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Community Structure Affects Annual Grass Weed Invasion During Restoration of a Shrub–Steppe Ecosystem

Phil S. Allen and Susan E. Meyer*

Ecological restoration of shrub–steppe communities in the western United States is often hampered by invasion of exotic annual grasses during the process. An important question is how to create restored communities that can better resist reinvasion by these weeds. One hypothesis is that communities comprised of species that are functionally similar to the invader will best resist invasion, while an alternative hypothesis is that structurally more complex and diverse communities will result in more effective competitive exclusion. In this field experiment, we examined the effects of restored community structure on the invasion success of three annual grass weeds (downy brome, jointed goatgrass, and cereal rye). We created replicated community plots that varied in species composition, structural complexity and density, then seeded in annual grass weeds and measured their biomass and seed production the following year, and their cover after 1 and 3 yr. Annual grass weeds were not strongly suppressed by any of the restored communities, indicating that it was difficult for native species to completely capture available resources and exclude annual grass weeds in the first years after planting. Perennial grass monocultures, particularly of the early seral grass bottlebrush squirreltail, were the most highly invaded communities, while structurally complex and diverse mixtures of shrubs (big sagebrush, rubber rabbitbrush), perennial grasses (bluebunch wheatgrass and bottlebrush squirreltail) and forbs (Lewis flax, Utah sweetvetch, hairy golden aster, gooseberryleaf globemallow) were more resistant to invasion. These results suggest that restoration of sagebrush steppe communities resistant to annual grass invasion benefits from higher species diversity; significant reduction of weed propagule pressure prior to restoration may be required.

Nomenclature: Cereal rye, *Secale cereale* L.; downy brome, *Bromus tectorum* L.; jointed goatgrass, *Aegilops cylindrica* Host; big sagebrush, *Artemisia tridentata* Nutt.; bluebunch wheatgrass, *Pseudoroegneria spicata* (Pursh) Á. Löve; bottlebrush squirreltail, *Elymus elymoides* (Raf.) Swezey; gooseberryleaf globemallow, *Sphaeralcea grossulariifolia* (Hook. and Arn.) Rydb.; hairy golden aster, *Heterotheca villosa* (Pursh) Shinners; Lewis flax, *Linum lewisii* Pursh; rubber rabbitbrush, *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird; Utah sweetvetch, *Hedysarum boreale* Nutt.

Key words: Ecological restoration, invasive plants, plant competition.

Many natural plant communities in semiarid regions of the western United States have been invaded by exotic species (DiTomaso 2000). For example, millions of hectares of former shrub–grasslands have been reduced to near monocultures of exotic annual grasses including cheatgrass or downy brome (*Bromus tectorum* L.), which probably represents the most successful plant invasion in the modern history of North America (D'Antonio and Vitousek 1992). In addition to greatly diminishing the abundance of native species, negative consequences of these plant invasions include dramatic alterations of fire regimes, nutrient cycling, hydrology, and energy budgets (Mack et al. 2000). Unfortunately, in spite of numerous studies devoted to understanding exotic invaders of shrub–grassland communities, the current trajectory points toward even more rapid invasion and degradation (Evans et al. 2001; Mack et al. 2000). Any large-scale solution to the problem of exotic plant invasion in the semiarid Western United States will require a synthesis of basic ecological principles with on-the-ground knowledge of

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* First author: Professor, Department of Plant and Wildlife Science, Brigham Young University, Provo, UT, 84602; second author, Research Ecologist, US Forest Service Rocky Mountain Research Station, Shrub Sciences Laboratory, 735 North 500 East, Provo UT 84606. Corresponding author's email address: Phil_Allen@byu.edu

Management Implications

Our study of annual grass weed invasion dynamics in a sagebrush steppe restoration experiment emphasizes the importance of combining the basic principles of ecological restoration and weed science to understand how the plant community at a particular site is likely to respond to restoration activities, and how the restoration species will interact with invasive exotic species in the area through time. Fundamental properties of a restoration site include its intrinsic productivity, as defined by climate and soils, its history of disturbance and use, and the pool of potential colonizing species, both native and exotic, that already occupy the area. Ecological theory indicates that sites with a history of disturbance are most invasible, as the absence of an intact plant community means resources are likely to be incompletely utilized, thus providing more resources for an invader. Sites subject to high propagule pressure from invasive species in the area are also at higher risk. The least invasible sites are generally those with low levels of disturbance and an absence of potential invaders. Restoration strategies will be different for sites at different points along this continuum of invasibility. Our study site was historically highly disturbed, with a history of fertilizer additions. Under this scenario the best strategy was to establish a native community that was structurally diverse, including the foundation species in this community, big sagebrush, as a major component, along with a mixture of perennial grasses and forbs. However, even though this combination reduced annual grass weed success, it did not prevent invasion. We subjected the site to relatively high propagule pressure by deliberately introducing seeds of annual grasses. In a practical restoration, the best strategy would have included reduction of propagule pressure as an integral component.

restoration practitioners, as well as a more effective utilization of the tools of weed science in the context of ecological restoration (D'Antonio et al. 2009; D'Antonio and Meyerson 2002). Invasive species control and ecological restoration clearly need to be applied in an integrated way in order to make progress in the effort to restore these degraded landscapes.

What Makes a Plant Community Vulnerable to Invasion?

Community Composition. The question of what makes a plant community vulnerable to invasion by exotic species has been the subject of intense theoretical analysis and a large number of experimental studies over the last few decades (Lonsdale 1999; Radford 2013; Reysner et al. 2013; Richardson and Pysek 2006). Much of this work has focused on the premise, originally proposed by Elton (1958), that plant communities with higher species diversity will be less vulnerable to invasion because the ecological niche space in the community will be filled more completely, leaving little niche space for invaders (Levine and D'Antonio 1999). While such a phenomenon has been demonstrated in some small plot studies (e.g., Fargione and Tilman 2005; Naeem et al. 2003; van Ruijven et al. 2003), the patterns on a landscape scale often support the opposite conclusion, namely that high-diversity communities are more subject to invasion (e.g., Lonsdale 1999; Stolhgren et al. 1999).

Another factor potentially influencing invasibility is the presence of dominant foundation species that could have an over-riding effect, with the expectation of decreased invasibility. This concept has been supported in at least one study in sagebrush steppe, where removal of the foundation species big sagebrush increased invasion success of downy brome and several weedy annual forbs, largely through increasing the availability of water (Prevey et al. 2010). In contrast, in a tallgrass prairie ecosystem, reducing the abundance of the foundation warm season grass actually reduced yellow sweetclover [*Melilotus officinalis* (L.) Lam.] invasion success, apparently because of reduction of facilitative effects (Smith et al. 2004).

In a different approach to how plant community structure might affect invasibility, a few studies have examined functional group diversity rather than species diversity, or the effect of a functional group in a community on an invader of the same functional group. For example, in an experimental study on factors controlling spotted knapweed invasion, Pokorney et al. (2005) showed that removal of both shallow-rooted and deep-rooted forbs increased knapweed invasion success in a cool-season grassland, while removal of perennial grasses generally did not. In a study involving removal of different functional groups (C3 grasses, C4 grasses, and forbs) in a prairie community in Minnesota, Symstad (2000) found evidence for decreased invasibility with increased functional group diversity, but there was only weak support for the idea that resident species decreased success of functionally similar invaders.

In sagebrush steppe ecosystems, early seral grasses like bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) are thought to be functionally similar to annual grasses. Several studies have shown that less productive sites dominated by this species are able to resist invasion by downy brome, yet allow recruitment of later seral native species such as big sagebrush (Booth et al. 2003; McClendon and Redente 1992; Stevens 1997). A related concept is the idea of 'assisted succession', where a perennial grass (in this case the exotic crested wheatgrass) is used to decrease competition from downy brome prior to the introduction of native species of diverse functional groups into the community (Cox and Anderson 2004).

Extrinsic Site Factors. Site factors, as opposed to characteristics of the resident plant community, can also have a major influence on the probability of invasion. One proposed explanation for the positive correlation between

resident species diversity and probability of invasion mentioned earlier (Lonsdale 1999) is that the same extrinsic site factors that have permitted a plant community to accrue high numbers of native species may also permit it to accrue more exotic species (Davis et al. 2005; Huston 2004). Huston (2004) proposed a scheme suggesting that sites that combine high productivity with high levels of disturbance have the highest probability of invasion and subsequent dominance by nonresident species, whether exotic or native. It has long been recognized that disturbance resulting in the removal or destruction of living plant biomass will result in an increase in the resources available to other plants, including invaders (Grime 1977). This phenomenon has been observed in sagebrush steppe removal experiments (Chambers et al. 2007). Disturbance can also result in an increase in the extrinsic supply of resources, for example, the nutrient augmentation that may accompany flooding in riparian communities. The positive relationship between productivity and invasibility is a consequence of the fact that highly productive sites present favorable conditions to a wider range of species. These sites also have more temporal and spatial fluctuation in resources than sites with low productivity, making it difficult for resident species to fully exploit the niche space and providing more windows for new species to invade (Davis et al. 2000).

Propagule Pressure. Whether or not a plant community is actually invaded by a nonresident species also depends on the arrival of propagules of that species at a time when resources are available for its establishment. Studies have shown that community resistance to invasion can be overwhelmed if propagule pressure from the invasive species is sufficiently high (e.g., von Holle and Simberloff 2005). This is a common phenomenon in the semiarid West, where intact plant communities with high resistance to invasion are eventually invaded by downy brome at some level regardless of their resistance, presumably because of the enormous propagule pressure from adjacent landscapes dominated by this weed.

Sagebrush Steppe Restoration. Pre-invasion landscapes in the semiarid West were characterized by perennial plant communities consisting of a shifting mosaic of shrubs, grasses, and forbs. Our long-term goal is to learn how to recreate native shrub–grassland plant communities that are resistant to reinvasion by exotic species, particularly annual grasses. For this study, we chose a site that had characteristics similar to a site in Rock Canyon near Provo, Utah, where we have been engaged in an intensive volunteer ecological restoration effort using transplant stock for over a decade (Peterson et al. 2004). In this experimental study, we used transplant stock to create replicated plots containing six combinations of native species at two densities and permitted them to establish for 2 yr. We then challenged these plant community plots with seed additions of three species of exotic annual grass that had been problematic in the Rock Canyon restoration effort [downy brome, jointed goatgrass (*Aegilops cylindrica* Host), and cereal rye (*Secale cereale* L.)], then quantified invasion success over 3 yr. Our objective was to develop best practices for restoration planting design by exploring four alternative hypotheses: (1) plant communities established at initially higher density will be more resistant to invasion, (2) plant communities comprised of native cool-season bunchgrasses, which are functionally more similar to annual grass weeds, will be more resistant to invasion, (3) herbaceous plant communities with higher species and functional diversity will be more resistant to invasion than herbaceous plant communities with lower species and functional diversity, and (4) more structurally complex communities that include shrubs will be more resistant to invasion than less structurally complex herbaceous communities.

Materials and Methods

Research Site. The experiment was conducted on a foothill shrub steppe site at the Brigham Young University Research Farm, Spanish Fork, Utah (elevation 1,500 m). Soil was a fine-loamy, calcareous Typic Calcixerol (Welby-Hillfield silt loam), with a pH of 7.3 to 7.7 and high water-holding capacity and fertility (Table 1). The study site had a southwest-facing slope of approximately 4%. Long-term weather records from a station located 1.5 km from the site indicate mean annual precipitation (100-yr average) of 49 cm, of which approximately 30% is from winter snowfall (Figure 1; Western Region Climate Center 2005). The study site had been previously planted to irrigated pasture dominated by perennial ryegrass (*Lolium perenne* L.).

Experimental Design. We arranged the experiment in a split-plot design with six block replications. The main plot factors were six restored community species combinations and two densities, for a total of twelve main plots per block and 72 main plots in the experiment. The subplot factor was seeded annual grass, with downy brome, jointed goatgrass, and cereal rye as seeding treatments along with a fourth control treatment with no seeded annual grass. This resulted in a total of 288 subplots in the experiment. Main plots were assigned randomly within blocks and subplots were assigned randomly within main plots. Each block measured 24 by 18 m (80 by 60 ft) and consisted of twelve 6 by 6 m main plots. Each main plot was subdivided into four 3 by 3 m subplots.

The six restored community species combinations consisted of two native bunchgrass monocultures, a mixture of the two bunchgrasses, grass mixture plus forbs, grass mixture plus shrubs, and grass mixture plus forbs plus

Table 1. Soil properties at the Spanish Fork Farm experimental restoration site in north central Utah. Analyses performed using standard protocols at the Brigham Young University Plant and Soil Analysis Laboratory, Provo, Utah.

	Soil horizon (depth in cm)					
Soil property	Ap (0–8)	Ap2 (8–23)	A (23–30)	AB (30–38)	B (38–71)	CB (71–178)
Texture						
% Sand	53.08	51.44	51.19	49.54	58.12	46.36
% Silt	25.21	25.15	24.43	24.08	19.74	27.42
% Clay	24.41	23.41	24.38	26.28	22.14	26.17
Bulk density	1.82	1.75	1.82	1.68	1.78	1.57
Calcium carbonate equiv. %	8.3	9.1	7.6	25.9	31.9	30.2
% water content at −15 bars	15.20	16.04	13.88	14.63	14.47	13.91
pH (saturated paste)	7.69	7.25	7.45	7.50	7.58	7.40
Electrical conductivity	0.56	2.25	0.53	0.40	0.32	0.56
Organic matter %	3.72	1.63	1.20	1.08	1.34	0.65
Cation exchange capacity	19.2	17.6	16.0	18.3	21.5	13.2
P (ppm)	39.6	18.6	9.2	3.7	2.2	1.6
Nitrate (ppm)	13.7	69.1	25.9	20.8	29.2	50.5
K (ppm)	630	592	259	198	112	99

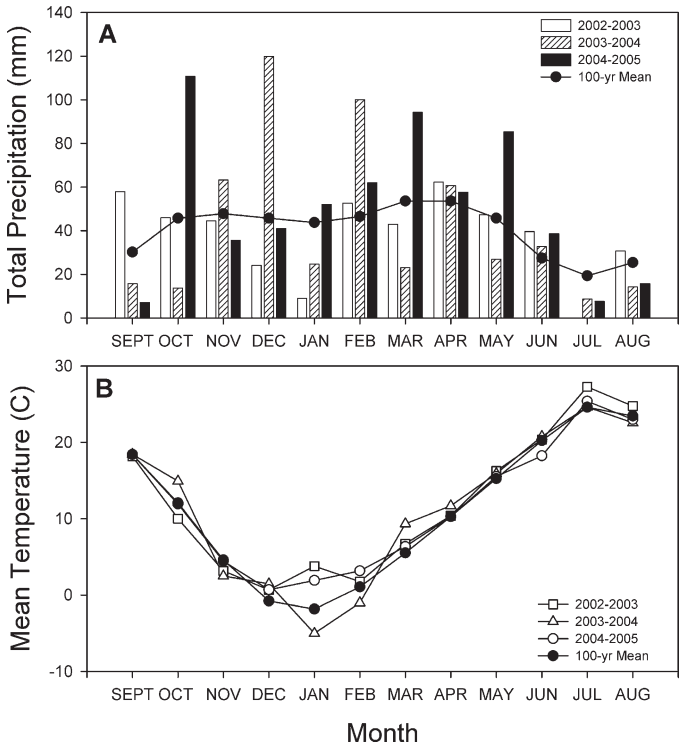

Figure 1. Mean monthly precipitation (A) and temperature (B) for the growing season year (September to August) at the Spanish Fork Powerhouse NOAA reporting station: long-term mean and growing season years during the course of the study (2002 to 2005).

shrubs. The experiment had a numerical replacement design, so that within each density treatment the total number of transplants was constant. In the low-density treatments, plant spacing was 53 cm (20 in) with a total of 111 plants per plot (3.6 plants m^{-2}). In the high-density treatments, plant spacing was 43 cm with a total of 196 plants per plot (5.4 plants m^{-2}). The two grass species were bottlebrush squirreltail and bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Á. Löve]. Four forb species were included: Lewis flax (*Linum lewisii* Pursh), gooseberryleaf globemallow [*Sphaeralcea grossulariifolia* (Hook. and Arn.) Rydb.], Utah sweetvetch (*Hedysarum boreale* Nutt.), and hairy goldenaster [*Heterotheca villosa* (Pursh) Shinners]. The two shrub species were rubber rabbitbrush [*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird] and mountain big sagebrush [*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle].

The grass mixture plots were planted to the two bunchgrasses at equal densities, while in the forb plots the forbs (four species in equal numbers) made up half of the total with the two bunchgrasses at equal densities making up the other half. In the shrub plus grass plots, half the grasses were replaced by the two shrub species at equal densities, while in the shrub plus grass plus forb plots the grass density was kept constant at half the plants, while the remaining half was divided evenly among the four forb and two shrub species. The shrubs were therefore planted at 3x greater density in the shrub plus grass plots relative to the shrub plus grass plus forb plots, while the grass densities were kept constant across the two shrub treatments. Within each multi-species plot the planting array featured regular alternation so that each species was distributed evenly throughout the plot.

Transplant Production and Field Plot Establishment. Existing vegetation in the study installation area was removed through application of glyphosate herbicide in April 2001. The area was not tilled or otherwise physically disturbed prior to planting. A wire fence 2.4 m high was erected around the study site to prevent foraging by mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*). The fence did not prevent occasional foraging by smaller mammals, especially voles (*Microtus* spp.) and deer mice (*Peromyscus maniculatus*).

Transplants were grown from locally collected seeds of each native species in the winter of 2000 to 2001 under greenhouse conditions in root-trainers (Spencer-Lemaire, Edmonton, Canada) containing a medium consisting of a 2 : 2 : 1 : 1 (volume) mixture of sieved peat, vermiculite, fine-grade Turface® montmorillonite clay and #16 quartz silica sand. A complete fertilizer formula was added during mixing (Meyer, unpublished data), and each batch of medium was steam-treated at 60 C (140 F) for 45 min. The production schedule (12 to 20 wk) was timed so that transplant roots of each species had just filled the containers at the time of transplanting. Transplants were hardened by placing them outdoors for 3 to 14 d before transplanting into the study site.

Transplanting and watering in of a total of 11,412 plants was completed during late April to early May 2001. Plots were then hand-weeded as needed and irrigated twice during the 2001 growing season, and any transplants that died ($< 10\%$) were replaced through the spring of 2002. During the spring and summer of 2002, plots were weeded but not irrigated. Survival at initiation of the seeding experiment in September 2002 exceeded 90%.

Experimental Protocol 2002 to 2003. Mature seeds of the annual weedy grasses (downy brome, jointed goatgrass, and cereal rye) were collected during the summer of 2002 from populations located within 1 km (0,62 mi) of the field site. Seeds were cleaned and stored in the laboratory over the summer to ensure dormancy loss. On September 10 and 11, 2002, seeds of each grass weed were hand-broadcast-seeded into their respective subplots at a rate of 80 seeds m^{-2}.

The following spring, in May 2003, plant cover was determined for native species and for seeded and volunteer weeds in each of the 288 subplots. Shrub cover for planted individuals was estimated by measuring the widest crown length and width, and calculating a circular area from the average of these two measurements (projected crown area). For herbaceous plants and volunteer seedling shrubs, cover was estimated in each subplot using a multiple-hit point intercept method with ten-pin frames (Elzinga et al. 1998), with the condition that no plant species could be counted more than once per point. The outer 0.5 m of each subplot was also avoided to minimize edge effects from surrounding plots. Four pin frame placements were made in each subplot for a total of 40 points per subplot (i.e., 160 points per plot). Forty points per subplot was large enough to detect the level of differences we were interested in.

All individuals of the seeded grass weeds were destructively harvested in June 2003. Harvest was timed to occur when seeds had reached maximum dry weight as indicated by inflorescence color changes. Above-ground annual grass weed biomass, seed biomass and seed number were estimated for each of the 216 seeded subplots. From near the center of each subplot, a 1 m^2 frame was lowered and all seeds harvested by clipping seed heads. All above-ground target grass weed vegetative biomass was then collected from the same 1 m^2 sample area, and seed head and vegetative biomass weights were determined separately. Samples were weighed fresh, dried in a hot greenhouse (approximately 50 C) for at least one week, then reweighed to determine the relationship between fresh and dry biomass. Subsamples of seed heads were quantified and the relationships between seed weight, seed number, and total plant biomass were estimated by linear regression for each annual grass weed species. For the remainder of each subplot, all above-ground target annual grass weed biomass was harvested and weighed fresh. Seed number, seed dry biomass, and total dry biomass per plot were then estimated using equations developed for each species from data based on the 1 m^2 sample plots.

Experimental Protocol 2004 to 2005. Our intention for the second year of data collection (2004 to 2005) was to repeat the weed addition experiment carried out the first year, with the same native plant communities and the same seeding rates of annual grass weeds. Survival of native herbaceous species was therefore evaluated in April 2004 and any plants that had died were reestablished by planting and watering in transplants produced during winter 2003 to 2004 for this purpose. Transplanting took place in May 2004. To minimize shrub growth into adjacent plots as well as competition with replacement herbaceous plants, we also pruned shrubs with a diameter > 1 m by removing four exterior stems. Approximately 10% of shrubs were pruned, and these were primarily in the two blocks located at the upper end of the slope.

Based on observations in spring 2004, we determined that adequate densities of annual grass weed seeds would already be present in their respective subplots in the fall as a result of plants produced in 2004 from seeds that inadvertently escaped harvest in 2003. We therefore chose not to add additional grass weed seeds to the subplots in fall 2004. Grass weed seed densities were not quantified and were not identical to those in the original planting, but were of approximately the same order of magnitude. It was clear from the spring 2004 observations that each annual grass weed was still almost completely confined to its originally seeded plots.

We then measured plant cover in May 2005 as described earlier. Cover of herbaceous plants and any seedling shrubs was determined using pin frames as in 2003, except that only three frame placements were made in each subplot for a total of 30 points. This was again sufficient sampling to detect meaningful treatment differences. Shrub cover was determined by measuring projected crown area as previously described.

Statistical Analysis. Experimental data were analyzed according to the split plot design using the SAS Proc Mixed procedure (SAS Institute, Cary, NC). The main plots were arrayed in a randomized block design with block as the random effect and restored community and planting density as fixed main effects, while grass weed treatment was included as a subplot fixed main effect. Response variables for the first year included annual grass weed total dry biomass, seed biomass, seed number m^{-2} and percent cover. Data for annual grass weed species were analyzed using the subset of plots into which each was seeded. We also analyzed absolute percent cover of other weeds (summed across all species), as well as total percent cover for all native herbaceous species combined and for shrubs combined. We included native plant community, planting density and annual grass weed treatment as main effects; in this case the unseeded control was included in the analysis. We analyzed the first and third year cover data sets separately because of possible differences in annual grass seeding rates. Proportional (percentage) variables were arcsine square root transformed to meet the assumptions of analysis of variance. Differences among least squares means were compared among treatments and treatment combinations (i.e., for significant treatment interactions) based on *a priori* planned comparisons.

Results and Discussion

Weather Patterns. Prolonged rainfall that began almost immediately after weeds were seeded in September 2002 produced ideal conditions for weed seedling establishment. Total precipitation for September was nearly twice the 100-yr mean (Figure 1). The winter in 2002 to 2003 was several degrees warmer than average and had precipitation well below average in December and January, resulting in very light snow cover. Weed seedlings experienced unusually favorable conditions for vigorous growth through much of the winter, and also received adequate precipitation for growth through the spring. In short, weather conditions were excellent for growth of annual grass weeds, other weed seedlings that emerged from the seed bank and for the cool-season native species included in the experiment. While not quantified, we noted that the annual grass weeds were much taller than typically observed, with cereal rye reaching $>$ 2 m in height.

Weather during the 2003 to 2004 growing year, when any residual grass weed seeds that escaped harvest in 2003 were establishing and producing seeds, was in sharp contrast to the previous year (Figure 1). There was insufficient precipitation for autumn emergence, and the winter was both colder than usual and exceptionally snowy because of a series of heavy storms in December and February. This delayed most grass weed emergence until April, and resulted in far lower emergence, survival, and fecundity than observed the previous year.

The autumn of 2004 was again favorable for autumn establishment of weedy annual grasses, although significant autumn precipitation inputs began a few weeks later than in 2002 (Figure 1). October precipitation was nearly triple the long-term mean, and the winter was again warmer than average, though monthly precipitation was near average through the winter months and snow cover was more persistent than in 2002 to 2003. The spring was exceptionally wet; rainfall totals in both March and May were far above average. This resulted in another above-average year for grass weed recruitment and seed production, though not as favorable as 2002 to 2003.

Native Species Cover Trends. The highest native plant cover by far was recorded in restored communities that contained shrubs, and much of this cover was contributed by the shrubs (Figure 2). Planting density had no significant effect on herbaceous cover. Plants grew more quickly at low density, resulting in similar cover values across densities. For shrubs, cover was significantly greater at higher density. Herbaceous cover declined from 2003 to 2005, though this effect varied by restored community type. Grass communities that included bluebunch wheatgrass showed little or no decline. In contrast, shrub cover continued to increase from 2003 to 2005. By spring 2005, shrub canopy cover measured as projected crown area in the high density plots exceeded a value of 1 (i.e., 100%), indicating that the canopies were effectively closed.

Herbaceous cover in both the grass plus forb and the squirreltail monoculture community types dropped precipitously from 2003 to 2005. This decline was largely because of high mortality of squirreltail (93%) and several of the forb species, most notably Lewis flax (overall forb mortality was 64%). Squirreltail and Lewis flax plants produced seeds in abundance in 2003, and these plants had also shown high seed production in 2002, the spring prior to introduction of annual grass weeds. Mortality therefore took place after two cycles of very high seed production, and could have been related to a tradeoff between reproduction and survival in these early seral species (Kozlowski 1992). All herbaceous species that died were replanted in spring 2004, but these new plants were small in size and apparently did not compensate for mortality of larger plants. Native herbaceous cover in restored communities

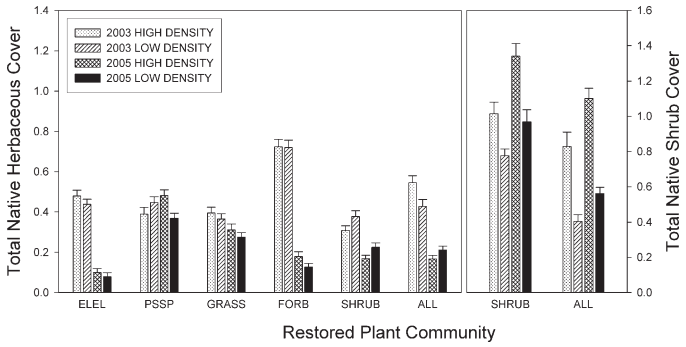

Figure 2. Total canopy cover of native species averaged across grass weed seeding treatments as a function of restored community type and planting density for 2003 and 2005. Restored community types are as follows: ELEL, squirreltail monoculture; PSSP, bluebunch wheatgrass monoculture; GRASS, squirreltail plus bluebunch wheatgrass; FORB, squirreltail plus bluebunch wheatgrass plus forb species; SHRUB, squirreltail plus bluebunch wheatgrass plus shrub species; and ALL, squirreltail plus bluebunch wheatgrass plus forb and shrub species. Error bars = standard error of the mean. 2003: Herbaceous cover: restored community main effect, d.f. = 5, 30, F = 6.95, P = 0.0002; density main effect d.f. = 1, 30, F = 0.14, n.s. Shrub cover (in restored communities that included shrubs): restored community main effect, d.f. = 1, 5, F = 26.16, P = 0.0037; density main effect d.f. = 1, 5, F = 18.21, P = 0.0080. 2005: Herbaceous cover: restored community main effect, d.f. = 5, 50, F = 21.15, P < 0.0001; density main effect, d.f. = 1.10, F = 0.53, n.s. Shrub cover (in restored communities that included shrubs): restored community main effect, d.f. = 1, 75, F = 33.38, P < 0.0001; density main effect d.f. = 1, 75, F = 67.66, P < 0.0001.

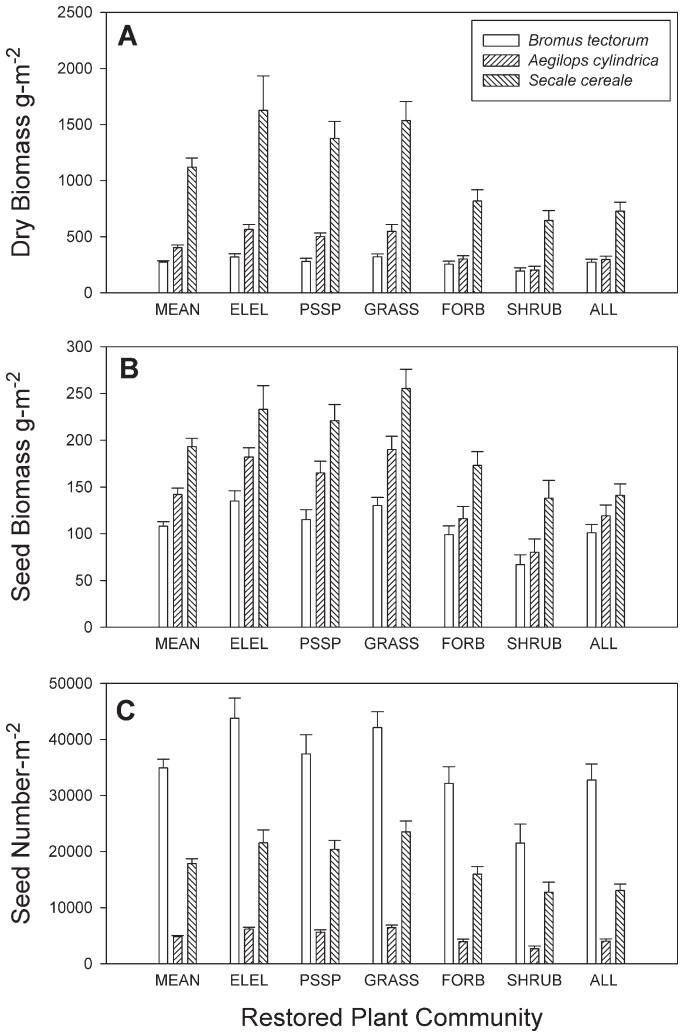

Figure 3. Mean 2003 yield data for each of three annual grass weeds (SECE, *Secale cereale*, cereal rye; AECY, *Aegilops cylindrica,* jointed goatgrass; BTEC, *Bromus tectorum,* downy brome) seeded into six restored communities. Restored community types are as follows: ELEL, squirreltail monoculture; PSSP, bluebunch wheatgrass monoculture; GRASS, squirreltail plus bluebunch wheatgrass; FORB, squirreltail plus bluebunch wheatgrass plus forb species; SHRUB, squirreltail plus bluebunch wheatgrass plus shrub species; and ALL, squirreltail plus bluebunch wheatgrass plus forb and shrub species. Error bars = standard error of the mean. (A) total dry biomass m^{-2} (grass weed main effect: d.f. = 2, 120, F = 18.74, P < 0.0001; restored community main effect: d.f .= 5, 25, F = 241.9, P < 0.0001; grass weed by restored community interaction: d. f. = 10, 120, F = 2.13, P = 0 .0268), (B) seed biomass m^{-2} (grass weed main effect: d.f .= 2, 120, F = 52.61, P < 0.0001; restored community main effect: d.f .= 5, 25, F = 15.58, P < 0.0001), and (3) seed number m^{-2} (grass weed main effect: d.f .= 2, 120, F = 639.1, P < 0.0001; restored community main effect: d.f .= 2, 25, F = 15.58, P < 0.0001).

that included shrubs was also much lower in 2005 than in 2003, possibly because of increased competition as the shrub canopies began to close.

Seeding annual grass weeds negatively impacted native herbaceous cover and survival but did not substantially impact shrub cover or survival relative to unseeded controls (data not shown). Cereal rye and jointed goatgrass had significantly stronger negative impacts than did downy brome. These impacts could not explain the high mortality of some of the herbaceous species, however, as mortality was as high in unseeded plots as in plots seeded to annual grass weeds.

Annual Grass Weed Performance. Measures of annual grass weed performance in 2003 indicated that all three of these weeds were highly successful in the restoration planting regardless of planting density or native species composition. Biomass production in 2003 differed significantly among annual grass weeds in the order cereal rye > jointed goatgrass > downy brome (Figure 3a), and this

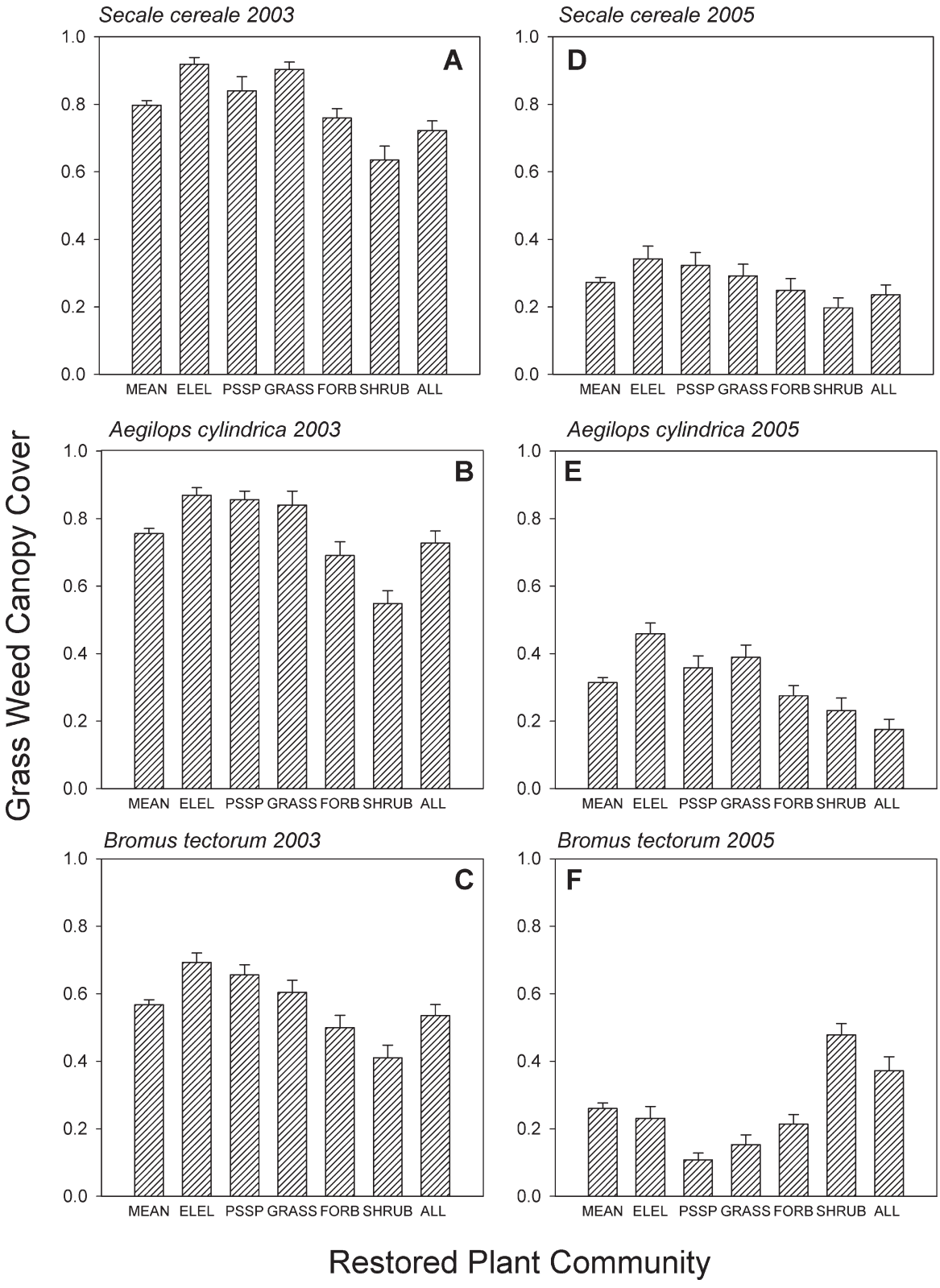

Figure 4. Canopy cover for three annual grass weeds as a function of restored community composition for 2003 and 2005. Data include means across all treatments and restored community types as follows: ELEL, squirreltail monoculture; PSSP, bluebunch wheatgrass monoculture; GRASS, squirreltail plus bluebunch wheatgrass; FORB, squirreltail plus bluebunch wheatgrass plus forb species; SHRUB, squirreltail plus bluebunch wheatgrass plus shrub species; and ALL, squirreltail plus bluebunch wheatgrass plus forb

same pattern was evident in seed biomass. These differences, though significant, were less dramatic (Figure 3b). However, downy brome produced an estimated 36,000 seeds m^{-2}, which was approximately twice as many as cereal rye and seven times as many as goatgrass (Figure 3c). This was because the average weight of a downy brome seed was only 3.1 mg (0.00011 oz), whereas cereal rye seeds averaged 10.8 mg and goatgrass seed units (which may contain 1 to 3 seeds) averaged 29.5 mg. Seed production for downy brome in 2003 was similar to seed production reported in monospecific stands (Smith et al. 2008).

Total grass weed dry biomass, seed biomass, and seed number in 2003 differed significantly among restored community types and showed similar patterns across weed species (Figure 3). The highest grass weed productivity was seen in the native grass community types. While differences among grass community types were not statistically significant, there was a consistent trend for reduced weed productivity in the bluebunch wheatgrass monoculture relative to grass communities that included squirreltail. Grass plus forb and grass plus forb plus shrub restored community types resulted in significantly lower grass weed total biomass, seed biomass, and seed numbers relative to native grass-only communities. However, the greatest reduction for these three variables was observed in the grass plus shrub community type, where all three measurements of weed productivity were reduced approximately by half relative to the all-grass communities (Figure 3). Weed seed production in the most weed-suppressive restored community (high density grass plus shrub) was decreased an average of 57% relative to the least weed-suppressive native community (low density squirreltail; mean 10,739 vs. 25,056 seeds m^{-2}). Total biomass for both cereal rye and goatgrass was reduced more than downy brome in the communities that included forbs and shrubs relative to the grass communities (Figure 3a). This interaction was not significant for total seed mass or seed number (Figure 3b, c). Native planting density had a marginally significant effect on grass weed productivity, with lower productivity at higher planting densities (21% decrease in total biomass m^{-2}: d.f. = 1, 5, F = 6.85, P = 0.0472; 13% decrease in seed number m^{-2}; d.f. = 1, 5, F = 6.42, P = 0.0524).

Canopy cover for annual grass weeds in 2003 exhibited the same patterns observed for other measures of weed productivity (Figure 4). Grass-only restored communities had the highest grass weed cover and the grass plus shrub community type had the lowest. Cereal rye and goatgrass produced maximum canopy cover values near 0.9 in 2003, while maximum values for downy brome did not exceed 0.7. Estimates of number of seeds produced m^{-2} in 2003 for each grass weed were significantly correlated with cover estimates at the restored community level (cereal rye: d.f. = 10, R^2 = 0.799, P < 0.0001; goatgrass: d.f. = 10, R^2 = 0.747, P < 0.0002; downy brome: d.f. = 10, R^2 = 0.738, P < 0.0004), showing that cover is a reasonable measurement surrogate for both biomass and seed production in these species.

Cover values for annual grass weeds were greatly reduced in 2005 relative to 2003, with an average reduction of 0.6 (Figure 4). Downy brome cover overall was again lower than cover for the other two species, but the difference among species was much less pronounced than in 2003. For cereal rye and goatgrass the pattern of lower canopy cover in the higher-diversity restored communities observed in 2003 was maintained, though the differences were not as strong and were not even significant for cereal rye. However, downy brome cover in 2005 was highest in the restored communities that contained shrubs, particularly the grass plus shrubs community, where downy brome cover values were as high as those observed in 2003 and were twice as high as 2005 cover values for cereal rye and goatgrass in this community. For downy brome, the differences in cover among restored community types were stronger in 2005 than in 2003 and actually showed a reversal, with the lowest cover values in grass-only community types and the highest values in community types with shrubs.

Annual grass weed cover did not vary significantly as a function of initial restoration planting density in either year, with two exceptions. In 2005 but not in 2003, cereal rye cover was lower on average in the high-density plantings (density main effect: 23.4 vs. 31.2%; d.f. = 1, 173, F = 11.72, P = 0.0009). Also in 2005 but not in 2003, downy brome cover was higher in the high-density community types that included shrubs and forbs, but lower in the high density grass-only community types (density by

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and shrub species. (A) *Secale cereale* (cereal rye) (B) *Aegilops cylindrica* (jointed goatgrass) and (C) *Bromus tectorum* (downy brome). Error bars = standard error of the mean. 2003: downy brome: restored community main effect: d.f. = 5, 26, F 7.51, P = 0.0002; goatgrass: restored community main effect: d.f. = 5, 25, F = 5.90, P = 0.0010; cereal rye: restored community main effect: d.f. = 5, 26, F = 6.97, P = 0.0003. 2005: downy brome: restored community main effect: d.f. = 5, 27, F = 12.21, P < 0.0001; goatgrass: restored community main effect: d.f. = 5, 25, F = 5.29, P = 0.0019; cereal rye: restored community main effect: d.f. = 5, 25, F = 0.93, n.s.

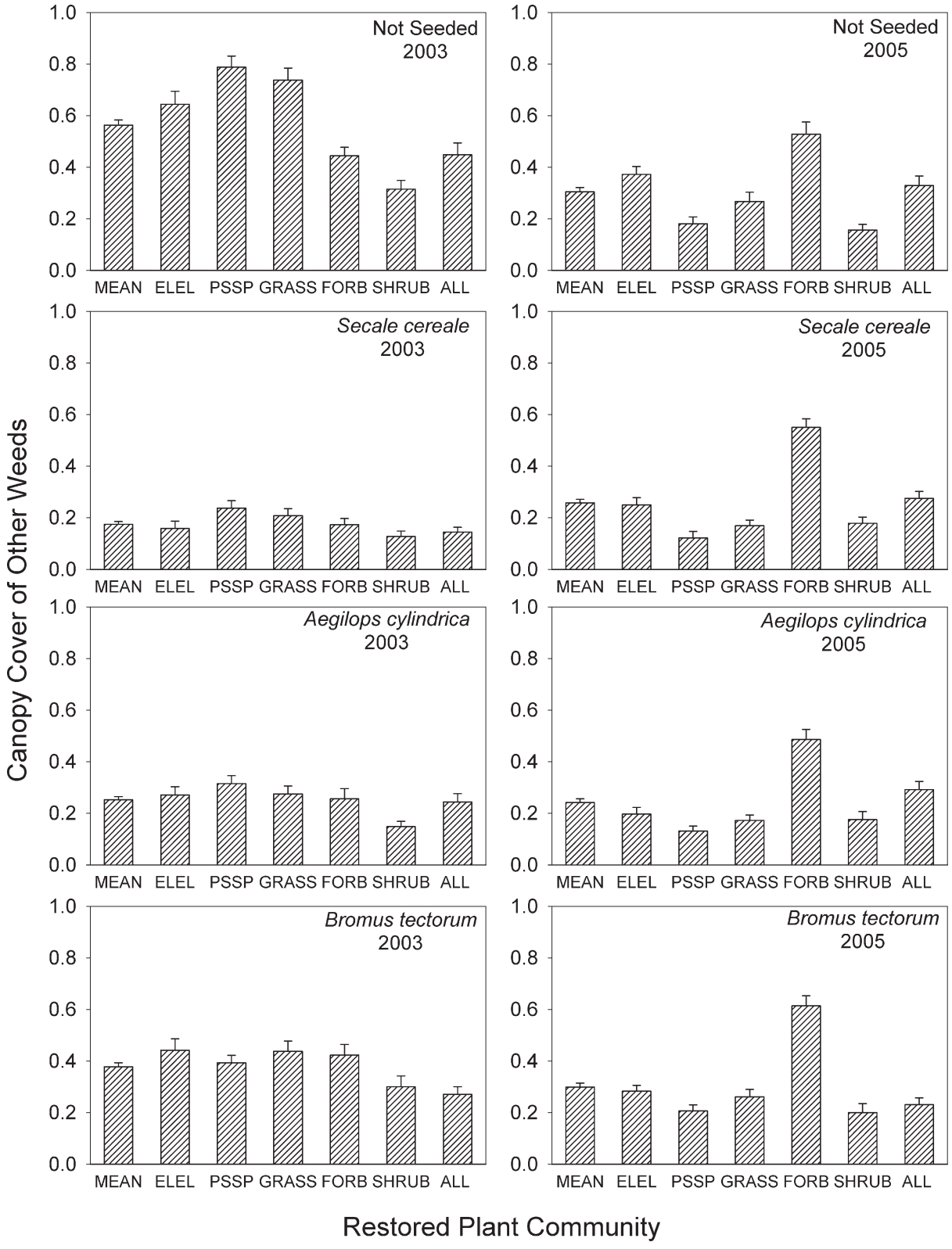

Figure 5. Canopy cover of weeds other than the three seeded annual grasses in 2003 and 2005 as a function of grass weed seeding treatment ("Not Seeded" = no invasive grass seeds added to subplot) and restored community type. Restored community types are: ELEL, squirreltail monoculture; PSSP, bluebunch wheatgrass monoculture; GRASS, squirreltail plus bluebunch wheatgrass; FORB, squirreltail plus bluebunch wheatgrass plus forb species; SHRUB, squirreltail plus bluebunch wheatgrass plus shrub species; and ALL,

restored community interaction: d.f. = 5, 168, F = 2.76, P = 0.0201).

Impact of Annual Grass Weeds and Restored Communities on Other Weeds. In addition to the target annual grass weeds seeded into native plant restored communities, we observed 21 annual or perennial herbaceous, mostly dicot weeds while taking cover data. While the majority of these other weeds were encountered relatively infrequently, four species, prickly lettuce (*Lactuca serriola* L.), tumble mustard (*Sisymbrium altissimum* L.), cheeseweed (*Malva neglecta* Wallr.) and shepherds' purse [*Capsella bursa-pastoris* (L.) Medik.], were encountered regularly. In 2003, control subplots (i.e., those not seeded to any of the annual grass weeds) had an average cover of other weeds of 0.56 (Figure 5). Other weed cover was progressively lower in subplots seeded to downy brome, goatgrass and cereal rye, respectively, which illustrates the ability of vigorous stands of annual grass weeds to suppress dicot weeds. In 2005, canopy cover of other weeds was greatly reduced (ranging from 0.25 to 0.3), with no strong suppressive effect of the annual grasses.

Restored community type also influenced canopy cover of other weeds. In both 2003 and 2005 there was significant reduction in cover of other weeds in the shrub plus grass community type relative to all-grass community types, particularly in the unseeded subplots. This restored community effect was similar to that observed for seeded grass weeds. But in contrast to the result for seeded grass weeds, other weeds reached maximum 2005 cover values in the grass plus forb community type and showed a sharp increase from 2003 to 2005 in this community type. This was especially pronounced in the seeded subplots, where annual grasses were less competitive than in 2003. Cover of other weeds generally showed a decrease from 2003 to 2005, but in the grass plus forb community type, apparent release from annual grass competition in 2005 resulted in other weeds reaching levels as high as or higher than the 2003 levels for unseeded subplots. Another possible explanation for this success is that the plots formerly planted with high densities of forbs exhibited a legacy effect that was positive for dicot weeds (Kardol et al. 2007). In contrast to these large effects of restored community type, there were no significant effects of planting density on cover of other weeds in either year.

Productivity, Disturbance, and Fluctuating Resource Effects. We obtained clear tests of our initial hypotheses, but the outcome of these tests must be interpreted in the context of specific conditions at the experimental site during the course of our study. We found that increasing initial restoration planting density by a factor of 1.75 had only a marginally significant effect on grass weed biomass and seed production and no effect on annual grass weed cover in 2003. In general it was not possible to prevent or even substantially reduce invasion by increasing restoration planting density.

The hypothesis that restored communities comprised of a functional group similar to the annual grass weed functional group (i.e. perennial grasses) would result in reduced invasion was strongly refuted in 2003. Grass-only restored communities had much higher levels of invasion than restored communities that also contained forbs and/or shrubs. Conversely, the hypothesis that higher species and functional group diversity in herbaceous communities would reduce invasion was supported in 2003; the grass plus forb community type was significantly less invaded than any of the all-grass community types. The hypothesis that structurally more complex communities that included foundation shrub species would be the most resistant to invasion was also supported for all three annual grass species in 2003.

In 2005, annual grass weeds were much less productive overall. We speculate this was because of the weather patterns that year, which included heavy winter snow cover that did not allow the winter growth observed in 2003. There was little evidence to credit increased competitive effects to restored communities for reduced annual grass production in 2005 except in the communities that included shrubs, which increased in canopy cover over the 2-yr period. Two of the herbaceous community types had significantly reduced perennial cover in 2005 and none had increased cover that would indicate higher competition from native species.

For cereal rye and jointed goatgrass, the overall pattern of reduced invasion with higher functional and structural diversity in the restored community was still evident. For downy brome, results in 2005 were reversed relative to 2003, with highest invasion in restored communities that included shrubs and lowest invasion in the bluebunch

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squirreltail plus bluebunch wheatgrass plus forb and shrub species. Error bars = standard error of the mean. 2003: Grass weed main effect: d.f. = 3, 1069, F = 169.8, P < 0.0001; restored community main effect: d.f. = 5, 25.6, F = 5.21, P < 0.0020; restored community by grass weed interaction: d.f. = 15, 1069, F = 6.10, P < 0.0001. 2005: Grass weed main effect: d.f. = 3, 784, F = 6.87, P = 0.0001; restored community main effect: d.f. = 5, 25, F = 30.98, P < 0.0001; restored community by grass weed interaction: d.f. = 15, 784, F = 2.16, P < 0.0064.

wheatgrass monoculture. Positive associations of downy brome with shrub canopies have been previously observed in both xeric and more mesic ecosystems (Griffith 2010; Meyer et al. 2001), but so have negative associations (Chambers et al. 2007, Prevey et al. 2010). Higher success of downy brome in restored communities containing shrubs the second year may also be partly because of the fact that these communities presented markedly reduced competition from the native understory.

The hallmark feature of the 2002 to 2003 season at our site was highly favorable conditions, with precipitation and temperature supporting a growing season that extended through fall, winter, and spring. This, coupled with nutrient levels related to the past history of agricultural use on this site, likely contributed to a scenario where resources were incompletely utilized and invisibility was favored (Davis et al. 2000). This interpretation is supported by soil test data (Table 1), where relatively high soil nutrient levels apparently resulted from the past history of chemical fertilization on this site. Thus, we conclude that the conditions of our study were probably close to ideal for annual grass weed invasion.

Sites in the process of ecological restoration are inevitably disturbed, and native plant communities in the early stages of development will not be able to fully exploit available resources and will leave openings for weed invasion. This disturbance could be less problematic in restoration of less productive sagebrush steppe sites, where lower levels of soil resources are more intrinsically limiting. Under soil-resource-limited conditions, our hypothesis that increased density will result in plant communities more resistant to invasion by annual grasses may be supported as has been observed in earlier studies (Booth et al. 2003; McClendon and Redente 1992; Stevens 1997).

Before conducting the study reported herein, we initiated an ongoing restoration project at Rock Canyon (Peterson et al. 2004). The Rock Canyon site is similar to the Spanish Fork Farm experimental site in several ways, including relatively high fertility, which at Rock Canyon was because of past agricultural use for the production of alfalfa hay. In both locations, including foundation shrub species early in the restoration process, as well as incorporating a diversity of herbaceous species, led to plant communities more resistant to invasion by annual grass weeds during the early years of establishment. However, it is also clear that propagule pressure must be reduced in order for the restoration to succeed. Because even moderate levels of downy brome can contribute to increased fire frequency, this could be a continued concern. We believe reduced levels of annual grass seeds will benefit similar restoration efforts. From our experience in nearby Rock Canyon, we learned that at least an 18-mo period of management of *in situ* annual grass weed populations prior to the initiation of restoration planting, with at least 2 yr of follow-up control, was necessary for restoration success (Allen, unpublished data; Peterson et al 2004). Complete reliance on transplants to suppress annual grass weeds under the conditions of this study did not result in successful community establishment. The hope is that, with time and the absence of continued disturbance, these restored communities will be able to sequester sufficient resources to reduce annual grass weed abundance to tolerable levels without the need for ongoing control.

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