Factors Mediating Cheatgrass Invasion of Intact Salt Desert Shrubland

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Abstract—Cheatgrass (*Bromus tectorum*) has recently displaced salt desert shrubland in many areas of the Great Basin. We studied the dynamics of cheatgrass invasion into an intact shadscale-gray molly community in Dugway Valley, Utah, by adding seeds and manipulating disturbance regime and resource availability. Shrub clipping or cryptobiotic crust trampling on large plots increased cheatgrass recruitment and biomass production slightly in a favorable moisture year (1997 to 1998), whereas in a less favorable moisture year (1998 to 1999) these disturbance treatments had a significant negative effect. In 1998 to 1999 small plot studies, recruitment was similar in intact shrub clumps and openings, but biomass and, therefore, seed production was three times greater in shrub clumps. Disturbance decreased recruitment but had no significant effect on biomass per plant. Added water had no effect in openings, but added N increased and reduced N decreased biomass. In shrub clumps, fertility manipulation had little effect, but added water increased biomass. Shrub simulation (water + N + shade) increased biomass per plant in openings, whether intact or disturbed. It had no effect in shrub clumps where shrubs were intact, but caused a large increase in both recruitment and biomass per plant where shrubs were removed. Shrub clumps provide foci of invasion because of their higher resource availability, but the shrubs have competitive as well as facilitative effects. In a dry year (1999 to 2000), there was no survival to reproduction in any treatment. There are no intrinsic obstacles to cheatgrass invasion at this site, but the process will be very slow because of low site productivity and the high probability of drought years. Disturbance is not a necessary precondition for invasion, but may facilitate the process in favorable years.

Introduction

Shrub steppe ecosystems of the Great Basin are in the process of a massive type conversion to low diversity annual grasslands heavily dominated by the exotic annual cheatgrass (*Bromus tectorum*). Fire frequency is a key factor in this conversion. The importance of fire in shrub steppe ecosystems depends on several factors. The long-term importance of infrequent but recurring fire in maintaining mosaics of shrub and perennial grass domination has been established for sagebrush steppe ecosystems (Peters and Bunting 1994). But overgrazing accompanied by invasion of exotic annual grasses that form a continuous layer of fine fuel has drastically increased fire frequency in these ecosystems, with fire return times decreasing from 50 to 200 years to 3 to 5 years (Whisenant 1990). This has resulted in complete loss of the shrub overstory and establishment of an annual grass dysclimax that perpetuates itself through repeated burning on ever-increasing areas (Billings 1994; D'Antonio and Vitousek 1992).

Shadscale-dominated ecosystems, which generally occur in areas of lower precipitation than sagebrush steppe ecosystems, experienced fire very infrequently if at all prior to the introduction of exotic annuals in the understory (West 1994). These ecosystems have been heavily impacted by a century and a half of livestock grazing and weed invasion, and few if any truly pristine areas exist. But the impact of fire in salt desert shrublands has manifested itself only recently, within the last 25 years (West 1994). The relatively sudden appearance of fire as a factor was associated with an increase in density and biomass production of cheatgrass that may already have been present in the understory. No one knows exactly what happened to open shadscale communities to massive understory dominance by cheatgrass, but a sequence of years of exceptionally high precipitation in the early 1980s is implicated in the effect. The result has been a rapid and extensive type conversion to a cheatgrass dysclimax with short fire return times, similar to the type conversion so widespread in sagebrush steppe ecosystems.

The question addressed in the work described here is how shadscale communities are placed at risk for understory takeover by cheatgrass, and whether there is any way to minimize this risk. We need to know how difficult it will be to manage these ecosystems as shrublands in the long term, and whether it is possible to restore shadscale ecosystems to a state that can resist massive annual grass invasion. This study represents a necessary step toward answering those questions.

One problem with descriptive studies of plant community change is difficulty in separating the effects of multiple causal factors. For example, heavy livestock grazing in a shadscale community can have many effects, including destruction of the cryptobiotic soil crust through trampling, selective elimination of palatable understory perennials, prevention of shadscale seed banking through consumption of fruits, and introduction of weed seeds. These in turn may have different effects on weed invasion success. In our

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experimental study, we introduced each of several factors independently, making it possible to examine the effect of each factor on invasion success, both alone and in combination. The study had two principal objectives: first, to determine the effect of seed introduction and systematic disturbance of an intact shadscale community on cheatgrass success, and second, to determine whether the effects of disturbance on cheatgrass success are mediated through soil nitrogen and/or water availability.

Study Site Description

Shrub steppe ecosystems dominated by shadscale (*Atriplex confertifolia*) occupy millions of acres in the Great Basin (Stutz 1978; Blauer and others 1976). Although referred to as salt desert shrublands, shadscale communities occur on fine-textured soils that are variably saline, in the zone between the greasewood (*Sarcobatus vermiculatus*) communities of the playa bottoms and the sagebrush (*Artemisia tridentata* and *A. nova*) communities of less xeric upland sites with coarser soils (Billings 1949).

The Camelback study site is located at an elevation of 1,310 m in Dugway Valley, on the Dugway Army Proving Grounds, approximately 170 km west of the Wasatch Front urban area. The army facility at Ditto is approximately 3 km to the north, and Camelback Hill is a few kilometers to the south. The vegetation on the site is a shrubland with shadscale (*Atriplex confertifolia*) and gray molly (*Kochia americana*) as the dominant species, and with a vascular plant cover value of 22 percent (Meyer and Garvin, unpublished data). Herbaceous perennial understory is essentially lacking. All surfaces, whether under shrubs or in openings, are inhabited by a well-developed cryptobiotic crust made up of lichens, mosses, and cyanobacteria. Weedy annuals present on the study site include perfoliate pepperweed (*Lepidium perfoliatum*) and bur buttercup (*Ranunculus testiculatus*), principally in the openings. In summer 1997, the only evident cheatgrass was along gravelly road shoulders, though there was a large population in a flooding area next to a gravel road a few hundred meters away.

Table 1—Monthly long-term precipitation totals and 1998, 1999, and 2000 water year (October 1 to September 30) monthly totals in millimeters at the Ditto Weather Station.

Month	WY1998	WY1999	WY2000	Longterm
October	15	45	0	20
November	26	8	1	15
December	10	6	1	15
January	14	25	19	12
February	41	5	29	14
March	44	5	4	21
April	21	52	8	21
May	16	28	20	26
Season total[a]	187	174	82	144
June	60	27	—	15
July	25	3	—	14
August	13	8	—	15
September	18	12	—	20
Grand total	303	224	—	208

[a]Total for 8-month season of growth for cheatgrass, a winter annual that emerges in autumn, winter, or early spring and matures by early summer.

The average annual precipitation at the study site, based on a station at nearby Ditto, is 208 mm (8.19 inches; table 1). The site has a history of sheep grazing but has been protected from grazing by livestock for over 50 years. Feral horses and pronghorn have access to the area but rarely visit. There is minimal vehicular disturbance.

Soils at the site are generally calcareous clay loams of moderately alkaline pH and moderate salinity and sodicity. In samples collected in November 1997, salinity, clay content, and carbonate content increased significantly with depth, while pH and sodicity (as measured by sodium adsorption ratio) did not (table 2). None of these parameters

Table 2—Mean values and significance tests for 10 soil parameters measured at 0 to 15 cm and 15 to 30 cm depths under shrub canopies and in openings at the Camelback study site. N = 4 per treatment combination.

	Under shrubs		In openings		Probability of significance from ANOVA		
Parameter	Surface (0 to 15 cm)	Sub-surface (15 to 30 cm)	Surface (0 to 15 cm)	Sub-surface (15 to 30 cm)	Shrub versus opening	Surface versus subsurface	Shrub/opening x surface/subsurface
Nitrate-N (ppm)[a]	12.2	7.6	6.9	6.8	<0.02	<0.06	<0.07
P (ppm)[b]	14.3	14.0	16.4	9.8	ns	ns	ns
K (ppm)[a]	704	818	809	867	<0.05	<0.06	ns
Org. Matter (percent) [c]	1.17	1.38	0.99	1.30	<0.06	<0.01	ns
Elec.Cond. (mmhos/cm)[a]	5.4	8.9	5.1	10.3	ns	<0.001	ns
pH[a]	7.9	7.9	7.8	8.0	ns	ns	ns
Sodium AR[a]	27.1	34.2	28.8	37.0	ns	ns	ns
Carbonate (percent)[d]	35.0	41.3	33.2	41.4	ns	<0.0001	ns
Sand (percent)	36.2	24.9	38.4	21.8	ns	<0.0001	ns
Clay (percent)	44.4	62.1	41.6	63.3	ns	<0.0001	ns

[a]In saturation extract.
[b]Bicarbonate-extractable.
[c]Walkley-Black method.
[d]Calcium carbonate equivalent.

differed significantly between shrub clumps and openings. Organic matter was generally low but was higher in shrub clumps and increased with depth, probably because of the high root:shoot ratios of the dominant shrub species (Holmgren and Brewster 1972). Phosphorus and potassium were present in nonlimiting amounts. Phosphorus concentration was not related to position or depth, while potassium was significantly higher in the subsoil and in openings. Nitrate-N was present at low levels, as would be expected with the low organic matter content. It was higher in shrub clumps than in openings and higher in the surface soil than in the subsoil. Nitrate-N was 50 percent higher in the surface soil under shrubs than in the open or in the subsoil. Surface soils under shrub clumps were also less compacted than soils in openings, with more surface roughness and lower bulk density.

Materials and Methods

Field experiments were initiated in September of each year. Disturbance studies utilizing large plots were carried out in 1997 to 1998, 1998 to 1999, and 1999 to 2000, while small plot resource manipulation studies were performed for 2 years starting in September 1998. Cheatgrass seeds were collected on the Whiterocks Road in former shadscale vegetation, ca. 28 km northeast of the study site, in June of each year, cleaned to >95 percent purity, tested for viability, and allowed to after-ripen under laboratory conditions until the broadcast planting without any covering treatment in September.

The large plot study initiated in 1997 consisted of four disturbance treatments, two seeding treatments, and 10 blocks for a total of eighty 1 x 3 m plots. The disturbance treatments included: intact shrubs and crust, shrubs clipped and left in place, crust trampled in place, and shrubs clipped in combination with crust trampled. The seeding treatments were no additional seed and 100 viable seeds (florets) per 0.1 m^2. This design was repeated the following 2 years with the exception that unseeded plots were not harvested, so that the plot total was 40. The same plots were used each year, with reclipping of any resprouted shrubs and redisturbance of the crust.

The small plot study was also a randomized block design, with eight replications. The treatment design was factorial with two positions (shrub clumps and openings), two disturbance treatments (intact and removal), and six resource manipulation treatments, for a total of 24 treatment combinations and 192 plots. The manipulations included: control, added water, added shade, added nitrogen, reduced nitrogen (by adding sucrose to immobilize nitrogen into microbial biomass), and shrub simulation (added shade, nitrogen, and water). Plot size was 0.1 m^2; the same plots were used each year.

Living shadscale shrubs >50 cm in crown diameter were selected for the shrub clump treatments. For the removal treatment, shrubs were clipped at ground level. Cryptobiotic crust was left intact in the shrub removal plots. For the open removal treatment, the cryptobiotic crust was physically removed to a depth of ca. 2 cm.

For the supplemental water treatment, water was added to simulate 25 mm of extra rainfall in mid-October and mid-March by suspending water-filled ziplock bags on hardware cloth platforms over the plots and allowing the water to drip through holes punched in the bottoms. Application took approximately an hour and resulted in little or no runoff. Nitrogen was added at a rate of 5.3 g per m^2 per yr in the form of ammonium nitrate, while sucrose was added at a rate of 50 g per m^2 per yr (McLendon and Redente 1992). Fertility treatments were applied dry at the same time as supplemental watering in the fall and spring, and plots were watered with a few milliliters of water to help prevent removal by wind. Shade was continuously applied through the course of the study by surrounding each shade plot with a quadrangular frame covered with 2 mm fiberglass window screening to a height of 45 cm. The shade frame tops were open.

Harvest took place in May each year after the plants had turned red and the seeds had reached maximum dry mass, but before any seed shatter. The first year, plants in the large plot experiment were counted after harvest, then dried at 40 °C for 48 hours and weighed to obtain total biomass per plot. In following years, only total biomass per plot was measured. For the small plot study, plants for each plot were counted during harvest and separated into seed (floret) and vegetative fractions. Each fraction was then dried and weighed to obtain biomass as above. Biomass per plant was a good predictor of seed biomass and, therefore, of seed number ($R^2 = 0.965$, d.f. = 190, $p < 0.0001$)

All count and biomass data were log-transformed prior to analysis of variance to increase homogeneity of variance (Zar 1984). Dependent variables for all analyses included number of plants setting seed per 0.1 m^2, dry biomass per 0.1 m^2, and biomass per plant. For the small plot study, seed fraction (floret mass/total mass) was also included. After determining that the block effect was not significant for any variable, it was pooled into the error term, and the data were analyzed as completely randomized designs. Data for the 1998 and 1999 large plot harvests were analyzed separately using fixed-effects two-way (1999 and 2000) or three-way (1998) analysis of variance. Data for the 1999 small plot study were analyzed as three-way fixed-effects models using a general linear models procedure. Control treatments for the four shrub/open intact/removal small plot treatment combinations were then compared with each other and with their respective manipulation treatments using orthogonal contrasts (Steel and Torrie 1980).

Results

Large Plot Study

The 1997 to 1998 fall-winter-spring season was favorable for cheatgrass at the Camelback study site, with adequate autumn, winter, and spring precipitation (table 1). Estimated seed return on the seeded plots averaged 28 percent, with 28 plants reaching reproductive maturity and mean biomass production of 1.2 g per 0.1 m^2 on seeded plots. Cheatgrass success in 1997 to 1998 was clearly limited by seed supply (table 3). There were 10 times as many plants on the seeded plots, and they produced five times as much biomass as the plants on the unseeded plots (fig. 1). The plants on the unseeded plots averaged twice the size of those on the seeded plots, however.

Table 3—Analysis of variance for the 1998 and 1999 harvests of the large plot experiment. Data were log transformed to increase homogeneity of variance prior to analysis. The block effect was not significant for any dependent variable: therefore, block and block interactions were pooled as the error term. Error degrees of freedom: 1998 = 62, 1999 = 36.

		Plant number		Plant biomass		Total plot biomass	
	d.f.	F	P	F	P	F	P
1998 experiment							
Seeded/unseeded	1	197.8	0.0001	58.3	0.0001	121.0	0.0001
Shrubs intact/clipped	1	0.1	ns	3.71	0.06	1.06	ns
Crust intact/trampled	1	0.57	ns	0	ns	0.57	ns
Seeding x clipping	1	0.10	ns	1.44	ns	0.88	ns
Seeding x trampling	1	0.31	ns	0.85	ns	1.05	ns
Clipping x trampling	1	4.35	0.05	0.02	ns	4.30	0.05
Seed x clip x tramp	1	0.42	ns	0.48	ns	1.05	ns
1999 experiment							
Shrubs intact/clipped	1	—	—	—	—	17.84	0.0002
Crust intact/trampled	1	—	—	—	—	8.11	0.0072
Interaction	1	—	—	—	—	1.00	ns

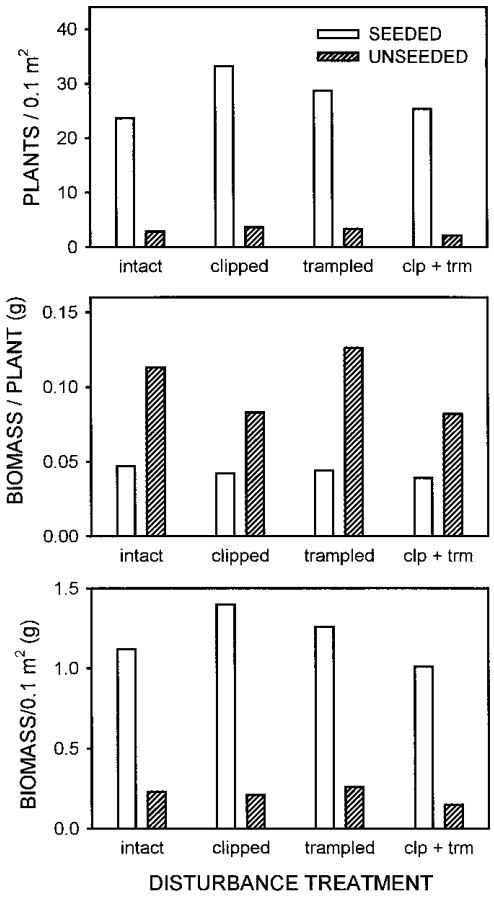

Figure 1—Plant number per 0.1 m^2 area, dry biomass per plant, and total dry biomass per 0.1 m^2 area for the large plot 1998 harvest. Disturbance treatments: intact (no disturbance), clipped (shrubs clipped at ground level), trampled (cryptobiotic crust trampled) and clp + trm (shrubs clipped in combination with crust trampled). Seeding treatments: seeds broadcast sown at 100 per 0.1 m^2 and no added seeds. See table 3 for significance tests.

Disturbance treatments had a slight but significant effect on cheatgrass success on the large plots in 1997 to 1998, and the effects were similar in seeded and unseeded plots (table 3). Plants were 30 percent larger overall where shrubs were left intact (table 3, nearly significant), but mild disturbance (either clipping or trampling but not both) resulted in a ca. 30 percent increase in recruitment and a ca. 20 percent increase in biomass per 0.1 m^2 (table 3, significant shrub treatment by crust treatment interactions; fig. 1). The severe disturbance treatment (shrubs clipped and crust trampled) did not show this beneficial effect, with numbers similar to those on intact plots and total biomass lower than any other treatment (fig. 1).

The 1998 to 1999 season was less favorable for cheatgrass at Camelback, with little late winter moisture (table 1). Biomass per 0.1 m^2 in the large plot study averaged only 0.262 g overall, little more than one-fifth of the value on seeded plots the previous year. In intact plots, biomass production was three times greater in 1998 than in 1999. Under this weather scenario, disturbance had a clear negative effect on biomass production, with the effects of both shrub clipping and crust trampling significant (table 2; fig. 2). Biomass production in the severe disturbance treatment was decreased by a factor of three relative to the intact plots.

The 1999 to 2000 season was categorically unfavorable for cheatgrass at Camelback, due to unusually dry conditions (table 1). Recruitment was minimal and no plants survived to reproduction, regardless of treatment, in either the large plot study or the small plot study described below.

Small Plot Study

Analysis of the 1999 harvest data for the small plot study showed that the shrub versus open treatment, the intact versus disturbed treatment, and the manipulation treatment main effects were all significant for plant number and total biomass per plot, but the intact versus removal treatment had no significant effect on plant size (table 4).

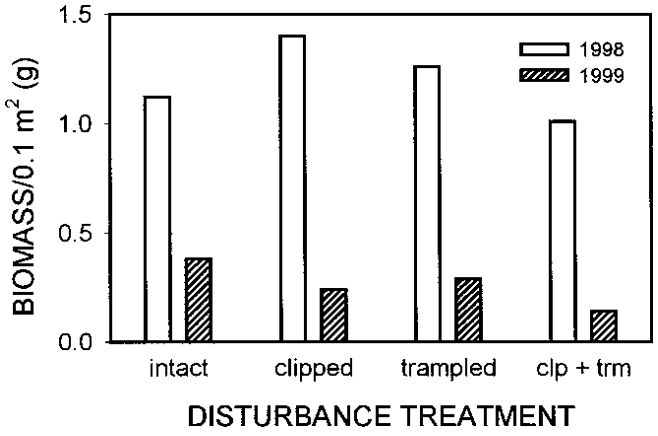

Figure 2—Total dry biomass per 0.1 m^2 area for the large plot 1998 and 1999 harvests. Disturbance treatments: intact (no disturbance), clipped (shrubs clipped at ground level), trampled (cryptobiotic crust trampled), and clp + trm (shrubs clipped in combination with crust trampled). See table 3 for significance tests.

Patterns for control plots were generally similar to patterns from the overall analysis, although sometimes not significant.

For plant number per plot, control and overall values were similar in shrub clumps and openings (fig. 3). Plant number was generally negatively impacted by disturbance, a result similar to the large plot study result from the same harvest year. This negative impact was greater in openings, resulting in a significant shrub clump versus opening intact versus removal interaction (table 4; fig. 3).

Biomass per plant was more than twice as high overall in shrub clumps as in openings, and this difference was even greater when intact control treatments were compared (table 4; fig. 4). The removal treatment had no significant effect on plant biomass overall in either shrub clumps or openings.

As a result of the interplay of the above two variables, biomass per 0.1 m^2 plot was significantly higher in shrub clumps than openings and significantly higher in intact plots than in removal plots overall (table 4; fig. 5). Total biomass was less impacted by disturbance in shrub clumps than in openings, resulting in a significant interaction for this variable. Control plots followed the same trends.

Only two manipulations significantly impacted plant number per plot, and these impacts were only sometimes evident. Shrub simulation had no effect on recruitment in intact shrub clumps, but had a large positive effect when shrubs were removed (fig. 3). Shrub simulation had no effect on recruitment in openings. Shade negatively impacted recruitment in openings but not in shrub clumps.

Biomass per plant was positively affected by supplemental water in shrub clumps, whether shrubs were intact or removed (fig. 4). Supplemental water had no effect on biomass per plant in openings. Conversely, added nitrogen increased and sucrose decreased biomass per plant in openings, but had no effect in shrub clumps. Shrub simulation (water + nitrogen + shade) had no effect in intact shrub clumps but a large positive effect when shrubs were removed. It had a significant positive effect on biomass per plant in openings whether or not crust was removed.

No manipulation treatment resulted in significantly increased biomass per plot relative to the control when shrubs were intact. With shrubs removed, shrub simulation had a large positive effect, while the positive effect of supplemental water alone was nearly significant (fig. 4). In openings, shrub simulation increased total biomass significantly over the control only when the crust was intact, although a similar but nonsignificant trend was evident in the removal treatment.

Seeds (florets) made up 29 to 48 percent of total dry mass, with a mean of 43 percent. Seed investment was significantly higher in shrub clumps than in openings and in intact versus removal treatments, although the differences in investment were not large (table 4; fig. 5). In control treatments, seed investment was higher in intact shrub clumps than in the other three treatments, and there was no significant manipulation effect with shrubs intact, although sucrose addition tended to reduce reproductive investment. With shrubs removed, added nitrogen decreased reproductive investment. In openings, which showed nitrogen limitation on plant biomass, added nitrogen had a null or positive effect on reproductive investment, while nitrogen depletion through sucrose addition resulted in a sharp decrease.

As mentioned above, the harvest for the 1999 to 2000 year in the small plot study was zero, regardless of position, disturbance treatment, or manipulation. There were, therefore, no significant treatment effects or interactions for any dependent variable.

Table 4—Analysis of variance for the 1999 harvest of the small plot factorial experiment. Data (except for seed fraction) were log transformed to increase homogeneity of variance prior to analysis. The block effect was not significant for any dependent variable; therefore, block and block interactions were pooled as the error term. Error degrees of freedom = 165.

		Number of plants		Plant biomass biomass		Total plot biomass		Seed fraction	
	d.f.	F	P	F	P	F	P	F	P
Shrub versus open	1	20.01	0.0001	237.2	0.0001	97.96	0.0001	4.77	0.0307
Intact versus removal	1	20.63	0.0001	0.67	ns	11.28	0.0010	4.41	0.0373
Manipulation	5	2.82	0.0178	18.88	0.0001	8.77	0.0001	9.03	0.0001
Shrub/open x intact/rem	1	19.07	0.0001	0.52	ns	10.61	0.0014	3.02	ns
Shrub/open x manip.	5	1.22	ns	8.09	0.0001	1.14	ns	7.70	0.0001
Intact/remove x manip.	5	2.09	ns	0.81	ns	1.93	ns	0.64	ns
Sh/op x int/rmv x manip.	5	0.66	ns	1.62	ns	1.22	ns	2.66	0.0427

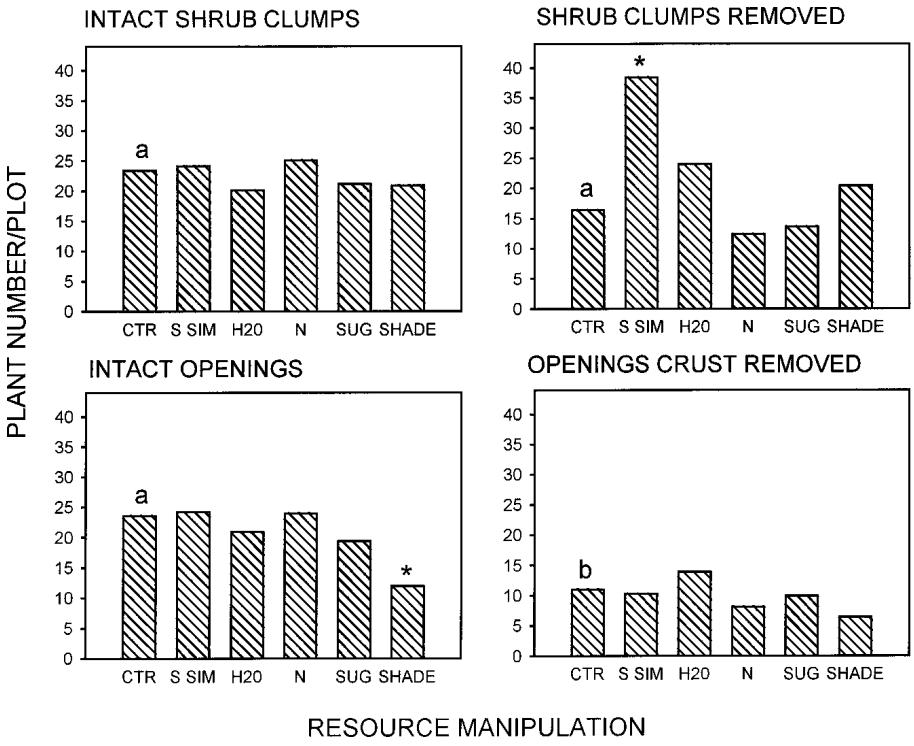

Figure 3—Plant number per 0.1 m^2 plot for each treatment combination in the small plot 1999 harvest. Control treatments with means not significantly different at the $p < 0.05$ level have columns headed by the same letter. Manipulation treatments that are significantly different from the control manipulation treatment within a shrub/open intact/removal treatment combination have columns headed by asterisks (*, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$; o, $p < 0.10$, marginally significant; CTR, control; S SIM, shrub simulation; H20, supplemental water; N, supplemental nitrogen; SUG, sucrose addition to reduce available nitrogen; SHADE, plots shaded).

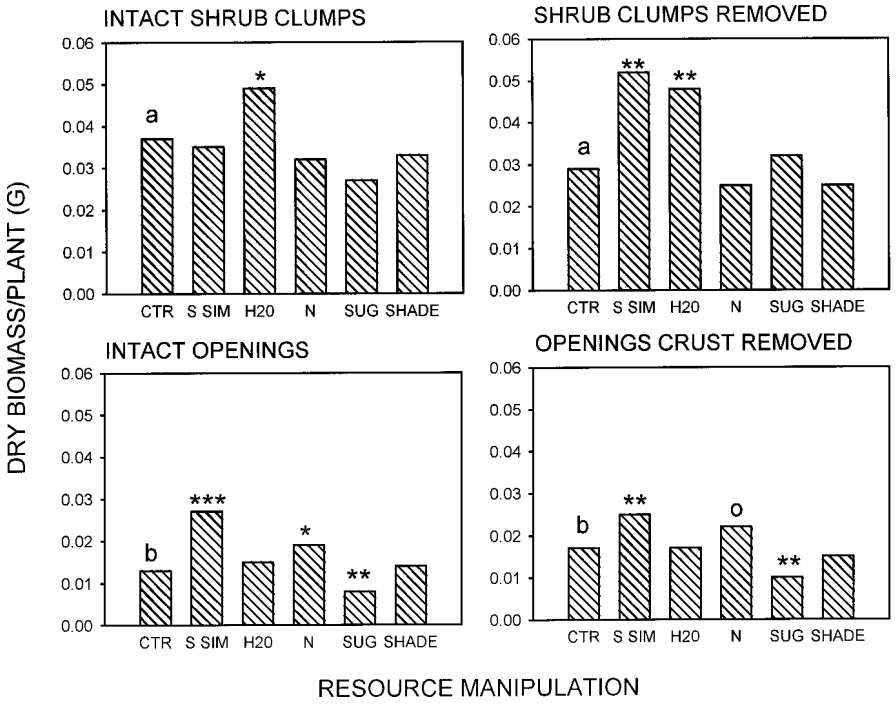

Figure 4—Dry biomass per plant for each treatment combination in the small plot 1999 harvest. Control treatments with means not significantly different at the $p < 0.05$ level have columns headed by the same letter. Manipulation treatments that are significantly different from the control manipulation treatment within a shrub/open intact/removal treatment combination have columns headed by asterisks (*, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$; o, $p < 0.10$, marginally significant; CTR, control; S SIM, shrub simulation; H20, supplemental water; N, supplemental nitrogen; SUG, sucrose addition to reduce available nitrogen; SHADE, plots shaded).

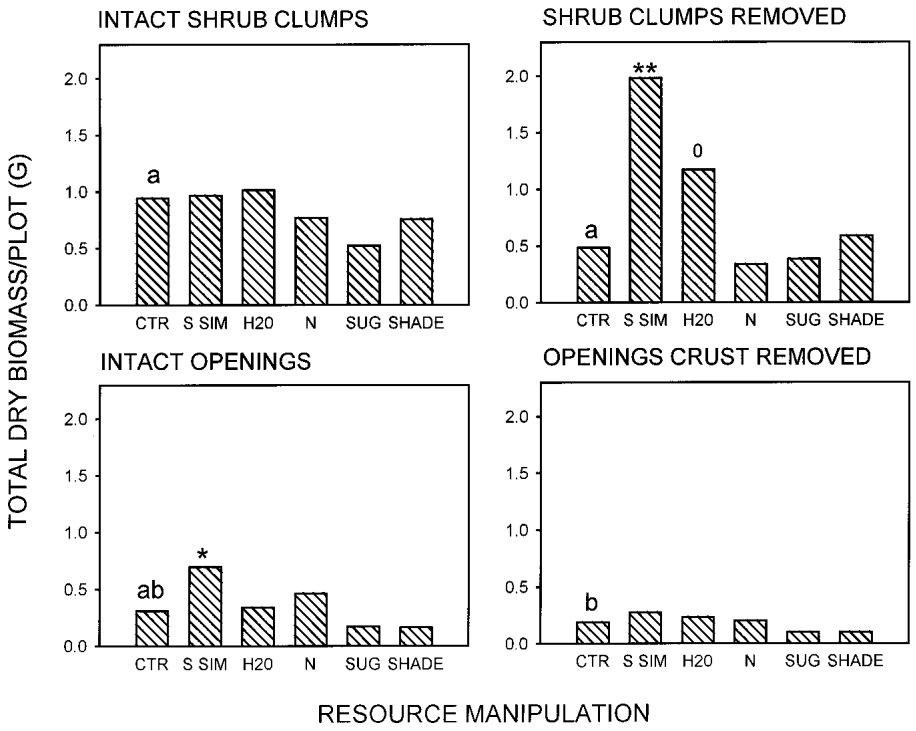

Figure 5—Total dry biomass per 0.1 m^2 plot for each treatment combination in the small plot 1999 harvest. Control treatments with means not significantly different at the $p < 0.05$ level have columns headed by the same letter. Manipulation treatments that are significantly different from the control manipulation treatment within a shrub/open intact/removal treatment combination have columns headed by asterisks (*, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$; o, $p < 0.10$, marginally significant; CTR, control; S SIM, shrub simulation; H20, supplemental water; N, supplemental nitrogen; SUG, sucrose addition to reduce available nitrogen; SHADE, plots shaded).

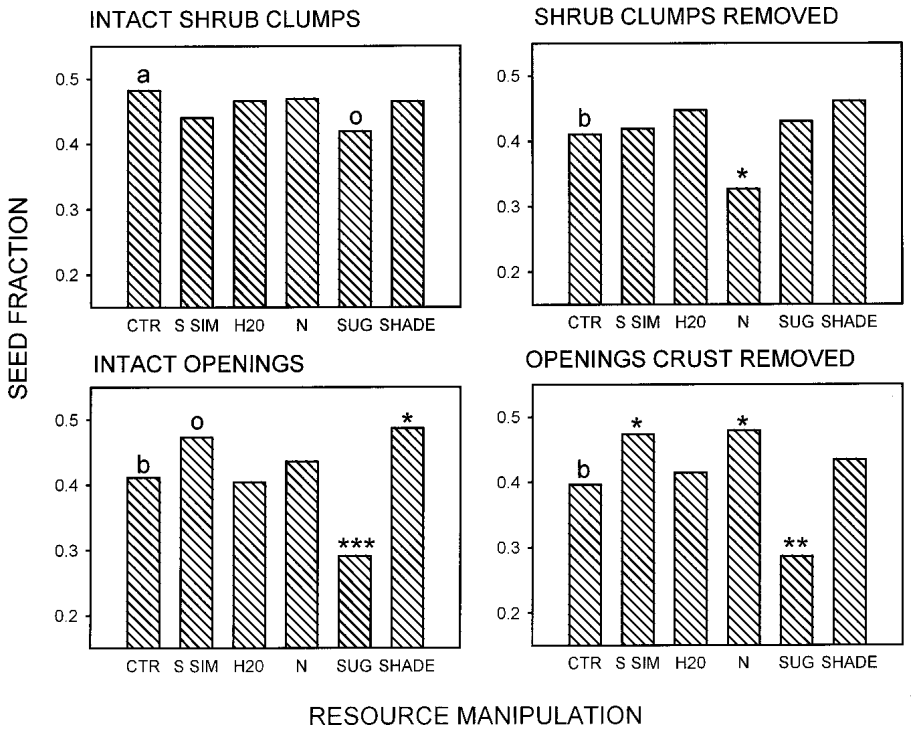

Figure 6—Fraction of dry mass invested in seeds (florets) for each of 24 treatment combinations in the small plot 1999 harvest. Control treatments with means not significantly different at the $p < 0.05$ level have columns headed by the same letter. Manipulation treatments that are significantly different from the control manipulation treatment within a shrub/open intact/removal treatment combination have columns headed by asterisks (*, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$; o, $p < 0.10$, marginally significant; CTR, control; S SIM, shrub simulation; H20, supplemental water; N, supplemental nitrogen; SUG, sucrose addition to reduce available nitrogen; SHADE, plots shaded).

Discussion

There appears to be little intrinsic resistance to cheatgrass invasion at the Camelback study site, in spite of its aridity, heavy soils, and high salinity. Seed supply or propagule pressure is the principal extrinsic factor mediating invasion rate. Resource availability determines the rate of recruitment from arriving propagules, and also regulates plant size and, therefore, seed production per plant. The degree of availability of "excess" resources to support cheatgrass recruitment and growth is related to effective precipitation and fluctuates from year to year (Davis and others 2000). The probable reasons that cheatgrass has not yet extensively invaded this plant community in Dugway Valley are at least twofold. First, dispersal into the area is minimized because human traffic is generally excluded or at least closely regulated, and herbivores that could transport seeds rarely enter this community type. Second, invasibility is greatly reduced in perhaps a majority of years by resource limitation related to the low and sporadic precipitation.

Recruitment from arriving propagules varied from 0 to 28 percent in our study. If we use 0.003 g as the average mass of a single cheatgrass propagule (Meyer, unpublished data), we can estimate seed production per plant from total biomass and seed investment values. In the 1997 to 1998 large plot study, plants in seeded plots averaged 0.050 g and produced an estimated seven seeds. At a return on seed for the following year of 24 percent (from 1998 to 1999 small plot study), those seven seeds would produce 1.7 plants, less than a doubling of the population. If we assume that in 1998 to 1999 recruitment was similar on intact large and small plots, namely 24 percent, then an individual plant on intact large plots would have averaged 0.016 g and would have produced 2.3 seeds. Given an optimistic return on seed for the following year of 25 percent, those seeds would produce on average 0.6 plants. Under this scenario, the population would experience no net growth across these three relatively favorable years.

In fact, the return on seed for 1999 to 2000 was much less than 25 percent; it was effectively zero. If all the seeds in the seed bank germinated but failed to survive, that would put the cheatgrass population at zero until the immigration of more seeds. An unknown fraction of the seeds produced in 1999 may have survived in the seed bank, although seed bank carryover is positively related to cheatgrass litter cover and, therefore, probably minimal at this site (Beckstead 2001). But even if, say, half of the seeds survived, the population would still be declining sharply, because recruitment from remaining seeds is not likely to exceed 25 to 30 percent, even in the most favorable year. This means that it would take a very unusual series of favorable water years to cause an exponential increase in cheatgrass biomass at this site.

Cheatgrass plants that occurred in intact shrub clumps in the 1999 small plot study were three times the size of those in openings and produced even more than three times as many seeds because of their higher reproductive investment. Even with an artificially equal initial distribution of propagules in the large plots and a shrub cover of 22 percent, almost as many seeds were produced in shrub clumps as in openings. Supplemental water increased this size advantage in shrub clumps. These facts may explain why plants in the unseeded plots in 1998 were twice as big as those in the seeded plots. Though we have no quantitative data to support this observation, it was clear that most of the plants in the unseeded plots were in shrub clumps. This would represent the natural invasion pattern. Shrub clumps are the foci of invasion because of their greater resource availability and the resulting increase in seed production per plant. Because 1998 was a more favorable water year than 1999 and because cheatgrass plants in shrub clumps respond more to additional water, the differential size advantage in shrub clumps would have been even greater in 1998. The shrubs apparently act as nurse plants for cheatgrass, ameliorating growing conditions for this understory species in an otherwise harsh environment, an effect commonly observed in warm desert ecosystems (Franco and Nobel 1989). The shrub clumps act as "fertile islands" surrounded by less productive openings (Garner and Steinberger 1989).

The impact of disturbance in opening the Camelback site to cheatgrass invasion was disappointingly small. In the most favorable water year, moderate disturbance (either trampling or clipping but not both) increased recruitment by 30 percent, and it increased biomass production and, therefore, seed production by 20 percent, but more severe disturbance (both trampling and clipping) had a null or negative effect. In a less favorable year, disturbance of any kind had a negative effect on cheatgrass biomass production. Disturbance is, therefore, not necessary for cheatgrass invasion at the Camelback site, but may speed the invasion process in favorable water years. This could have impact, because favorable water years are the only years when there can be net cheatgrass population growth at this site.

Because of low cheatgrass biomass and seed production even in favorable years, it may be hard to see how openings at Camelback could ever support closed stands of cheatgrass (Beckstead 2000). This would limit disturbance from fire, because the fuel would remain discontinuous even in high water years. But cheatgrass dominance results in a redistribution of organic matter and fertility from the subsurface to the surface (Meyer and Garvin, unpublished data). Heavy cheatgrass production in shrub clumps over a period of unusually wet years could result in a gradual encroachment and eventual coalescing of litter across the openings, resulting in less N limitation and more favorable soil physical characteristics for cheatgrass production. We have seen this process occurring in heavily invaded shadscale communities in adjacent, less xeric, Skull Valley. Once this happens, cheatgrass can thrive in the openings, the fuel can become continuous, and the vegetation can carry fire.

The shrub simulation treatment with shrubs removed dramatically increased cheatgrass recruitment and biomass production. This treatment may mimic what happens after a shadscale plant dies. The soil and microsite characteristics that make shrub clumps more favorable persist and, in the case of fertility, may even be enhanced in the years after shrub death, making dead shrub clumps highly favorable microsites for cheatgrass. This effect became important on a landscape scale in the early 1980s, when the same series of high water years that speeded cheatgrass invasion also resulted in widespread shadscale stand loss (Nelson and others 1990). Stand loss itself does not result in local

extinction, because shadscale is able to recruit from a persistent seed bank (Meyer and others 1998). But the concomitant increase in cheatgrass biomass production within these communities greatly increases the probability of recurring fire and rapid conversion to cheatgrass domination.

This scenario was not played out in Dugway Valley as it was in many other eastern Great Basin desert valleys, principally because of its greater aridity and seed limitation. The probability that cheatgrass will eventually take over and displace shadscale communities in Dugway Valley depends on weather patterns as well as on seed availability. The best hope for protecting the salt desert shrub communities in Dugway Valley, therefore, lies in reducing the probability of propagule arrival by restricting entry and by eradicating adjacent populations, as well as limiting levels of anthropogenic disturbance.

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