The Mark of Zorro: Effects of the Exotic Annual Grass *Vulpia myuros* on California Native Perennial Grasses

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Abstract

Native perennial grasses were once common in California prairies that are now dominated by annual grasses introduced from Europe. Competition from exotics may be a principal impediment to reestablishment of native perennial grasses. Introduced annual grasses, such as *Vulpia myuros* (zorro fescue), are often included with native perennial species in revegetation seed mixtures used in California. To examine the potential suppressive effect of this graminoid, we evaluated the growth and performance of a mixture of California native perennial grasses and resident weeds when grown with varying densities of *V. myuros*. The annual fescue exhibited a strongly plastic growth response to plant density, producing similar amounts of above-ground biomass at all seeding densities. Perennial grass seedling survival and above-ground biomass decreased and individuals became thinner (i.e., reduced weight-to-height ratio) with increasing *V. myuros* seeding density. *V. myuros* also significantly suppressed above-ground biomass and densities of weeds and had a more negative effect on weed densities than on native perennial grass densities. Biomass of native grasses and weeds was not differentially affected by increasing densities of *V. myuros*. Overall, because *V. myuros* significantly reduced the survival and performance of the mixture of native perennial grasses and this effect increased with increasing *V. myuros* density, we conclude that including this exotic annual in native seed mixtures is counterproductive to restoration efforts.

Key words: *Nassella pulchra, Hordeum brachyantherum* **ssp.** *brachyantherum, Elymus glaucus, Melica californica, Nassella cernua, Poa secunda* **ssp.** *secunda, Vulpia myuros*, **California prairie restoration, California native perennial grasses, competition.**

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Introduction

Native perennial grasses were once a major component of the grasslands of California (Clements 1934; Beetle 1947; Burcham 1957; Heady 1988). These grasslands became dominated by non-native annual species with the introduction of annual grasses from the Mediterranean region, changes in disturbance patterns owing to human activity (Heady 1988), and drought (Burcham 1957).

Although competition from annual grasses can negatively impact perennial grass establishment (Bartolome & Gemmill 1981; Dyer et al. 1996; Dyer & Rice 1997), native perennial grasses have shown promise for ecosystem restoration, reduction of erosion, and weed control. Grasses have long been known to substantially reduce erosion and perennial grasses have been of special interest to soil conservationists for erosion control (Magette et al. 1989; Kemper et al. 1992; Aase & Pikul 1995; Dabney et al. 1995; Meyer et al. 1995; Daniels & Gilliam 1996; Dewald et al. 1996). Over the long term, perennial grasses may provide more consistent soil cover than annual grasses. Extreme fluctuations of annual grass populations (Talbot et al. 1939) may reduce their effectiveness in erosion control. In contrast, long-lived perennial grasses may be more consistent producers of biomass than annual grasses because of their life history, persistent root system, and ability to tap deep soil water sources once established (Holmes & Rice 1996).

In addition to soil erosion control benefits, California's native perennial grasses may be effective in suppressing weeds. Seedlings of some species of native perennial grasses, e.g., *Hordeum brachyantherum* ssp. *brachyantherum* (meadow barley) (Bugg et al., unpublished data) and *Koeleria cristata* (junegrass) (Borman et al. 1991), are competitive with annual grasses during their first year of growth. Once established, long-lived perennials are good competitors, persisting in plant communities for decades (White 1967). Bugg et al. (1997) showed that perennial grasses could be established in the Sacramento Valley of California on roadsides, and healthy stands of many species persisted into the fourth year after seeding. Although perennial grasses generally grow more slowly than annual grasses (Chapin 1980), they may be more effective in controlling weeds such as *Centaurea solstitialis* (yellow starthistle) that are dependent on residual summer soil moisture (Northam & Callihan 1988; Larson & McInnis 1989; Roché et al. 1994).

Perennial grasses are good competitors once established, but evidence from both field and greenhouse studies indicates that native perennial grasses have difficulty competing with introduced annual plants as seedlings (Bartolome & Gemmill 1981; Dyer et al. 1996; Dyer & Rice 1997; Dyer & Rice 1999). In California, seedlings of the perennial grass *Nassella pulchra* (purple needlegrass) often do not survive the rapid spring growth period typical of the Mediterranean annual grassland. In a study by Dyer et al. (1996) only 0.01% of *N. pulchra* seedlings that grew from seeds planted into an annual-dominated grassland survived to the fourth year. As further evidence for poor seedling survival, the density of this species did not increase over a 20-year period at Hopland Field Station in northern California (Bartolome & Gemmill 1981). Dyer and Rice (1999) showed that the growth of *N. pulchra* seedlings was reduced owing to competition with annuals for light during spring, which resulted in a reduction in the ability of the perennial to utilize water deep in the soil profile during the dry California summer. Container studies by Bartolome and Gemmill (1981) showed that both densities and growth of *N. pulchra* seedlings were reduced when they were grown with high densities of the introduced annual species *Bromus hordeaceus* (soft chess) and *Vulpia myuros* (zorro fescue). These findings were supported by results from a container study by Dremann (1989).

There is strong evidence that introduced annual grasses interfere with establishment and growth of native perennial grasses, yet annuals are often included with perennials in seed mixtures for revegetation. One rationale for this practice is that annuals typically have faster emergence rates (Bartolome & Gemmill 1981) and higher relative growth rates (Chapin 1980; Jackson & Roy 1986; Muller & Garnier 1990; Garnier 1992) resulting in more rapid protection of soil from erosion than perennial grasses. In addition, the competitive nature of the annuals may help to reduce the growth of resident weed species as suggested by the literature on annual grass cover crops (e.g., Konesky et al. 1989; Pérez & Ormeño-Núñez 1993; Bugg 1996).

Despite a great deal of evidence to the contrary, annual grasses may improve establishment and survival of perennial grasses. Annual grass cover crops have been reported to suppress weeds while increasing forage yields (Bendixen & Lanini 1994) and either not affecting (Smeda & Putnam 1988) or increasing strawberry yields (Newenhouse & Dana 1989). It has also been anecdotally suggested that annual grasses may serve as nurse plants for perennial seedlings. Several studies have shown that perennial plants can promote establishment of other species by protecting seedlings from intense sun, heat, herbivores, and frost (Muller 1953; Niering et al. 1963; Franco & Nobel 1989). It is possible that annual grasses may protect native perennial seedlings similarly under some conditions, although Mediterranean annual grasses were found to interfere with the establishment of *Artemisia californica* (California sagebrush) (Marquez & Allen 1996; Eliason & Allen 1997).

V. myuros (hereafter referred to as annual fescue) is one of the most common annual grasses included with native perennial grasses in seed mixtures in California. It has been thought to exert minimal competitive pressure on other species within the mixtures because its canopy is neither tall nor dense. However, its effects have not been tested experimentally under field conditions. The purpose of this experiment was to investigate whether the presence of annual fescue positively or negatively affected native perennial grass above-ground biomass, density, and seedling size. Increases in these performance measures would indicate that annual fescue acts as a nurse plant, promoting growth and establishment of the perennials; decreases would suggest competitive suppression of the perennials. We also evaluated the effects of annual fescue on the above-ground biomass and density of resident weeds (species that were not seeded), and assessed whether the weeds were affected relatively more strongly than native perennial grasses. This comparison allowed us to address the proposal that annual fescue might suppress weeds without negatively affecting native perennial species.

Methods

Experimental Design, Site Preparation, and Seeding

From the fall of 1993 through the spring of 1995, a randomized complete block experiment with four replicates and five treatment levels (20 plots in total) was conducted in Yolo County, California. The experiment was located in an agricultural field that had been planted in dryland wheat and then left fallow and untilled for several years before initiation of the experiment. The soil was predominantly Corning red gravelly loam (Typic Palexeralf). It is a well-drained, terrace soil, of capability class IV, that is suitable for dry-farmed grain or pasture (Andrews 1990). The Corning soil extractable nitrogen levels (Table 1) were comparable to those for soils of California annual grasslands (Gulmon 1979, Davidson et al. 1990), an unvegetated granitic road-cut slope in northern California (Claassen & Zasoski 1993), and a low nutrient grassland in Greece (Mamolos et al. 1995). According to soil analyses (A&L Laboratories, Fresno, CA), phosphorus levels were low

Table 1. Summary of soil nutrient analysis results for Corning soil; soils were taken from the west end of the area used for the experiment.

Sample Depth	*% Organic Matter*	*Available P (ppm)*	*K (ppm)*	*Mg (ppm)*	*Ca (ppm)*	*Na (ppm)*	*pH*	*C.E.C. (meq/100 g)*	*NO_3 (ppm)*	*S (ppm)*	*Zn (ppm)*	*Mn (ppm)*	*Fe (ppm)*	*Cu (ppm)*	*B (ppm)*	*Soluble Salts (mmhos/cm)*
0–10 cm	0.2	17	89	697	2,600	89	7	20.9	2	3	0.6	11	11	1.1	1.6	0.5
20–30 cm	0.8	35	202	515	3,220	35	7	21	9	8	2.2	17	24	0.9	2.2	0.2

for the 0–10-cm sample and high for the 20–30-cm sample, with a minimum of 20 ppm recommended for average crop production. Potassium levels were low for the 1–10-cm sample and medium for the 20–30-cm sample.

The eastern end of the field included a Marvin silty clay loam (Aquic Haploxeralf). It is not as well-drained as the Corning soil and is capability class II, which is suitable for row crops (Andrews 1990). These soils are typical of perennial grass revegetation sites, but are probably more fertile than roadside revegetation sites where hillsides have been cut away and topsoil has not been replaced. There was a fertility gradient between the two soil types and the experimental blocks were placed along the gradient to minimize the variation within blocks as much as possible given logistical constraints.

The field was ripped to a depth of about 60 to 90 cm, laser-leveled, disced, and cultivated. Beds 152 cm wide were created and the seed was planted on the top of the beds. The native perennial grass seed mixture was planted at one density consistent with current standard practice (Table 2) (J. Haynes, personal communication). The seed was mixed with equal proportions of rice hulls in order to achieve the desired final seeding density and to aid in even distribution. The mixture of native perennial grasses was planted on 21 November 1993 at the rates listed in Table 2, using a wildflower broadcast seeder (Truax Company, Inc., Minneapolis, MN) followed by a flexible chain harrow. On 24 November 1993 the annual fescue seed was planted into plots 3 m wide, spanning 2 beds previously seeded with the perennial grass mixture, and 6.1 m long at densities of 0.09, 0.46, 1.38, and 2.75 g/m^2 (Table 3). A treatment of the native grass seed mixture without annual fescue was included as a control. Plots were cultivated by hand immediately after the annual fescue seed was broadcast to incorporate it into the top layer of soil. The soil and weather were dry during the entire planting process so there was no possibility that initial germination of the perennial grasses could have preceded that of annual fescue.

Purity of seed was determined using methods of the Association of Official Seed Analysts (Wiesner 1989). Germination tests were conducted with 100 to 400 seeds of each species at room temperature. These estimates were used to calculate the pure live seed percentage (P.L.S.), the standard used for determining seeding densities in the revegetation industry [percent P.L.S. = (proportion of pure seed in the seed lot) × (proportion of germinable seed) × 100].

The climate at the study site is Mediterranean; rain falls during the cool winter months with little or no precipitation during the hot summer months. The experiment received ambient rainfall with no supplemental watering. The 30-year average annual precipitation for Davis, California (71.3 km southeast of the study site) for 1961–90 is 46.0 cm (Owenby & Ezell 1992). At the study site, 35.4 cm of precipitation were measured in 1994 and 78.3 cm in 1995; the distribution and amount of rainfall at the site was similar to Davis. Although the annual precipitation during 1994 was lower than the 30-year average for the area, 3.2 cm of rain fell during May in Davis, where the 30-year average for that month is 0.7 cm. This rain effectively lengthened the time that conditions were

Table 2. Seeding densities for species included in the native perennial grass mixture.*

	Perennial Grass		*Seeding Density*		
Common Name	*Scientific Name*	*Cultivar-Year Produced*	*P.L.S. lb/acre*	*P.L.S. g/m^2*	*P.L.S. seeds/m^2*
Blue wildrye	*Elymus glaucus*	Anderson 1993	2.5	0.28	77
Meadow barley	*Hordeum brachyantherum* ssp. *brachyantherum*	Cosumnes 1993	0.86	0.09	24
California melic	*Melica californica*	Winters 1993	2.25	0.25	145
Nodding needlegrass	*Nassella cernua*	Benicia 1993	2.06	0.23	97
Purple needlegrass	*Nassella pulchra*	Unknown 1993	4.42	0.49	71
Pine bluegrass	*Poa secunda* ssp. *secunda*	Fisk Creek 1993	0.58	0.07	48
		TOTAL	12.67	1.41	462

*Seeding densities were based on pure live seed (P.L.S.) estimates, a revegetation standard for estimating seeding densities. Percent P.L.S. = (proportion of pure seed in the seed lot) × (proportion of germinable seed) × 100. Nomenclature is according to Hickman 1993.

Table 3. *Vulpia myuros* seeding densities based on pure live seed (P.L.S.) estimates.*

Seeding Density		
lb/acre	*g/m²*	*seeds/m²*
0.82	0.09	139
4.18	0.46	710
12.54	1.38	2,129
25	2.75	4,243

*Percent P.L.S. = (proportion of pure seed in the seed lot) × (proportion of germinable seed) × 100.

favorable for plant growth in that temperatures were warm and soil was moist. Also, rainless periods were not longer than 14 days from December through February and did not appear to reduce survival of seeded species (C. S. Brown, unpublished data). In 1995 the annual rainfall was well above the 30-year average in Davis with 3.8 cm of rain falling during May and 1.8 cm during June. Thus, the precipitation pattern in 1995 made it an exceptionally wet year with an extended growing season.

Sampling Methods

Plant density was estimated in each treatment plot by counting the number of individual plants that occurred within two randomly located 0.1-m^2 circular quadrats. Densities of annual fescue and native perennial grasses were estimated 9 March and 12–19 April in 1994. Native perennial grass densities were also estimated 24 October 1994 and 22 April 1995. Species that were not seeded were considered weeds. About 70% of the weed biomass was from forbs, with the remainder from annual rushes and grasses. The most abundant dicotyledonous weeds were *Calandrinia ciliata* (red maids), *Convolvulus arvensis* (field bindweed), *C. solstitialis* (yellow starthistle), and a *Silene* sp. (catchfly). The monocotyledonous weeds were predominantly *Avena fatua* (wild oat) and *Juncus bufonius* (toad rush). Densities of weeds were estimated 12–19 April 1994.

Heights of annual fescue and native perennial grasses were estimated 12–19 April 1994 (two plants per plot). Above-ground biomass samples of annual fescue, native perennial grasses, and weeds were taken 3–10 May 1994 by clipping the vegetation from two 0.1-m^2 circular quadrats, randomly placed within each treatment plot. Biomass samples were sorted, dried to constant weight at 65°C, and weighed. Treatment plot values were means of the two subsamples. Weed species composition was determined using the dried biomass samples.

Statistical Analyses

Annual fescue seedling density and biomass data were log transformed and analyzed using simple linear regression. Perennial grass density data collected over the duration of the experiment were analyzed using repeated measures analysis of variance (ANOVA) with time as the repeated measure. The hypothesis that the perennial grass data satisfied the assumption of sphericity (equal variance and independence) could not be rejected based on Mauchly's Criterion so results from the unadjusted ANOVA (i.e., degrees of freedom not reduced to compensate for dependence of residuals) were used (von Ende 1993). Linear contrasts were used to determine differences between the native grass mixture grown alone and grown in the presence of annual fescue at any density, and between the native grass mixture grown with annual fescue seeded at 0.09 g/m^2 and the three higher densities.

One-way ANOVA was performed on variables that were measured once during the experiment if visual inspection of the data suggested highly nonlinear treatment responses. Square-root-transformed weed density and log-transformed weed biomass were analyzed with ANOVA. Tukey's Studentized Range Test was used for a posteriori comparison of means. For native grass data, linear regression was conducted on the log of biomass per square meter, the log of biomass per individual, and untransformed density and height data. Statistical power analysis was performed for the test of the effect of annual fescue seeding density on perennial grass densities (Cohen 1977). Comparisons between weed and native grass densities and biomass were based on data taken during the April and May 1994 sampling periods, respectively. For analyses exploring the relative effects of annual fescue seeding density on native grass and weed density and biomass, the data were square-root transformed, differences between the two vegetation types at each of the treatment levels were calculated, and the differences were analyzed with linear regression.

SAS for Windows (Release 6.10, 1994, SAS Institute Inc., Cary, NC) was used for repeated measures and one-way ANOVA. BMDP New System for Windows (Version 1.0, 1994, BMDP Statistical Software, Inc., Los Angeles, CA) was used for regressions. Power analysis was performed with JMP (Version 3.1, 1995, SAS Institute Inc., Cary, NC).

Results

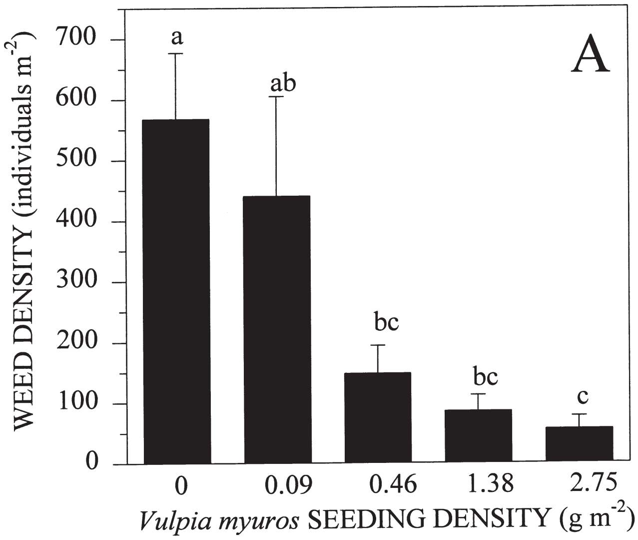
Effects of *V. myuros* Density Variation on Perennial Grass and Weed Density

The number of annual fescue seedlings increased as seeding density increased ($p = 2.1 \times 10^{-7}$, $r^2 = 0.71$); however, its biomass per area did not increase significantly with seeding density ($p = 0.16$, $r^2 = 0.07$). Native perennial grass densities decreased over time with increasing annual fescue seeding density ($p = 0.0017$) (Fig. 1) and were higher for the native grass mixture grown alone, compared to the mixture grown with annual fescue at any density (linear contrasts $p < 0.01$). Additional contrasts showed no significant difference between native grass densities in plots with the lowest seeding rate of annual fescue (0.09 g/m^2) and plots at higher seeding density (0.46, 1.38, and 2.75 g/m^2). Weed densities were reduced by more than an order of magnitude by increasing annual fescue seeding density ($p = 0.0015$) (Fig. 2A) and plots without annual fescue had significantly greater weed densities than the 0.46, 1.38, and 2.75 g/m^2 treatment levels.

Differences between weed and grass densities decreased as annual fescue seeding density increased ($p = 0.0035$, $r^2 = 0.38$) (Fig. 2B), which could have resulted from differences in sensitivity of either plant type to changing annual fescue densities. There was no significant relationship between perennial grass density and annual fescue seeding density at the 12–19 April 1994 sampling date ($p = 0.96$, $r^2 = 0.0001$). In contrast, weed densities decreased with increasing annual fescue seeding density ($p = 0.0007$, $r^2 = 0.48$) (Fig. 2A).

Effects of Annual Fescue on Growth of Perennial Grasses and Weeds

Above-ground biomass of native perennial grasses and weeds decreased with increasing annual fescue seeding



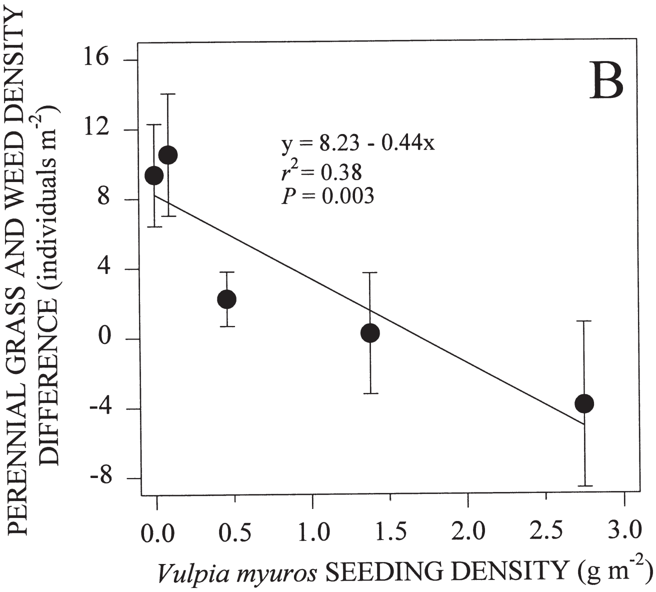


Figure 2. (A) Density of weeds (±1 SEM, $n = 4$) at various *Vulpia myuros* seeding rates on 12–19 April 1994. Means with different letters are significantly different from one another according to Tukey's Studentized Range Test ($\alpha = 0.05$). (B) Regression of the difference between square-root transformed weed and native perennial grass densities (±1 SEM, $n = 4$).

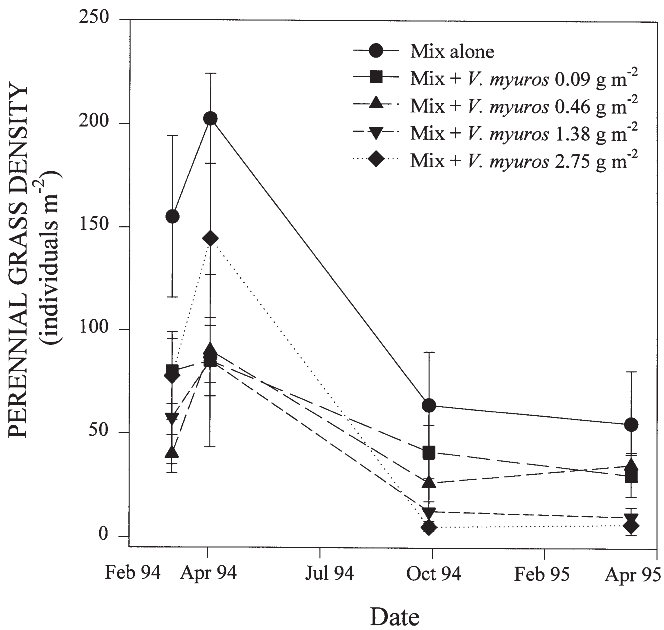


Figure 1. Changes in density of a mixture of California native perennial grass species (±1 SEM, $n = 4$) over four sampling dates when planted alone and with *Vulpia myuros* at 0.09, 0.46, 1.38, and 2.75 g/m^2.

density ($p = 0.002$ and $p = 0.01$, respectively) (Fig. 3). Suppressive effects on the two plant types were similar in that the difference between weed and native grass biomass did not change significantly with increasing annual fescue density ($p = 0.30$, $r^2 = 0.06$).

Increasing annual fescue seeding density did not affect perennial seedling height ($p = 0.58$) (Fig. 4A). However, weights of individual perennial grass seedlings differed among seeding density treatments ($p = 0.008$) (Fig. 4B); seedlings tended to be smaller at the higher annual fescue seeding densities.

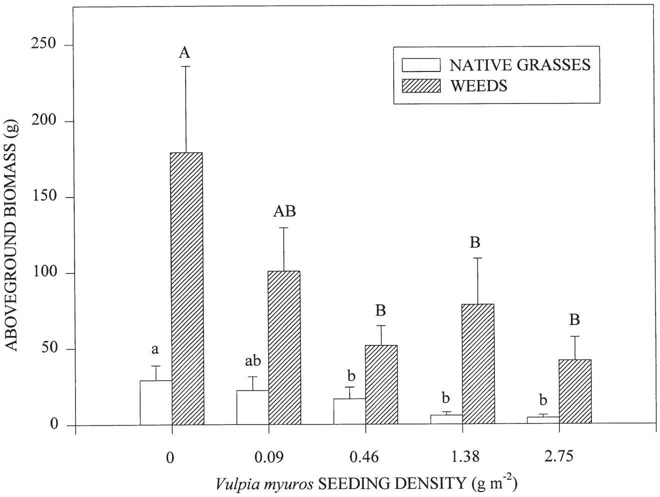


Figure 3. Above-ground biomass of native perennial grasses and weeds (±1 SEM, n = 4) at various *Vulpia myuros* seeding densities on 3–10 May 1994. Means with different letters are significantly different from one another according to Tukey's Studentized Range Test (α = 0.05).

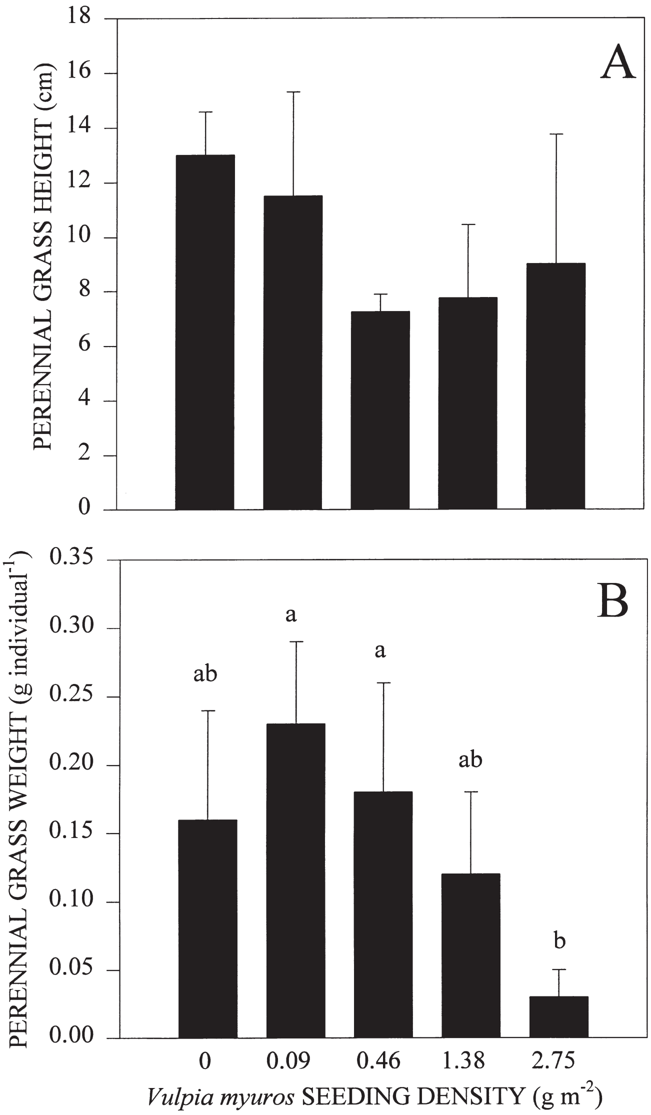


Figure 4. (A) Perennial grass height (±1 SEM, n = 4) and (B) perennial grass biomass per individual (±1 SEM, n = 4) with variation in *Vulpia myuros* seeding densities. Means with different letters are significantly different from one another according to Tukey's Studentized Range Test (α = 0.05).

Discussion

The results of our experiment show that increasing seeding densities of annual fescue reduced above-ground biomass and densities of both native perennial grasses and weeds. Perennial grass and weed above-ground biomass were suppressed to the same degree at the 3–10 May 1994 sampling date. However, only weed densities, not perennial grass densities, were reduced significantly by increased annual fescue seeding density at that time. The statistical power to detect a relationship between perennial grass densities and annual fescue seeding density was 0.68. With this level of statistical power we suggest that if a relationship had existed, it would have been detected and that native grass survival was less sensitive than weed survival to increasing annual fescue densities. However, across all sampling dates, perennial grass densities were reduced when annual fescue was present, even at the lowest seeding density.

This overall response may reflect the growth capacity of annual fescue more than sensitivity of the native grasses to its competitive effects. Although annual fescue seedling densities increased with increasing seed density, biomass production reached maximum levels at low seed density. This may explain why low-density stands of annual fescue suppressed native grasses nearly as much as high-density stands.

When we considered the effect of increasing annual fescue seeding densities on native perennial grass seedling morphology, we found that perennial individuals weighed less for a given height at higher annual fescue density. This suggests that competition for soil resources or light, or both, inhibited native perennial grass seedling biomass accumulation. Seedlings in this weakened state may be less likely to survive than larger individuals (Harper 1977).

These experimental results demonstrate a number of negative effects of annual fescue on native perennial grasses, but the decision of whether or not to include it in a revegetation seed mixture should be driven by the goals of the reseeding effort. Two of the most common purposes for reseeding are establishment of native vegetation and erosion control. Our results provide reasons to believe that including annual fescue in seed mixes will not promote either of these goals. The suggestion that annual grasses may act as nurse plants to native perennial grasses is not supported by our results. This is consistent with the findings of Marquez and Allen (1996), and Eliason and Allen (1997), who found that annual legumes and grasses, respectively, reduced establishment of *A. californica.*

The differential effects of annual fescue (i.e., weeds were more negatively affected than perennial grasses) might seem to warrant including it in mixtures with native perennial grasses in order to control weeds. However, both the amount (density and biomass) and identities of weeds should be taken into account before coming to this conclusion. In our experiment, weed densities were equal to or greater than perennial grass densities and above-ground weed biomass was many times greater than perennial grass biomass. Weed seedling densities at annual grassland sites present formidable obstacles to native grass establishment, as has been shown by others (Dyer et al. 1996). Most reports of soil seed bank numbers in California grasslands range between 7,500 and 60,000 seeds/m^2 (Heady 1988), numbers much higher than the seeding densities we used (Table 2). Using annual fescue to suppress weeds might seem to be a sensible option in situations where the resident weedy vegetation presents a greater impediment to native perennial grass establishment than annual fescue. However, because weeds are generally prolific seed producers, it is doubtful that the initial reductions of weed density and biomass that we observed would be sufficient to prevent growth of weed populations in subsequent years. In addition, the combined suppressive effect of weeds and annual fescue on native grasses would probably result in very low survival of perennial grass seedlings. We suggest that more active means of weed control are needed to provide conditions conducive to native perennial grass establishment.

When erosion control is the primary objective of a reseeding project, one should consider that the amount of protection provided by quick germinating, fast growing annual grasses depends greatly on the rainfall pattern after seeding. If a rainy season begins with torrential storms, it is unlikely that even annuals will reduce erosion significantly. Mechanical or chemical means of slowing run-off and increasing infiltration, such as mulch and wetting agents, would probably be more effective than any seeded species in reducing early-season erosion.

Overall, when considering whether or not to include annual fescue in seed mixtures with native perennial grasses, restorationists and revegetation specialists should consider its potential effects on resident weeds and native species included in the mixtures, the importance of erosion control, and the goals and resources of the project. Our experiment showed that native perennial grasses were suppressed by the presence of annual fescue. Although weeds were reduced by fescue, their biomass was many times greater and their densities equal to, if not greater than, those of native perennial grasses. Given these results, as well as the fact that erosion control by annual grasses is contingent on weather patterns, we consider it unwise to include annual fescue in seed mixtures with California native perennial grasses. We suggest that emphasizing mechanical means of erosion control in the short term may be the best use of resources in order to reach long-term native vegetation establishment and erosion control goals.

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