

## SHRUB EXPANSION IN MONTANE MEADOWS: THE INTERACTION OF LOCAL-SCALE DISTURBANCE AND SITE ARIDITY

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**Abstract.** Montane meadows in the Sierra Nevada of California have experienced dramatic expansion of shrubs (*Artemisia rothrockii*) and reduction in herbaceous species cover since the introduction of livestock in the late 1800s. Increases in meadow aridity due to livestock use has been proposed as the primary factor facilitating sagebrush dominance in these areas. However, our data suggest that sagebrush can readily expand into moist meadow areas where the water table is shallow. We explored how the relative importance of local processes influencing seedling establishment vary with changes in site aridity. We quantified patterns of sagebrush abundance in relation to water table depth and surface soil moisture and sagebrush seedling occurrence relative to distance from reproductive sagebrush plants and the presence of gopher disturbance. We tested the independent and interactive effects of vegetation clipping and surface soil disturbances on sagebrush germination, survival, and growth using experiments established in four vegetation types that differed in water table depth, surface soil moisture, and herbaceous species cover. Experiments were conducted over two growing seasons that differed in water availability. Our results suggest that small (<1 m<sup>2</sup>) soil disturbances promote the germination and growth of sagebrush seedlings in intact, ungrazed, moist, herbaceous meadow areas. In the absence of disturbance, dense herbs, whether clipped or not, prevented germination. The effects of disturbance were strongest in sites with moist surface soil that support a dense herbaceous canopy and were less important in sites with lower surface-soil moisture, where seedling establishment rates were low despite abundant exposed soil. The spatial distribution of sagebrush seedlings is consistent with these experimental results. Sagebrush seedling density decreased dramatically with distance from reproductive shrubs, and seedlings were almost always preferentially associated with gopher mounds in moist herbaceous areas. Clipping aboveground biomass of herbs on a relatively small scale (4 m<sup>2</sup>) had no effect on sagebrush germination or early seedling growth; however, the growth and survival of larger transplanted seedlings was enhanced by clipping. We conclude that, while sagebrush expansion is traditionally associated with increased meadow aridity, it exhibits the greatest potential for seedling germination, growth, and survival in mesic, rather than xeric, sites. Realization of this potential is dependent on the confluence of exposed soil, a nearby seed source, and reduction of aboveground herb biomass.

**Key words:** *Artemisia; competition; desertification; disturbance; grazing; meadows; pocket gopher; rangeland; sagebrush; seedling establishment; shrub invasion; Sierra Nevada, California.*

### INTRODUCTION

Throughout semi-arid rangeland woody species have expanded at the expense of herbaceous graminoids and forbs over the past 150 yr (e.g., Humphrey and Mehroff 1958, West 1983, West et al. 1984, Archer 1989, Brown and Archer 1989, Schlesinger et al. 1990, Vavra et al. 1994, Miller and Rose 1995, Van Auken 2000). Several conceptual models suggest that shrub expansion can lead to an “alternate stable state” (West 1983, Archer 1989, Westoby et al. 1989, Schlesinger et al. 1990, Friedel 1991, Laycock 1991, Wilson and Agnew 1992, Vavra et al. 1994). These models are supported by in-

creasing evidence that large-scale conversion of grasslands to shrublands can have important feedbacks on local climatic and soil conditions that promote aridification and further facilitate the expansion of shrubs (West 1983, Archer 1989, Schlesinger et al. 1990, Galardo and Schlesinger 1992, Hobbie 1992, Sturges 1993, Blackburn et al. 1994, Halvorson et al. 1994, Vavra et al. 1994, Wondzell et al. 1996, Connin et al. 1997, Kleb and Wilson 1997, Van Breeman and Frizi 1998). The development of positive feedbacks requires that shrubs become established over a relatively large area. Multiple factors operating on both large and small scales have been proposed to initiate the invasion of woody plants into herb-dominated sites, and the relative importance and interactions among these factors appear to vary considerably over space and time (West 1983, Milchunas and Lauenroth 1993, Vavra et al. 1994, Miller and Halpern 1998). Consequently, it is

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difficult to apply existing general conceptual models to predict site-specific risks of shrub expansion.

Some proposed factors at the scale of a site or geographic region that set the stage for initial shrub expansion include (1) reduced fire frequency due to livestock grazing of herbaceous species (e.g., Milchunas and Lauenroth 1993, Vavra et al. 1994, Van Auken and Bush 1997); (2) decreased soil moisture from widespread soil compaction and disturbance due to trampling by livestock (Schlesinger et al. 1990, Vavra et al. 1994); (3) increased aridity from livestock-induced changes in stream and watershed hydrology (Platts 1979, Magilligan and McDowell 1997, Kirchner et al. 1998); (4) changes in regional climate or the frequency of extreme weather events (Williams et al. 1987, Wiegand and Milton 1996, Millar and Woolfenden 1999); (5) regional changes in the abundance of native herbivores and granivores (Brown and Heske 1990, Weltzin et al. 1997); (6) increases in shrub seed dispersal by livestock (Brown and Archer 1987, Brown and Archer 1999); (7) elevated concentration of atmospheric CO<sub>2</sub> (Polley 1997); and (8) interactions among two or more of these factors (Grover and Musick 1990, Milchunas and Lauenroth 1993, Vavra et al. 1994, Wiegand and Milton 1996, Brown and Archer 1999, Arnalds and Archer 1999, Van Auken 2000). The distribution of shrubs can also be influenced by local, or neighborhood, factors that affect individual germination and establishment. These include local competition with neighboring graminoids and forbs, seed or seedling predation, local seed supply, and small disturbances or gaps created by burrowing mammals (Platt 1975, Fowler 1981, Gross and Werner 1982, Goldberg and Werner 1983, Brown and Archer 1987, Peart 1989, Bossard 1991, D'Antonio 1993, Burke and Grime 1996, Van Auken and Bush 1997). It is the interaction of these local factors and broader site conditions that are critical to determining patterns of shrub expansion and shrub-herb ecotone boundaries (e.g., Brown and Archer 1989, 1999, Van Auken and Bush 1989, Williams and Hobbs 1989, Harrington 1991, Gosz 1993, Bush and Van Auken 1995, O'Connor 1995, Scholes and Archer 1997, Weltzin et al. 1997, De Simone and Zedler 1999). Thus, predicting shrub invasion at a particular site requires an understanding of how the relative importance of local processes that influence seedling establishment vary with broader environmental gradients or anthropogenic changes in site conditions.

We explore factors that initiate the expansion of shrubs (here sagebrush, *Artemisia rothrockii*) into moist montane meadows of the southern Sierra Nevada, California, USA. Shrubs have expanded in these meadows since the introduction of livestock in the late 19th century (Ratcliff 1985, Odion et al. 1988, Dull 1999). Sagebrush expansion is commonly attributed to increased meadow aridity due to historic changes in stream hydrology (e.g., Schoenherr 1995). However, two patterns that we observed pose a challenge to this

view and to predicting areas most at risk of further sagebrush encroachment. First, sagebrush appears to be invading moist regions within individual meadows, including areas that have been protected from livestock grazing for at least 10 yr. Second, the patterns of sagebrush colonization into moist herbaceous areas are spatially variable and not easily explained by patterns of livestock grazing, water table depth, or surface soil characteristics. Using a combination of observational data and field experiments replicated across different soil and water table conditions, we explore how local processes that might influence sagebrush seedling establishment interact with broader patterns of site aridity.

Specifically, we (1) quantified sagebrush abundance in relation to water table depth and surface soil moisture; (2) quantified the occurrence patterns of sagebrush seedlings and gopher disturbances; (3) tested the independent and interactive effects of clipping vegetation and simulating small (<1 m<sup>2</sup>) gopher disturbances on sagebrush germination, survival, and growth; and (4) compared the effects of clipping and disturbance among four vegetation types that differed in surface soil moisture, herbaceous species cover, and water table depth over two growing seasons that differed in water availability.

#### THE STUDY SYSTEM

This study was conducted in two large (up to ~15 km<sup>2</sup>) montane meadows of the Golden Trout Wilderness (GTW) in the southern Sierra Nevada, California, USA (36° N, 118° W) that are part of a complex of the largest meadows of the Sierra Nevada. These are found at elevations between ~2500 m to 3000 m in a series of open basins on the Kern Plateau along the South Fork Kern River and its tributaries. The meadow vegetation is almost entirely native, with the only common exotic, *Taraxicum officinale*, <0.1% cover in all the vegetation types included in the study. The meadows are moist but occur within a semiarid landscape: annual precipitation of the region is ~50 cm (Albert 1982, Odion et al. 1988). Although brief summer thunderstorms occur, snowmelt is the most important source of water for the meadow vegetation. Water availability is an important predictor of plant species composition in this system (Benedict 1983, Sarr 1995). Spring snowpack in the southern Sierra Nevada is highly variable among years. Our study included one wet El Niño year (1998), when the spring snowpack was 200% of the 30-yr mean and the meadows were not snow-free until early June; and one dry year (1999), when the spring snowpack was 50% of the 30-yr mean and snowmelt was one month earlier (California Department of Water Resources, California Data Exchange Center).<sup>4</sup>

The meadows in the entire Sierra Nevada were intensively grazed by domestic livestock in the late 1800s

<sup>4</sup> URL = <http://cdec.water.ca.gov/>

and early 1900s (Ratliff 1985, Menke et al. 1996), and some are still an important source of summer forage for cattle. Before 1850, *A. rothrockii* (hereafter "sagebrush") appears to have been restricted to the dry soils at meadow fringes, between the meadow and the lodgepole pine (*Pinus contorta*) forest on adjacent hillslopes, and it expanded into the meadows after the onset of intensive grazing (Ratliff 1985, Odion et al. 1988, Dull 1999).

Sagebrush expansion has been attributed to increases in meadow aridity due to anthropogenic impacts to streams and stream channels. Grazing and trampling of vegetation along the stream banks can cause erosion, channel incision, and an associated lowering of the water table in the adjacent meadow (Odion et al. 1988, Schoenherr 1995, Knapp and Mathews 1996, Kirchner et al. 1998). Channel incision has left "abandoned" meadow terraces that are sometimes >2 m above the level of the stream (Bryant and Nelson 2000). The U.S. Forest Service installed large fenced cattle enclosures in four meadows in 1983 and 1991 (Knapp et al. 1998). The observational data reported in this study were collected in Mulkey (36°24' N, 118°12' W, 2700 m), and Templeton Meadows (36°20' N, 118°12' W, 2500 m). All of the experimental data were collected in Mulkey Meadow.

Sagebrush is predictably abundant on high meadow terraces along incised stream channels where the water table is consistently >1 m deep (Benedict 1983, Sarr 1995). This distribution pattern is consistent with the notion that sagebrush expansion has occurred in response to increased site aridity. However, low terraces (where the late summer water table is only 50–95 cm deep) contain co-occurring patches of sagebrush with and without an herbaceous understory as well as meadow areas with no sagebrush. Low terrace vegetation patches vary in size from 5 m to ~100 m in diameter. Thus, a lowered water table does not explain all of the patterns of sagebrush encroachment. Hereafter these different vegetation types will be referred to as "Herb" (low terrace herbaceous meadow), "Sage-Herb" (low terrace sagebrush patches with an herbaceous understory), "Low-terrace Sage" (low terrace sagebrush patches with exposed soil and low herbaceous cover), and "High-terrace Sage" (high terrace sagebrush communities with exposed soil and low herbaceous cover). We took advantage of these different vegetation types to examine how the factors that regulate sagebrush establishment vary across sites that differ in soil moisture, water table depth, and herbaceous cover.

#### METHODS

##### *Patterns of sagebrush, water table, soil moisture, and gopher disturbance*

To quantify the general relationship between sagebrush density and water table depth, we used a series of piezometers along transects perpendicular to the wa-

ter table gradient (i.e., perpendicular to the streams that bisect each meadow) that were installed by Sarr (1995). At each piezometer, depth to the water table was recorded and the number of sagebrush individuals was counted within 1 m radius of the piezometer. These observational data were collected at the end of the summer growing season (August) of 1995.

To explore whether the sagebrush-herb mosaic in the low terrace was associated with small scale variation in water table depth and/or surface soil moisture, we installed additional piezometers and collected soil samples from the four vegetation types (Herb, Sage-Herb, Low-terrace Sage, and High-terrace Sage) which co-occurred within each of five stream reaches (blocks) within the Mulkey Meadow cattle enclosure. The entire meadow is ~7 km long and 3 km<sup>2</sup> in aerial extent, and the cattle enclosure extends ~2 km along the stream, and ~50–100 m to either side. The blocks within the enclosure were separated by at least 100 m.

Piezometers were constructed with 2 m long PVC pipe perforated with holes that were covered with fiberglass mesh to allow water to enter while excluding soil. Piezometers were placed in holes created with a soil auger in late summer when the water table is generally at its lowest point for the year. Surface soil moisture was monitored using two methods. In the summer of 1997, 10 cm diameter × 15 cm deep soil samples were collected monthly from each of the four vegetation types at a location near each piezometer in that area. Soil samples were immediately placed in airtight plastic bags and stored in the shade before transporting to the lab for measurements of gravimetric soil moisture. In the patches with sagebrush, samples were collected both under shrub canopies and in the intershrub spaces. In 1998 and 1999, soil moisture in the top 30 cm was measured monthly with Time Domain Reflectometry (TDR) probes at each vegetation type within each site. TDR values of volumetric moisture were converted to gravimetric moisture using bulk density measurements from 20 cm deep cores sampled concurrently with the July 1998 TDR readings. We compared gravimetric moisture from these samples to the converted TDR measurements. Gravimetric TDR estimates showed close to a 1:1 correspondence with the gravimetric moisture measurements from soil cores ( $R^2 = 0.91$ , slope = 1.1,  $P < 0.0001$ ).

We quantified sagebrush seedling occurrence relative to vegetation type and gopher disturbance along permanently marked 10-m transects in each vegetation type within each block. Because seedling occurrence appeared to be more spatially variable in Herb and Sage-Herb vegetation than in either the Low- or High-terrace Sage, we sampled three transects in the former two vegetation types and one transect for each of the Low- and High-terrace Sage at each block. The three transects within each block for Herb and Sage-Herb were averaged prior to analysis (i.e., replication was five blocks for all vegetation types). For each transect,

the frequency of occurrence of gopher disturbances and sagebrush seedlings was quantified using twenty  $0.5 \times 0.5$  m quadrats positioned contiguously along the transect. Sagebrush individuals were classified as seedlings if they were  $<10$  cm tall and their maximum canopy diameter was  $<10$  cm. Gopher disturbance and seedlings were monitored in July 1998 and June 1999. Very few seedlings recruited in the summer of 1999, so only the 1998 data are presented.

In the summer of 2000, we quantified sagebrush seedling occurrence relative to distance from a seed source by counting seedlings in four distance categories (0–0.5 m, 0.5–1 m, 1–1.5 m, 1.5–5 m) within a wedge radiating out from isolated clumps of one to four reproductively mature sagebrush individuals. No other reproductive sagebrush individuals were located within 5 m of the edge of the wedge. All sampling was done outside the livestock enclosure. Within the first two distance categories seedlings were counted within the entire  $360^\circ$  around the shrub. For the further distance categories, seedlings within a randomly oriented  $90^\circ$  wedge with a 5 m radius were counted. For each seedling we recorded the substrate type on which it occurred (i.e., intact meadow or disturbed soil). For each distance category we also visually estimated the percentage of the area sampled that was disturbed soil. Because total seedling abundance varied among clumps the density of seedlings within each distance category was standardized by total seedling density for each group of shrubs.

#### *Competition–disturbance experiment*

To quantify the effects of aboveground competition and soil disturbance on the establishment of sagebrush we manipulated all combinations of aboveground vegetation (clipped or unclipped) and soil disturbance (similar in size to natural gopher mounds, or  $30 \times 30$  cm disturbed or undisturbed). To explore how the effects of these local factors vary with site aridity (water table depth and surface soil moisture), we replicated these treatments in each of the four vegetation types (Herb, Sage–Herb, Low- and High-terrace Sage) at each of the five blocks discussed above within the cattle enclosure of Mulkey Meadow. The experiment was confined to the livestock enclosure in order to examine factors that promote continued sagebrush establishment after livestock removal.

The main experimental plots were  $4 \text{ m}^2$  and included the following treatments: sagebrush clipped or unmanipulated (hereafter “–Sage” and “+Sage”), and aboveground herbaceous biomass clipped, approximately every 2–3 wk over the growing season, or unmanipulated (hereafter “–Herbs” and “+Herbs”). It was only possible to have orthogonal manipulations of the sage and herb clipping treatments in Sage–Herb patches. Within each main plot, four  $30 \times 30$  cm subplots received one of two treatments: disturbed (existing vegetation and roots removed and the top 15 cm

of soil manually turned over), or undisturbed (unmanipulated). All the treatments were replicated in each of the four vegetation types at each of the five blocks.

In one pair of disturbed and undisturbed subplots within each  $4\text{-m}^2$  plot, we planted 500 sagebrush seeds. In the other pair we transplanted sagebrush seedlings obtained from a common area within each block. Sagebrush seeds were collected in October 1997 and stored in paper bags in a cold room at  $4^\circ\text{C}$  over the winter. Seeds were planted in early June 1998, soon after snowmelt. Sagebrush seedlings were transplanted in mid-June 1997, and had a mean initial maximum height of 2.5 cm and mean initial maximum canopy diameter of 1 cm. Transplants were watered regularly the first week after planting. Transplants that died during the first 6 wk were assumed to have died because of transplanting stress and were replaced with new ones.

Seedling and transplant growth was monitored by measuring maximum height and two canopy dimensions (maximum diameter and the diameter perpendicular to the maximum) at monthly intervals during each growing season. Seedling size ( $\text{cm}^3$ ) was calculated as the product of seedling maximum height and the area of the canopy (estimated as  $\pi r^2$ , assuming the canopy was circular). Seedling relative growth over a given time interval was measured as  $\log(\text{size}_{\text{time}2}/\text{size}_{\text{time}1})$ .

Because space constraints within the livestock enclosure limited the number of experimental replicates, we attempted to minimize mortality due to gopher activity by excluding gophers from all the experimental plots in the low terrace vegetation types. Gophers were excluded by burying 0.6-cm aviary netting 40 cm deep, leaving a 5-cm extension above ground. Observations suggest that the aviary netting was successful at excluding gophers from the experimental plots. Thus results of these experiments should be interpreted in the context of both gopher and livestock enclosure.

General patterns of plant community structure within the four vegetation types of the experiment were quantified within the unmanipulated  $4\text{-m}^2$  plots in July 1999, the period of peak flowering and biomass of the growing season. Canopy cover (%) of all plant species was estimated in two  $0.5 \times 0.5$  m point-intercept quadrats in the center of each  $4\text{-m}^2$  plot. Cover for each species was estimated from the proportion of intersections with the grid of 162 points for each  $4\text{-m}^2$  plot (two quadrats with 81 points each).

#### *Data analysis for the competition–disturbance experiment*

Germination rate was measured as the number of seeds (of 500 planted) that germinated and survived to the end of the first growing season (September 1998). The growth of seedlings (both those germinated from seed and those transplanted) was evaluated over two complete growing seasons. Although seedlings were transplanted in mid-June 1997, we used August 1997 as the starting date for measuring growth in order to

TABLE 1. Summary of the factors and levels used in separate factorial ANOVAs (analogous to a priori contrasts) used to quantify interactive effects using orthogonal components of the competition–disturbance experiment.

ANOVA	Factors				Tests
	Vegetation type	Sagebrush	Herbs	Disturbance	
1) Sagebrush × Herbs	Low-terrace Sage–Herb	+, –	+, –	D, U	Does the effect of herbs vary with the presence of sagebrush?
2) Herbs × Vegetation type	Low-terrace Herb	N/A	+, –	D, U	Does the effect of herbs vary between vegetation types that have an herbaceous understory?
	Low-terrace Sage–Herb	+/- pooled	+, –	D, U	
3) Sagebrush × Vegetation type	Low-terrace Sage–Herb	+, –	+/- pooled	D, U	Does the effect of clipping sagebrush vary among the three sagebrush vegetation types?
	Low-terrace Sage	+, –	N/A	D, U	
	High-terrace Sage	+, –	N/A	D, U	
4) Vegetation type × Disturbance	Low-terrace Herb	N/A	+/- pooled	D, U	Are there overall differences among vegetation types?
	Low-terrace Sage–Herb	+/- pooled	+/- pooled	D, U	Does the effect of soil disturbance vary with vegetation type?
	Low-terrace Sage	+/- pooled	N/A	D, U	
	High-terrace Sage	+/- pooled	N/A	D, U	

Notes: Sagebrush is coded as clipped (–) or present (+); herbs are coded as clipped (–) or present (+); disturbance is coded as soil disturbed (D) or undisturbed (U). For all response variables analyzed, the Sage × Herb interaction was not significant (see Tables 5–7). Thus, to increase our power to evaluate Herb (or Sage) effects across the different vegetation types, +/- Sage (or Herb) treatments were pooled in these subsequent ANOVAs (Underwood 1997). “N/A” means not applicable in that sagebrush (or herbs) do not grow in that habitat type.

allow time to overcome transplanting shock. Since August is near the end of the active growing season, transplant growth at the end of 1997 was negligible. Treatment effects on seedling growth were evaluated with separate ANOVAs for the 1998 and 1999 summer growing seasons because mortality of individuals over the 1998–1999 winter and during the drought summer of 1999 meant that repeated-measures ANOVA would ignore information about those replicates in 1998. Since seedling growth in 1999 was very low in all treatments due to a drought, we wanted to maximize the information about treatment effects on growth in 1998. The two summer growing seasons were separated by almost 9 mo of dormancy.

Since not all treatment combinations were present in each vegetation type, we used separate factorial ANOVAs on orthogonal subsets of the data to test for interaction terms that were, a priori, of particular interest. While this entails using some of the data more than once, it is analogous to using a priori contrasts to test for differences between individual treatments and to test for nonadditivity among treatments (Table 1). The disturbance treatments were nested within sage and/or herb treatments, and the latter were nested within vegetation type (Herb, Sage–Herb, Low-terrace Sage, High-terrace Sage) in all the ANOVAs described. Specific error terms used to test main plot vs. subplot effects are specified in the resulting ANOVA tables. For both the germination and growth data, the variance tended to increase with the mean, thus data were log-transformed (see table legends).

## RESULTS

### *Patterns of community structure, water table, and soil moisture*

Sagebrush density was greater on high terraces where the late season water table is deeper than 1 m (Fig. 1a), and low on streamside terraces where the late season water table is <50 cm and the soil is often saturated in the spring. However, sagebrush density was highly variable on low terraces where the late summer water table is 50–95 cm deep (Fig. 1a).

Herb meadow patches had dense cover of perennial grasses, sedges, rushes, and forbs, with very little bare soil (Fig. 1b). In contrast, both Low- and High-terrace Sage had >50% bare soil and had similar sagebrush and herb cover despite differences in water table depth (see water table results in next paragraph). Sage–Herb patches had similar cover of sagebrush as the Low- and High-terrace Sage, but significantly less cover of bare soil. (Fig. 1b). However, total herbaceous cover in the Sage–Herb patches was more sparse than that in the Herb vegetation type (Fig. 1b).

The water table depth in the low terrace was shallowest in the spring and declined throughout the summer in 1997 and 1998 (Fig. 2a; repeated-measures ANOVA within-subjects effect of Time, Wilk's  $\lambda = 0.14$ ,  $P = 0.0003$  for 1997 and Wilk's  $\lambda = 0.06$ ,  $P = 0.0003$  for 1998). In 1999, however, the water table did not drop significantly over the summer because it started off relatively deep due to low snowpack the previous winter (rm-ANOVA within-subjects effect of Time,

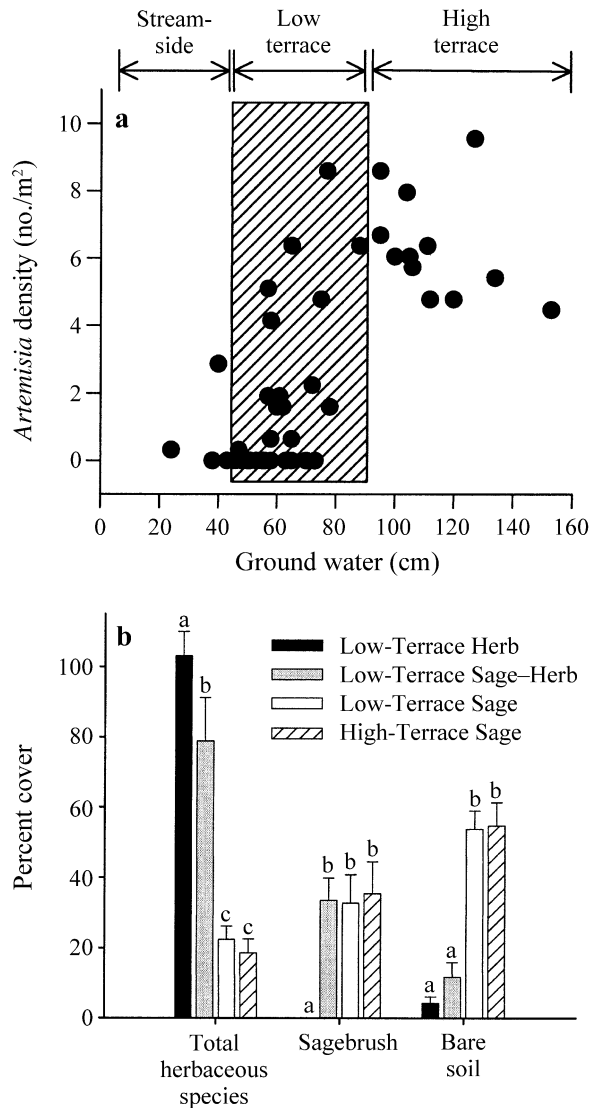


FIG. 1. (a) The relationship between water table depth and sagebrush density sampled within a 1-m radius of each piezometer in August 1995. The hatched area indicates samples from low meadow terraces, where the Herb, Sage-Herb, and Low-terrace Sage vegetation types co-occur. (b) Mean ( $\pm 1$  SE) percent cover of sagebrush canopy, herbaceous species (grasses, sedges, rushes, and forbs), and exposed soil in July 1999, the time of peak summer flowering and biomass, in the unmanipulated plots of the competition-disturbance experiment for each of the four vegetation types. Since data are canopy cover, the sum of all species can be greater than 100%. For each group of bars, different letters indicate that the cover differed significantly between vegetation types ( $\alpha < 0.05$ ,  $F$ -protected least-squares means). To meet the assumptions of ANOVA, cover data were arcsine-square-root transformed prior to analysis.

Wilk's  $\lambda = 0.43$ ,  $P = 0.29$ ; Fig. 2a). Striking differences between low-terrace vegetation types were not associated with any local discontinuity in the water table, which was almost identical among low-terrace vegetation types at any point in time (Fig. 2a, rm-ANOVA  $F$ -

protected least-squares means,  $P > 0.30$  for all dates). However, moisture in the top 30 cm of soil differed significantly among these low-terrace vegetation types (Fig. 2b, rm-ANOVA  $F$ -protected least-squares means, Herb>Sage-Herb>Sage;  $P < 0.01$  for all dates except July 1997). While Low-terrace Sage had a consistently shallower water table than High-terrace Sage (Fig. 2a, rm-ANOVA  $F$ -protected least-squares means,  $P < 0.01$  for all dates), the surface soil was similarly dry in each (Fig. 2, rm-ANOVA  $F$ -protected least-squares means,  $P > 0.60$  for all dates). Mean surface soil moisture in Low-terrace Sage patches is significantly lower than in adjacent Herb areas due to coarser gravelly soil with lower water holding capacity in the latter (C. M. D'Antonio and E. L. Berlow, unpublished data). Note that the small peak in soil moisture in July 1997, due to midsummer thunderstorms (Fig. 2b), did not recharge the groundwater (Fig. 2a).

Both gopher disturbance and sagebrush seedlings were most abundant in Sage-Herb patches (Fig. 3a). While persistent gopher mounds were less abundant in the Low- and High-terrace Sage, observations of go-

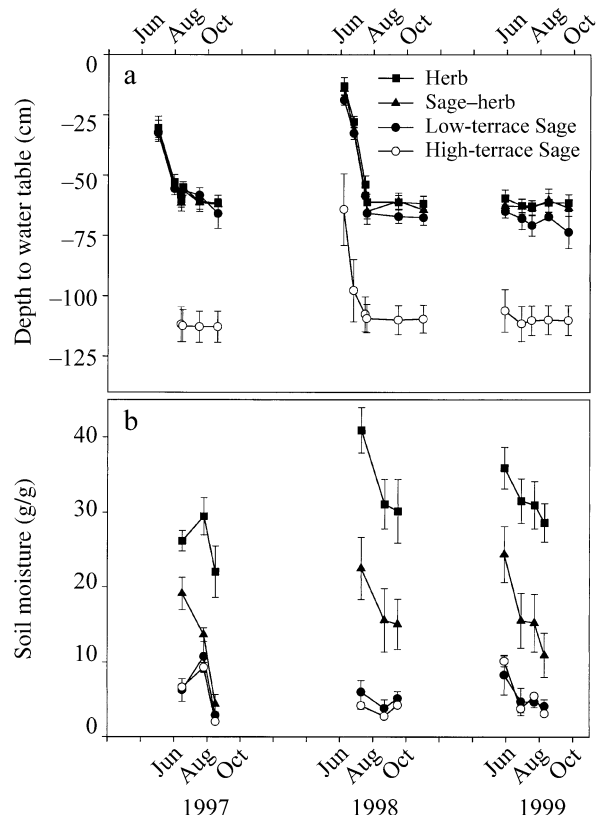


FIG. 2. Mean ( $\pm 1$  SE;  $n = 5$  blocks) (a) water table depth and (b) gravimetric surface soil moisture over the time course of three growing seasons for each of the four vegetation types in the competition-disturbance experiment. Note that there are no data for High-terrace Sage in spring of 1997. The first sample date for each year varies due to the timing of snowmelt.

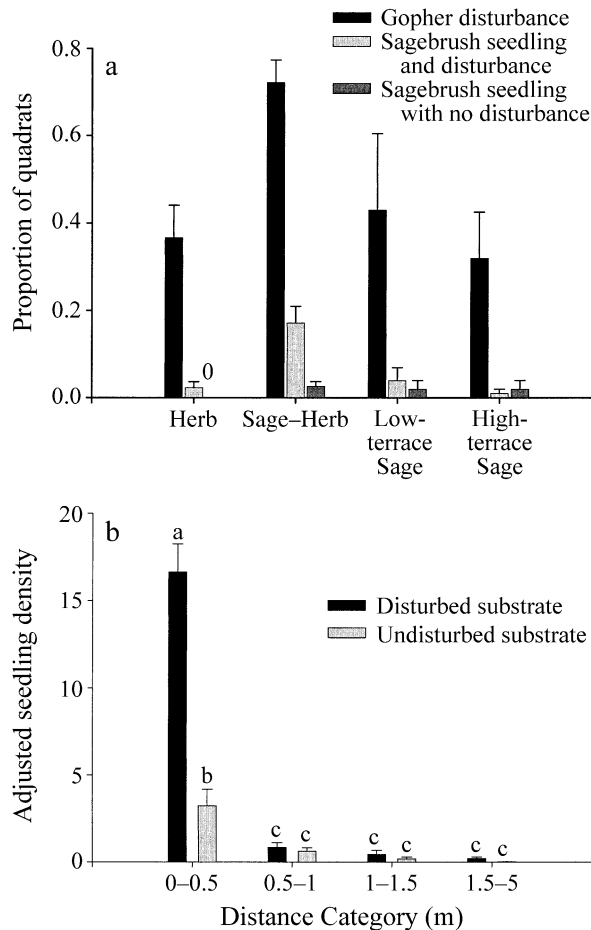


FIG. 3. (a) Mean ( $\pm$  1 SE) proportion of 0.025-m<sup>2</sup> quadrats along 10-m belt transects that contained sagebrush seedlings (individuals <10 cm in height or in maximum canopy diameter) and gopher disturbances for each vegetation type in June 1998;  $n = 5$  sites for each vegetation type. (b) Mean ( $\pm$  1 SE) proportion of sagebrush seedlings at different distances from reproductive shrubs. Seedling density in each distance category was adjusted by the total seedling density around each shrub because of high variation in total seedling abundance among shrubs. Different letters indicate that the adjusted density differed significantly between distance and substrate combinations ( $F$ -protected least-squares means,  $P < 0.05$ ).

pher activity suggest that mounds may disappear faster in these vegetation types due to looser and more coarse soil. In Herb areas, where bare space in the absence of disturbance is rare, sagebrush seedlings occurred exclusively on gopher disturbances (Fig. 3a,  $\chi^2 = 12.38$ ,  $P < 0.001$ ). In mesic Sage-Herb, sagebrush seedlings were more frequently associated with gopher disturbances than expected based on the relative abundance of gopher disturbances in this vegetation type (Fig. 3a,  $\chi^2 = 6.73$ ,  $P < 0.01$ ). In Low- and High-terrace Sage, where bare space is abundant, sagebrush seedlings exhibited no preferential association with disturbed soil (Fig. 3a,  $\chi^2 = 1.71$ ,  $P > 0.10$ ; and  $\chi^2 = 1.25$ ,  $P < 0.25$ , respectively).

Seedling density decreased significantly beyond 0.5 m from a seed source (Fig. 3b). Within the 0–0.5 m distance category, seedlings were preferentially associated with disturbed substrate (Fig. 3b). In order to determine whether the spatial distribution of seedlings was simply mapping onto the distribution of disturbed substrate, we included percent disturbance as a covariate. Neither percent disturbance nor its interaction with distance were significant ( $P > 0.15$ ), and their inclusion in the model did not change the significance of the other factors.

#### Competition–disturbance experiment

*Seedling germination, establishment, growth, and survival.*—There was no significant effect of either clipping sagebrush adults or clipping herbs on the number of sagebrush seedlings that emerged and survived to the end of the first summer (Fig. 4a; Table 2, ANOVAs 1–3). However, soil disturbance significantly increased seedling establishment in both Herb and Sage-Herb vegetation types (Fig. 4a; Table 2, ANOVAs 1 and 2). Overall, seedling establishment was highest in disturbances within Herb areas (Fig. 4a; Table 2, ANOVA 4, Disturbance  $\times$  Vegetation type,  $P < 0.0001$ ). No seedlings emerged in undisturbed plots in the Herb vegetation type. There was very low seedling establishment in both the Low- or High-terrace Sage independent of soil disturbance (Fig. 4a; Table 2, ANOVA 3, Disturbance  $\times$  Vegetation type,  $P < 0.0002$ ).

Of the plots where germination occurred, there were no significant effects of clipping herbs or removing sagebrush adults on seedling growth in the first year (Fig. 4b; Table 2, ANOVAs 1–4,  $P > 0.1$  in all cases). There were also no differences in seedling size among vegetation types (Fig. 4b). It was not possible to evaluate effects of disturbance on seedling growth rates because of low germination in the undisturbed plots (Fig. 4a). Of the seedlings that survived the first year, survivorship during the dry 1999 growing season was relatively high in most treatments ( $74 \pm 12\%$ , mean  $\pm$  1 SE). However, growth in 1999 was minimal (or negative due to dieback), with no discernable patterns among treatments (Fig. 4b; Table 2, ANOVAs 1–4,  $P > 0.1$  in all cases).

Growth of transplanted seedlings was significantly enhanced by disturbance and by clipping either herbs or adult sagebrush (Fig. 5a; Table 3, ANOVAs 1–3, Wet Year). Disturbance had a stronger positive effect on transplant growth in Sage-Herb than in either of the Sage areas without an herbaceous understory (Fig. 5a; Table 3, ANOVA 3, Disturbance  $\times$  Vegetation type). Of the transplants that survived the first year,  $97 \pm 2\%$  survived the subsequent drought year. The relative growth of these individuals, however, was an order of magnitude lower than during the previous wet year (Fig. 5). Transplant growth the second year was similar among all treatments, with the exception of a positive

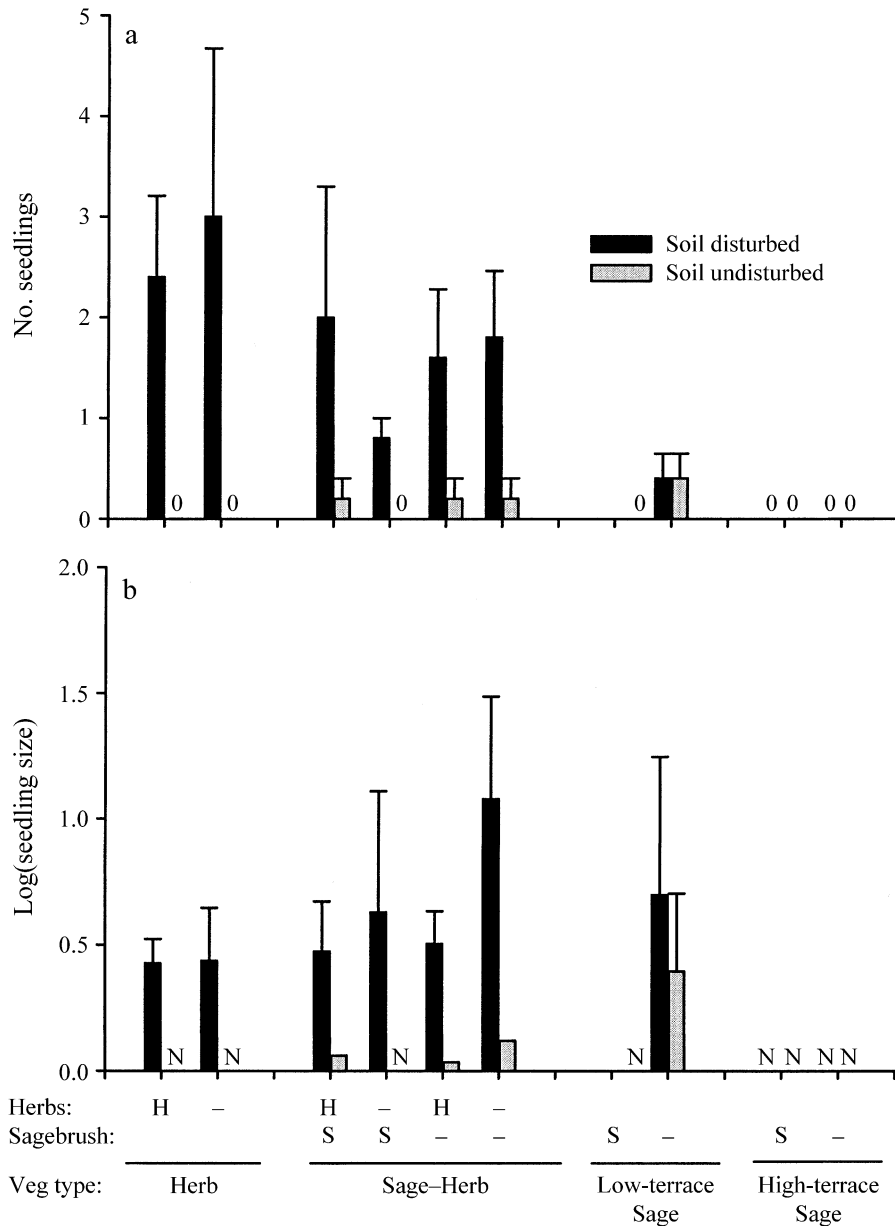


FIG. 4. (a) Mean (+ 1 SE) number of sagebrush seeds (out of 500 planted) that germinated and survived until the end of the first growing season (September 1998) for each treatment in the competition-disturbance experiment. Treatments where no seeds germinated are indicated by "0." (b) Mean (+ 1 SE) size of seedlings at the end of the first growing season (September 1998) for each treatment in the competition-disturbance experiment. Treatments within the same vegetation type are indicated with the horizontal lines below the x-axis. Codes for treatments are as follows: "S" for sagebrush present, "-" for sagebrush clipped, "H" for herbs intact, "-" for herbs clipped. No "S" (or "H") indicates that there was no sagebrush (or herb) treatment for that vegetation type. "N" indicates that none germinated or survived in that treatment. See *Methods: Competition-disturbance experiment* for details about how seedling size was measured.

effect of removing sagebrush in Low- and High-terrace Sage. (Fig. 5b; Table 3, Dry Year).

Four years after transplanting, no seedlings survived in any of the Herb plots that were undisturbed and unclipped (Table 4). By contrast, 100% survived in Herb plots that were both disturbed and clipped, with 40% of those reaching reproductive maturity (Table 4).

In Sage-Herb areas, 4-yr transplant survival was also zero in all undisturbed plots where herbs were not clipped. Averaged over disturbed and sagebrush removal treatments in the Sage-Herb vegetation type,  $60 \pm 8\%$  of the seedlings survived in plots with clipped herbs, while only  $30 \pm 19\%$  survived in unclipped plots. In the Low- and High-terrace Sage, transplant

TABLE 2. Summary of factorial ANOVAs used to quantify interactive effects of vegetation type, sagebrush, herbs, and disturbance on sagebrush seedling germination in the competition–disturbance experiment.

Source	df	<i>F</i>	<i>P</i>
1) Sagebrush × Herbs interaction			
Block	4	3.46	<b>0.03</b>
Sagebrush	1	0.99	0.34
Herbs	1	0.35	0.56
Sagebrush × Herbs	1	0.99	0.34
Error 1 (Block × Sagebrush × Herbs)	12		
Disturbance	1	17.4	<b>0.0001</b>
Error 2	17		
2) Herbs × Vegetation type interaction			
Block	4	1.56	0.21
Vegetation type	1	0.15	0.72
Error 1 (Block × Vegetation type)	4		
Herbs	1	0.10	0.76
Herbs × Vegetation type	1	0.01	0.92
Error 2 (Block × Herb × Vegetation type)	8		
Disturbance	1	41.51	<b>0.0001</b>
Disturbance × Vegetation type	1	2.15	0.15
Error 3	36		
3) Sage × Vegetation type interaction			
Block	4	2.43	0.06
Vegetation type	2	7.39	<b>0.015</b>
Error 1 (Block × Vegetation type)	8		
Sagebrush	1	2.72	0.12
Sagebrush × Vegetation type	2	0.72	0.51
Error 2 (Block × Sage × Vegetation type)	12		
Disturbance	1	8.50	<b>0.006</b>
Disturbance × Vegetation type	2	10.41	<b>0.0002</b>
Error 3	45		
4) Vegetation type × Disturbance interaction			
Block	4	0.94	0.45
Vegetation type	3	3.92	<b>0.04</b>
Error 1 (Block × Vegetation type)	12		
Disturbance	1	26.95	<b>0.0001</b>
Disturbance × Vegetation type	3	9.15	<b>0.0001</b>
Error 2	74		

Notes: In all cases, data were log-transformed number of seedlings (planted in June 1998) that germinated and survived to the end of the first growing season (September 1998). All plots received 500 seeds. Because disturbance treatments were nested within sage/herb treatments, and the latter were nested within vegetation types, different error terms were used to test effects at different scales. Error terms are listed directly below the effects being tested. Boldface type indicates  $P < 0.05$ .

survival averaged  $35 \pm 10\%$  and  $30 \pm 13\%$  respectively, with no effects of disturbance or sagebrush removal (Table 4).

In sum, clipping herbs had little effect on germination and first-year seedling growth, but facilitated the growth and longer term (4 yr) survival of larger (2–3 cm initial height) transplants. Soil disturbance also consistently facilitated transplant growth and survival, with the strongest effect in the moist habitats with dense herbs. Soil disturbance was critical for germination in habitats with dense herbs, but had no effect in the more arid Sage habitats, where exposed soil was abundant but germination rates were consistently low.

#### DISCUSSION

While shrub expansion in montane meadows is commonly attributed to an increase in meadow aridity (e.g., Schoenherr 1995), we found that sagebrush exhibited

the highest rates of germination and seedling growth within moist meadow microhabitats if small-scale (<1 m<sup>2</sup>) soil disturbances were present. In the absence of disturbance, intact moist herbaceous meadow effectively prevented sagebrush germination and strongly inhibited transplanted seedling growth and survival. These results are consistent with studies demonstrating that small soil disturbances and canopy gaps in grasslands can be critical to the establishment of invading species (Platts 1979, Gross and Werner 1982, 1983, Brown and Archer 1987, Peart 1989, Bossard 1991, D'Antonio 1993, Burke and Grime 1996, D'Antonio et al. 1999, De Simone and Zedler 1999). Thus, while shrub encroachment of meadows is commonly assumed to be in response to increased site aridity, local disturbances can strongly promote invasion of microhabitats at the moist end of the gradient.

Our results underscore the fact that replicating ex-

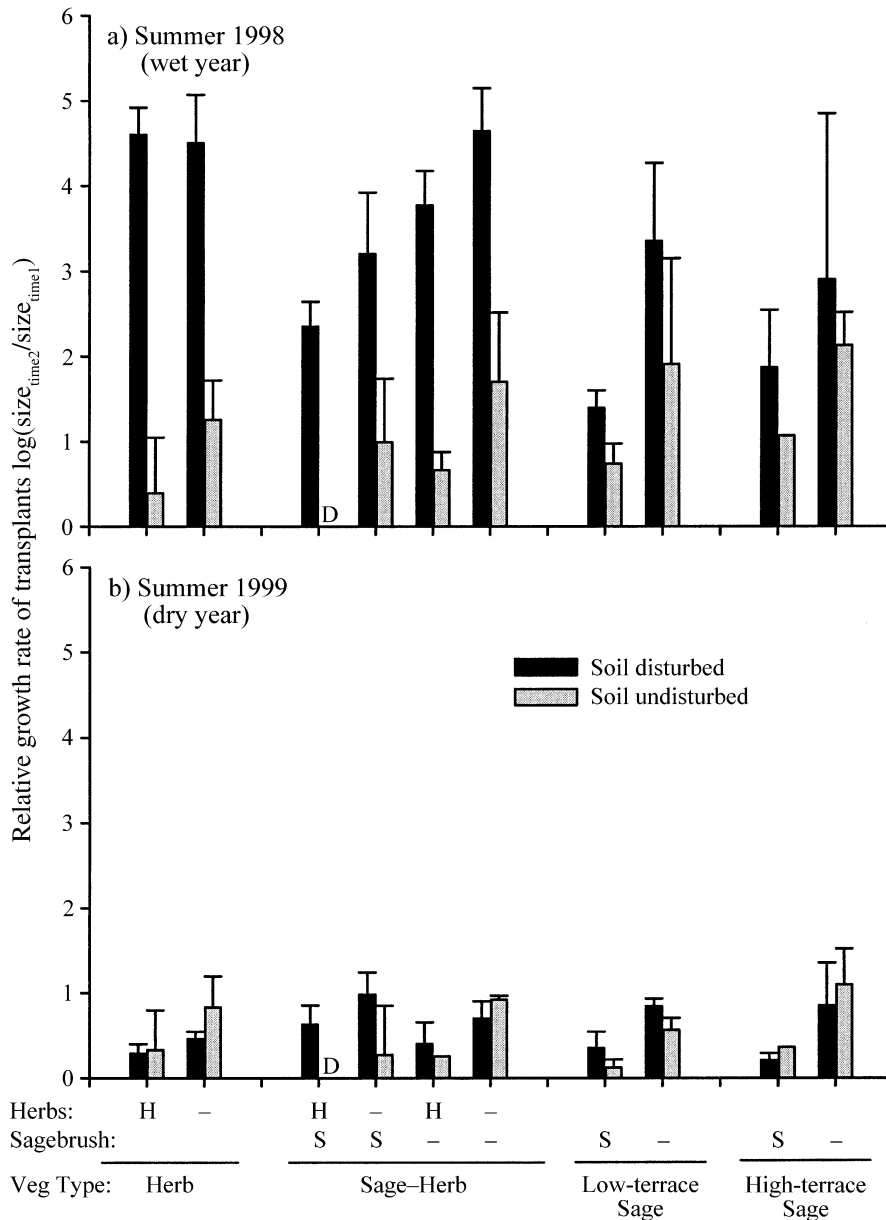


FIG. 5. (a) Mean (+ 1 SE) growth of transplanted seedlings that survived through the first (wet) summer (1998) for each treatment in the competition–disturbance experiment. Growth was measured as  $\log(\text{size}_{\text{time}2}/\text{size}_{\text{time}1})$  where  $\text{time}2 = \text{September } 1998$  and  $\text{time}1 = \text{time of initial transplant}$ . See *Methods: Competition–disturbance experiment* for details about how size was measured. (b) Mean (+ 1 SE) growth of the same transplanted seedlings during the second (drought) summer (May–August 1999). “D” indicates that all individuals of that treatment were dead by the end of that summer. See legend of Fig. 4 for x-axis codes.

perimental manipulations across environmental gradients or habitat types and over time can be a powerful efficient way to quantify how local, or neighborhood, processes vary with site conditions (e.g., D’Antonio 1993, Menge et al. 1994, Berlow 1997, 1999). While our field experiment was limited to a cattle enclosure within one large meadow, the treatment blocks were separated by at least 100 m across almost 2 km of stream, and the treatments within each block were rep-

licated across contrasting vegetation types, surface soil conditions, and water table depths. This “comparative experimental” approach (sensu Menge 1991) can elucidate “contingent generalizations” about how the relative importance of different processes that promote species invasions is likely to vary across habitats or over time (e.g., Bossard 1991, D’Antonio 1993). In montane meadows of the eastern Sierra Nevada, disturbance had the strongest effect in moist Herb and

TABLE 3. Summary of separate ANOVAs used to quantify interactive effects of vegetation type, sagebrush, herbs, and disturbance on transplanted sagebrush seedling growth.

Source	Wet year (1998)			Dry year (1999)		
	df	F	P	df	F	P
1) Sagebrush × Herbs						
Block	4	5.46	<b>0.03</b>	4	1.44	0.34
Sagebrush	1	6.46	<b>0.03</b>	1	0.06	0.81
Herbs	1	5.20	<b>0.04</b>	1	1.69	0.22
Sagebrush × Herbs	1	0.17	0.69	1	0.25	0.63
Error 1 (Block × Sage × Herbs)	10			10		
Disturbance	1	46.30	<b>0.001</b>	1	2.25	0.19
Sagebrush × Disturbance	1	0.02	0.90	1	0.50	0.51
Herbs × Disturbance	1	2.44	0.16	1	0.61	0.47
Error 2	8			5		
2) Herbs × Vegetation type						
Block	4	2.76	<b>0.05</b>	4	1.78	0.17
Vegetation type	1	1.20	0.33	1	0.12	0.75
Error 1 (Block × Vegetation type)	4			4		
Herbs	1	9.14	<b>0.02</b>	1	0.67	0.45
Herbs × Vegetation type	1	0.07	0.80	1	0.00	0.98
Error 2 (Block × Herbs × Vegetation type)	5			5		
Disturbance	1	66.39	<b>0.0001</b>	1	0.00	0.95
Disturbance × Vegetation type	1	0.82	0.38	1	2.00	0.17
Error 3	23			19		
3) Sagebrush × Vegetation type						
Block	4	3.28	<b>0.03</b>	4	0.28	0.88
Vegetation type	2	0.46	0.65	2	0.11	0.90
Error 1 (Block × Vegetation type)	7			7		
Sagebrush	1	5.22	<b>0.05</b>	1	6.50	<b>0.03</b>
Sagebrush × Vegetation type	2	0.40	0.68	2	2.35	0.16
Error 2 (Block × Sage × Vegetation type)	8			8		
Disturbance	1	12.58	<b>0.001</b>	1	0.05	0.83
Disturbance × Vegetation type	2	3.96	<b>0.03</b>	2	1.02	0.34
Error 3	23			20		
4) Vegetation type × Disturbance						
Block	4	2.59	<b>0.05</b>	4	0.74	0.57
Vegetation type	3	1.42	0.29	3	0.30	0.82
Error 1 (Block × Vegetation type)	11			11		
Disturbance	1	30.62	<b>0.0001</b>	1	0.00	0.95
Disturbance × Vegetation type	3	2.04	0.12	3	1.23	0.31
Error 2	43			37		

Notes: Growth over each growing season (May to August/September) was measured as  $\log(\text{size}_{\text{time1}}/\text{size}_{\text{time2}})$ . In the first (wet) summer final size was measured in September 1998. In the subsequent (dry) summer, final size was measured in August 1999. Error terms are listed below the effects being tested. Boldface type indicates  $P < 0.05$ .

Sage-Herb vegetation types, and was unimportant in the more xeric Low- and High-terrace Sage habitat, where bare soil was abundant but germination rates were consistently low. This result is consistent with the observation that natural sagebrush seedlings were preferentially associated with gopher disturbances in Herb and Sage-Herb vegetation types, but not in either the Low- or High-terrace Sage areas.

Dense herbs, whether clipped or not, prevented sagebrush germination. Of the seeds that germinated in disturbed plots, germinants grew equally well during the first growing season regardless of whether the surrounding herbs were clipped. However, the growth and survival of larger transplanted seedlings (2–3 cm initial height) was enhanced by clipping herbs. These results are consistent with other studies that suggest the strength of aboveground competition from herbs may

vary between the different early life stages of shrub seedlings (Bush and Van Auken 1995, Van Auken and Bush 1997, Brown and Archer 1999). Thus, sagebrush seedling germination rates were highest when exposed soil co-occurred with moist conditions, and longer term seedling growth and survival were enhanced by both disturbance and clipping aboveground herbaceous vegetation.

Our results are consistent with a general conceptual model of community organization that suggests local biotic interactions should increase in importance with decreasing environmental stress (Menge and Sutherland 1976, 1987). D'Antonio (1993) also found that local disturbances were more important in facilitating invasion by a long-lived perennial species in mesic sites that supported dense herbaceous vegetation than in xeric sites with more sparse vegetation. These pat-

TABLE 4. Proportion of sagebrush seedlings transplanted July/August 1997 that survived until July 2001 for each vegetation type and treatment in the competition–disturbance experiment.

Vegetation Type	Sagebrush	Herbs	Disturbance	Survival (%)	Reproductive (%)
Low-terrace Herb	N/A	–H	disturbed	100	40
	N/A	–H	undisturbed	40	0
	N/A	+H	disturbed	40	0
	N/A	+H	undisturbed	0	0
Low-terrace Sage–Herb	–S	–H	disturbed	80	0
	–S	–H	undisturbed	40	0
	–S	+H	disturbed	80	0
	–S	+H	undisturbed	0	0
	+S	–H	disturbed	60	0
	+S	–H	undisturbed	60	0
	+S	+H	disturbed	40	0
	+S	+H	undisturbed	0	0
Low-terrace Sage	–S	N/A	disturbed	40	0
	–S	N/A	undisturbed	60	0
	+S	N/A	disturbed	20	0
	+S	N/A	undisturbed	20	0
High-terrace Sage	–S	N/A	disturbed	20	0
	–S	N/A	undisturbed	60	0
	+S	N/A	disturbed	40	0
	+S	N/A	undisturbed	0	0

Note: Sagebrush is coded as clipped (–S) or present (+S); herbs are coded as clipped (–H) or present (+H). “N/A” means not applicable in that sagebrush (or herbs) do not grow in that habitat type.

terns suggest that, more generally, in arid and semi-arid grasslands, local biotic interactions may be more important in regulating shrub establishment at sites that are mesic enough to support continuous herbaceous cover.

However, at the more mesic end of the grassland/savanna gradient, where soils are relatively well drained, succession may lead to dominance by woody species in the absence of disturbances such as fire or seed/seedling predation (e.g., McBride and Heady 1968, Bragg and Hulbert 1976, Weltzin et al. 1997, Brown and Archer 1999, Ludwig et al. 1999). In several temperate and subtropical savannas, experimental field studies of shrub seedling establishment have found that seedlings are able to germinate and grow even in the presence of dense herbaceous vegetation (e.g., Meyer and Bovey 1982, Brown and Archer 1989, 1999, Williams and Hobbs 1989, O'Connor 1995, Scholes and Archer 1997, Weltzin et al. 1997). In these ecosystems, it appears that, in the absence of disturbances such as fire or seed/seedling predation, succession leads to dominance by woody plants (e.g., McBride and Heady 1968, Bragg and Hulbert 1976, Weltzin et al. 1997, Brown and Archer 1999). Thus, whether disturbances promote, prevent, or have no effect on the conversion of grassland to shrubland may vary predictably, but nonlinearly, across a gradient of site moisture availability. In arid sites characterized by discontinuous herb cover and exposed soil, local disturbances are unlikely to play a role in shrub establishment. At sites of intermediate soil moisture that support dense continuous cover of herbs, disturbance and other factors that reduce competition from herbs may be critical for shrub

establishment. At wetter sites with well-drained soil, disturbances such as fire and seedling predation may instead be the key source of woody plant mortality that maintains high herb cover.

#### *Historic factors preventing sagebrush encroachment*

Given the potential for sagebrush to colonize, persist, and grow vigorously in moist meadow terraces where livestock are excluded, it is unclear what prevented sagebrush from dominating mesic portions of these basins before the onset of grazing and stream incision (i.e., before 1850). Possible factors include differences in past climate, fire frequency, flooding frequency, soil disturbance patterns, sagebrush seed supply, grazing, and interactions among these factors. These factors are discussed in turn here.

Millar and Woolfenden (1999) have proposed that vegetation change in the Sierra Nevada could be due to a significant warming trend that has occurred since 1900, the end of the “little ice age.” There is evidence from aging sagebrush in Mulkey Meadow that new patches of Sage–Herb and Low-terrace Sage were synchronously established during a period of drought that followed the wetter than average 1982–1983 El Niño (Bauer et al., *in press*). It is not clear from these data whether sagebrush expansion was promoted by the drought, by the preceding wetter than average El Niño year, or a combination of both. However, the data do suggest that changes in the frequency and intensity of El Niño's over the past century (Timmermann et al. 1999, Urban et al. 2000) may have facilitated sagebrush in low meadow terraces.

Unlike other grassland systems, there is little evi-

dence that fire was historically responsible for preventing the establishment of sagebrush in the montane meadows of the southern Sierra Nevada (Dull 1999). Charcoal layers in the meadow soil profile suggest that only five major fire episodes occurred during the past 1200 yr (Wood 1975), and all appear to indicate upland forest fires (i.e., allochthonous charcoal), rather than in situ burning of meadow vegetation (Dull 1999). Small lightning-caused fires in the sparse lodgepole pine forests surrounding the meadows are common, but the likelihood of fires spreading downslope to the meadow is low due to extremely low fuel availability in the rocky forest understory and the high fuel moisture of meadow vegetation (Dull 1999; E. L. Berlow, C. M. D'Antonio, and S. A. Reynolds, *personal observations*). Fuel availability in the forest is low due to naturally arid conditions and gravelly soils, rather than due to livestock grazing. In addition, fire suppression was not an active management policy in this area until the 1960s, well after the main expansion of sagebrush occurred. Finally, exotic annuals that have altered fire regimes in other grassland ecosystems (e.g., *Bromus tectorum*) are not present.

Before stream channel incision, flooding during peak spring snowmelt may have been frequent enough to kill any sagebrush seedlings that colonized between flood events. In a study of a nearby meadow on the Kern Plateau, Kirchner et al. (1998) estimated that, given the current incised channel, complete inundation of the meadow would occur once every 100 yr. Under a scenario of no channel incision (the assumed prelivestock condition), the meadows may have been inundated as frequently as every 5 yr (Kirchner et al. 1998). However, the degree to which *A. rothrockii* can tolerate inundation is not clear. While there is evidence that a related species of sagebrush common to the Great Basin (*A. tridentata*) is very sensitive to saturated and anoxic soil conditions (Lunt et al. 1973), our observations suggest *A. rothrockii* is tolerant of very high soil moisture. We have observed individuals survive periods of standing water in the spring, or even complete submergence. Further studies are necessary to evaluate *A. rothrockii*'s tolerance of saturated soils and the relative importance of mortality due to flooding in this system.

It is impossible to evaluate whether the frequency of gopher disturbances in the mesic meadow has increased over time, and thus facilitated recent expansion of sagebrush in mesic terraces. While some have suggested that gopher populations increase after livestock grazing (Laycock and Richardson 1975, Ratliff 1985), there are no data available to address this hypothesis for these meadows. However, there is strong evidence from other systems that gophers can be sensitive to both plant species composition and soil characteristics (Chase et al. 1982, Tilman 1983, Huntly and Inouye 1988, Engeman et al. 1997, Inouye et al. 1997, Rezsutek and Cameron 1998), both of which may have been directly and indirectly altered by grazing, trampling, stream in-

cision, or climatic change. More frequent flooding in the past also could have resulted in less gopher activity in mesic meadow areas, and thus fewer opportunities for shrub establishment.

Even if gopher disturbance frequency has not changed significantly, it is possible that sagebrush colonization of disturbances was historically limited by low seed supply (e.g., Platt 1975). While sagebrush was abundant on high terraces prior to the onset of livestock grazing, these terraces were probably more limited in extent prior to stream incision. The observed spatial patterns of seedling distribution suggest that sagebrush may have limited dispersal ability, and studies of other *Artemisia* species suggest that most seeds fall within 1 m of the shrub (Friedman and Orshan 1975, Wambolt et al. 1989). Hence, seed dispersal from sagebrush in high terraces at the meadow fringes to gopher mounds in the mesic meadow may have been infrequent. Studies of other grasslands have suggested that shrub expansion was limited by seed dispersal and that livestock have become important dispersal agents (e.g., Humphrey and Mehrhoff 1958, Brown and Archer 1987, 1989). Using an individually based spatial invasion model developed by Higgins et al. (1998, 2000), we have conducted preliminary simulations that suggest the combination of low dispersal, low germination and seedling survival rates, and germination restricted to disturbances may be enough to prevent sagebrush expansion from the meadow fringes, despite high frequencies of soil disturbance in the meadow (E. L. Berlow and C. M. D'Antonio, *unpublished data*).

Grazing may have directly triggered the initial expansion of sagebrush by increasing survival rates of the few seedlings that became established in the meadow. Our results suggest that regular clipping of the aboveground herb biomass increased the long-term survival of seedlings that were transplanted into herbaceous meadow. Seedlings that were transplanted to soil disturbances in plots that also were clipped exhibited 100% survival after 4 yr and were the first to reach reproductive maturity. In comparison, seedlings transplanted to undisturbed and unclipped herbaceous plots exhibited 0% survival after 4 yr. Our preliminary simulations suggest that once scattered reproductively mature sagebrush become established within the meadow, further colonization accelerates rapidly, despite limited dispersal ability. Further experiments, field observations, and simulations are required to determine how interactions of the above-mentioned factors may have triggered an increase in sagebrush dispersal, germination, and survival in the meadow over the past century.

### Conclusions

Based on the assumption that a lowered water table is the primary factor promoting shrub expansion in the montane meadows, current management efforts focus on preventing further stream incision (Odion et al.

1988; D. Hubbs, *personal communication*). These efforts are essential for preventing further increases in meadow aridity, however, they also implicitly assume that existing meadow terraces with a shallow water table are safe from sagebrush expansion. One important, and perhaps counterintuitive, conclusion from this and other recent studies (e.g., Brown and Archer 1997, 1999, Williams and Hobbs 1989, Harrington 1991, O'Connor 1995, Brown et al. 1997) is that, while shrub expansion is often associated with rangeland desertification, mesic habitats may be more susceptible to seedling establishment than xeric ones if seed supply and suitable substrate (i.e., exposed moist soil) are abundant. Thus, even if stream-channel incision is prevented, moist meadow areas are at risk of being rapidly colonized by sagebrush. To prevent further invasion it is essential to focus management and restoration efforts on mesic areas near to sagebrush seed sources where gopher disturbances create gaps in the herb canopy.

While the general patterns of shrub invasion are similar across a wide variety of grassland or meadow ecosystems and general conceptual models of this process have been proposed, the mechanisms that promote or prevent shrub establishment appear to be context dependent. Thus comparative experimental field studies are critical to determine how the processes that regulate shrub invasion vary among habitats or across physical and biological gradients. Understanding these contingencies is important for developing site-specific management plans and for effectively targeting management activities.

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