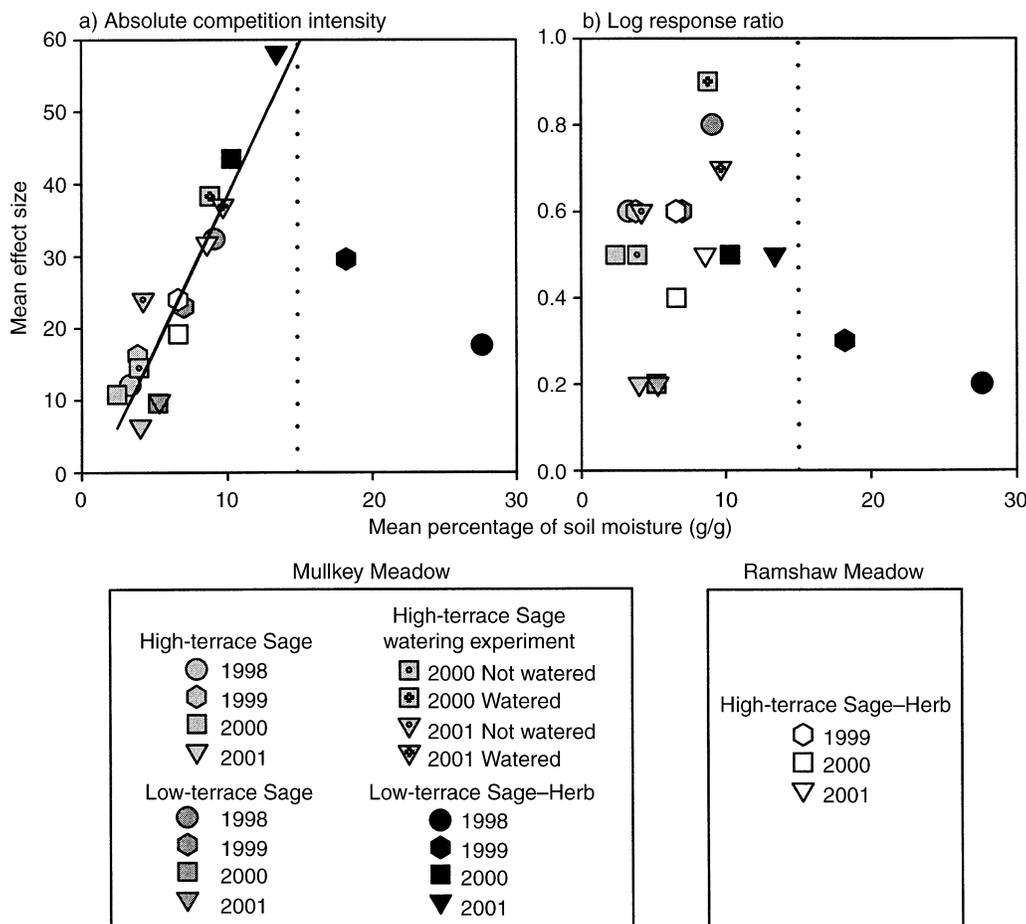


FIG. 4. Mean magnitude of herb-cover increase with shrub removal vs. mean midsummer soil moisture for each vegetation type, year, and watering treatment. The dotted vertical line indicates 15% soil moisture. (a) Absolute competition intensity. Herb response magnitude was measured as the absolute difference in total herb cover between paired shrub removal and control plots. The solid line is a linear regression ( $R^2 = 0.71$ ,  $P < 0.0001$ ) using data for each paired shrub removal and control replicate and mean midsummer soil moisture for that habitat and year combination. The regression was estimated using only data from Mullkey Meadow plots (closed symbols), and only years that were statistically independent (1998, 1999, and 2001). (b) Log response ratio. Herb response magnitude was measured as the log of the ratio of total herb cover in shrub removals divided by total herb cover in the paired shrub controls. Regression of effect magnitude versus soil moisture was not significant ( $R^2 = 0.03$ ,  $P = 0.3$ ) and is not shown.

symbols), there may be a reversal of this trend with high soil moisture, but this pattern was driven by only two cases with  $>15\%$  moisture. Standardizing herb response to shrub removal by total herb cover in the absence of shrubs (log response ratio), we found no consistent pattern of effect size with soil moisture (Fig. 4b). In contrast to the patterns for absolute competition intensity, midsummer soil moisture only explained 3% of the variation in the log response ratio ( $P = 0.3$ ).

c) *Does sagebrush growth differ among habitats, years, and with watering?*—In all three vegetation types in Mulkey, sagebrush branch elongation rates over the growing season were greater in the wet summer of 1998 than in the subsequent two drought years (Fig. 5). There are no data for branch elongation in the Ramshaw High-terrace Sage-Herb in 1998 because the experiment was not initiated until July of that year.

Branch elongation rates did not differ significantly between 1999 and 2000 in any of the four vegetation types. Branch elongation rates were greatest in the Low-terrace Sage-Herb within any given year. Growth rates were not significantly different between the Low- and High-terrace Sage in any year ( $F$ -protected least-squares means,  $P > 0.50$  in all cases), despite large differences in water table between these habitats (Berlow et al. 2002). When High-terrace Sage was watered, branch elongation rate almost doubled. When all habitats, years, and watering treatments are considered, sagebrush growth was significantly correlated with midsummer surface soil moisture ( $R^2 = 0.46$ ,  $P = 0.01$ ). However, sagebrush branch growth in control plots was not correlated with the magnitude of herb response to shrub removal in adjacent plot ( $R^2 = 0.014$ ,  $P = 0.4$ ).

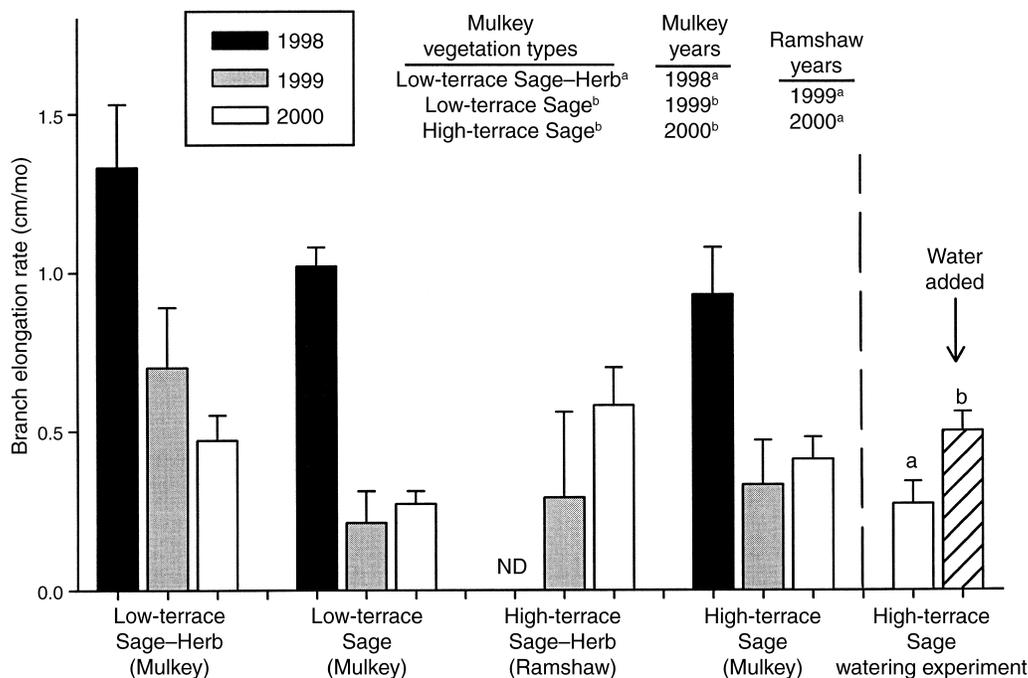


FIG. 5. Mean ( $\pm 1$  SE) sagebrush vegetative branch elongation rates for all four sagebrush vegetation types over each growing season (histogram bars left of dashed vertical line), and the Mulkey watering experiment in 2000 (histogram bars to right of dashed line). ND = no data, because branch elongation was not measured that year in Ramshaw Meadow. Different letters above bars (or appearing as superscripts in columns at top of figure) indicate that there were significant differences ( $P < 0.05$ ) in branch elongation rates among vegetation types, among years, or between watering treatments.

#### DISCUSSION

The absolute difference in herb cover between shrub removal and control plots increased linearly with soil moisture in the xeric to mesic range in this system (i.e., soil moisture  $< 15\%$ ). This pattern was consistent regardless of whether the variation in moisture was due to natural variation among vegetation types or among years, or to experimental addition of water. The relationship between herb response and midsummer soil moisture, generated from experiments in one meadow, successfully predicted the effect of shrub removal in a novel sagebrush habitat in a separate meadow located 200 m lower in elevation. In this semiarid system, midsummer soil moisture was correlated with spring snow pack, total nitrogen and carbon, initial herbaceous cover, and initial shrub biomass. In other arid and semiarid systems, variability in the outcome of shrub control has been attributed to variation in precipitation (Clary and Jameson 1981, Georgetii et al. 1997), water table depth (Chambers and Linnerooth 2001, Wright and Chambers 2002), initial herbaceous cover and/or composition (Hyder and Sneva 1956, Hedrick et al. 1966, West and Hassan 1985), and initial shrub cover (Passera et al. 1996). Together with our experimental results, these patterns suggest that soil moisture may be a useful general predictor of the absolute increase in herbaceous cover/biomass with shrub control in a variety of systems where water is a critical limiting resource.

From our data, we could not make strong conclusions about the relationship between competition intensity and soil moisture under wetter conditions. One would expect a weaker relationship at higher moisture levels because herb cover in the presence of sagebrush is dense enough that competition among herb species for other resources (e.g., light) would likely preclude a strong response to shrub removal (e.g., Miller 1996). It is noteworthy that when the wettest habitat (Low-terrace Sage-Herb) dropped below 15% soil moisture in 2000 and 2001, the herbaceous response to shrub removal fit the positive linear relationship described by the more xeric vegetation types. Other studies have suggested a positive relationship between competition intensity and productivity is more likely when low productivity levels are included in the study (e.g., Campbell and Grime 1992, Turkington et al. 1993, Bonser and Reader 1995). While we did not directly measure productivity, soil moisture was strongly correlated with peak annual standing herbaceous biomass, which completely dies back each winter in this montane system.

It has been suggested that at the very low end of a productivity gradient, competition should be weaker than facilitation, resulting in net positive interactions (Bertness and Callaway 1994, Callaway and Walker 1997, Choler et al. 2001, Callaway et al. 2002). Variable response of herbs to shrub removal in arid environments can result from shifts in the balance be-

tween competition and facilitation under vs. away from shrub canopies (Aguar and Sala 1994, Facelli and Temby 2002). Facilitation in our experiments, expressed by declines in herb cover with sagebrush removal, was rarely observed. However, our estimates of herbaceous response were integrated across locations both under and away from shrub canopies. Thus, we may not have sampled at a fine enough scale to detect microsite variation in facilitation vs. competition.

While total herbaceous cover consistently increased with shrub removal, the individual species that responded varied among vegetation types and among blocks within a vegetation type. In this high-elevation, perennial-dominated system with a short growing season, most herbaceous response to shrub removal was likely due to vegetative growth of existing perennials (E. L. Berlow, C. M. D'Antonio; H. Swartz, *personal observations*). Longer term monitoring may be necessary to evaluate community-level change resulting from recruitment of perennial species from seed. From the perspective of restoration, these results suggest that initial potential effects of shrub removal will be strongly influenced by which perennial herbs are already present at a site. Thus, removal should be targeted in areas where species of interest are relatively abundant, or it should be conducted in combination with seeding or transplanting of target species. Preliminary seeding trials in the watering experiment have resulted in germination of perennial herb species in plots where they were previously absent (E. L. Berlow and C. M. D'Antonio, *unpublished data*).

While shrubs and herbs often use water from different depths (e.g., Sala et al. 1989, Wilson 1998), this has not precluded competition between them in semiarid systems (e.g., see references in D'Antonio and Vitousek 1992, Briones et al. 1998). Our results suggest that sagebrush growth responds to soil moisture in the top 30 cm; thus, competition for water with shallow-rooted herbs is possible. While competition is often the inferred mechanism in simple removal experiments such as those in this study, potential experimental artifacts may also influence the response of the target species. For example, soil disturbance in the removal treatments, rather than competition, could increase herb growth by facilitating germination from the seed bank. By clipping sagebrush at the base of the stem rather than removing the entire plant, we attempted to minimize soil disturbance in removal plots. Decomposition of residual shrub roots in the removal plots could have helped to stimulate an initial pulse of herb growth independent of competition (e.g., Underwood 1986). However, it is unlikely that this was the only explanation, since our observed herb growth responses were maintained over time.

#### *Theory and practice*

One tension between basic and applied ecology is that the former tries to develop general theory, while

the latter must address context-specific concerns (Higgins et al. 2000). Our objective was to apply recent advances in general competition theory for predicting site-specific variation in the response of herbaceous meadow species to shrub removal. The relationship between competition intensity and productivity, environmental stress, or some surrogate of these, has been the subject of considerable debate (e.g., Thompson 1987, Tilman 1987, Thompson and Grime 1988, also reviewed in Goldberg and Barton 1992). One obstacle to incorporating this body of theory into management is that the relationship clearly depends on many factors. Among these are the metric used (relative vs. absolute competition), the response variable (growth, survival, etc.), the source and range of variation in productivity, and most importantly, the particular objectives or questions of interest (Goldberg and Novoplansky 1997, Goldberg et al. 1999). However, one consistent result has been that absolute competition tends to increase with productivity (e.g., Reader et al. 1994, Kadmon 1995).

Absolute competition intensity is problematic for interpreting the strength of competition because it confounds the direct effect of site productivity on a target species' growth with the indirect effects of competition (Goldberg and Barton 1992, Grace 1995, Miller 1996). Yet in the context of restoration, land managers are interested in absolute increases of herbaceous cover, particularly where exposed soil is susceptible to erosion (USDA Forest Service 1998). We observed a predictable increase in absolute magnitude of herbaceous response to shrub removal over a specified range of soil moisture (0–15%). Independent of the exact mechanisms governing the herb response, this pattern was consistent across a range of environments and methodologies and correctly predicted the effect of shrub removal under novel conditions. These results suggest that shrub removal will have the strongest positive effects on herbaceous species at mesic sites or during wet years at xeric sites. Increasing water availability alone to xeric sites dominated by sagebrush is unlikely to increase herbaceous biomass because the suppression by shrubs negates the positive effect of watering.

#### ACKNOWLEDGMENTS

For assistance in the field we are grateful to L. Anneron, T. Baisden, K. Bauer, L. Gallardo, C. Gott, K. Haubensak, D. Gluesenkamp, S. Green, N. Hausmann, K. Miller, A. Darrouzet-Nardi, J. Pangburn, C. Rakunas, S. Reynolds, W. Riley, R. S. Schneider, J. Thorne, and numerous student interns from the Summer Immersion Program in Education and Research, of the Eastern Sierra Institute for Collaborative Education and the U.C. White Mountain Research Station. T. Dudley, D. Sarr, R. Knapp, B. Langford, D. Hooper, D. Hubbs, L. Bryant, K. Nelson, and the D'Antonio lab group provided valuable advice during the study. S. Szweczak, the U.C. White Mountain Research Station, the Sierra Nevada Aquatic Research Lab, and the Inyo National Forest provided essential logistical support. Financial support was provided by a NSF Postdoctoral Fellowship, the Jepson Herbarium Heckard Fund, the Hellman Family Fund, the U.C. Berkeley

Faculty Fund for Research in Biology, and a NSF grant (DEB-9815813) to C. M. D'Antonio and E. L. Berlow.

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