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Germination Speeds of Exotic Annual and Native Perennial Grasses in California and the Potential Benefits of Seed Priming for Grassland Restoration

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Introduction

Many western grasslands and scrublands are being overrun by Mediterranean annual grasses that are a limiting impediment to grassland restoration throughout the western United States (Kay et al. 1981; Dyer and Rice 1997, 1999; Brown and Rice 2000). Conserving and restoring these invaded ecosystems are important biodiversity goals. Restoring perennial grasslands can also increase the forage quality of these systems (Menke 1992; Stromberg and Kephart 1996).

The continued persistence of exotic annual grasses, and their initial success as invaders may be related to their more vigorous growth (Jackson and Roy 1986), a shift in soil–water utilization patterns (Holmes and Rice 1996), the lack of adequate native grass seed inputs, and heavy competition between alien and native species during early stages of establishment and growth (Dyer et al. 1996; Dyer and Rice 1997, 1999). The phenology of the annuals, including their germination ecology, may play a major role in their competitive dominance.

Germination in the grasslands of California's Central Valley is initiated by the first autumn rains of 15–25 mm (Bartolome 1979), and germination and establishment of annual grasses are rapid. Although exotic annual grasses are generally believed to germinate more quickly than native perennials, this has rarely been tested (Hardegree 1994; but see Reynolds et al. 2001). This earlier germination, coupled with the greater initial growth rates of annual grasses, appears to give a competitive advantage to exotic annual grasses over later-germinating and slower-growing native perennial grasses (Verdu and Travese 2005; see also Rice and Dyer 2001).

Bartolome (1979) found that seedling densities reached a maximum within 2 weeks of initial germination. Initial seedling density of annuals can be as high as 200,000 plants per m^2 (Biswell and Graham 1956). The slower-germinating perennial grass seeds face intense competition from these annuals for water, light, and nutrients at establishment. Increasing the germination speed of perennial grasses could increase their establishment success. Techniques that could increase the germination speeds of perennial grass seeds could potentially contribute to the restoration of grassland communities.

Initially developed for agronomic crops, seed priming has been used to increase seed germination speed in native perennial grass seeds of the

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western United States (Hardegree 1994). Seed priming, also known as hydropedesis (Baskin and Baskin 1998), is a technique by which seeds are partially hydrated to a point where germination processes begin, but emergence of the radicle (the embryonic seedling root) has not yet occurred (Bradford 1986; Hardegree and Emmerich 1992).

The restoration potential of seed priming depends on the degree of increase of germination speed attained. For perennial grasses of the Great Basin region of western North America, Hardegree (1994) used seed priming to induce five native grasses to germinate more rapidly than cheatgrass (*Bromus tectorum*). Several studies examine the effects of priming on western perennial grasses (Hardegree 1994; Hardegree and Van Vactor 2000; Hardegree et al. 2002), but none examine if these priming gains were significant in a competitive field setting.

Our goal here was to determine the germination speed of native perennial and exotic annual grasses, and to explore the potential of seed priming for improving the restoration of perennial grasslands in California. For seed priming to be a valuable restoration technique it must (1) improve the germination speed of California native perennial grasses, and (2) do so enough to significantly reduce the competitive advantage of the exotic annuals.

Although exotic annual grasses are generally believed to germinate more quickly than native perennials, this has rarely been tested

Methods

Germination trials

We carried out two trials of germination speed for three common exotic, invasive annual grass species and five native perennial grass species. The native perennial species studied were *Elymus glaucus, E. trachycaulus, Hordeum brachyantherum, Nassella pulchra,* and *Poa secunda.* The exotic annual species studied were *Bromus diandrus, B. madritensis,* and *B. hordeaceus.* We acquired local ecotypes (Yolo County) of the native perennial grass seeds from Hedgerow Farms in Winters, California. We bought the exotic annual grass seeds from Valley Seed Service in Fresno, California.

In the first trial in November 1999, we placed arrays of 50 seeds in individual clear, 5-inch-square plastic boxes on sterile blotter paper saturated with distilled water. There were two replicates per species. We placed the germination boxes in a growth chamber at 10°C (50°F) where they were subjected to 10 hours of light to mimic winter conditions. We checked the seeds every day and considered them germinated once the radicle had emerged to a length of at least 2 mm. We counted and removed germinated seeds for 2 weeks, at which time no further germination occurred.

In the second trial, we sent samples of three native grasses, *N. pulchra, P. secunda,* and *E. glaucus,* to Kamterter, LLC (a seed priming facility in Durham, KS) to be primed in January 2000. The seeds were matric-primed using a proprietary process similar to other seed priming techniques (Hardegree and Emmerich 1992; Hardegree et al. 2002; Lee et al. 2004). Matric-priming involves initiating the imbibing of water by seeds in a wet solid (vermiculite) mixture, then drying seeds before full germination. In March 2000, we carried out a second set of germination trials using seeds of the three annual *Bromus* species, as well as primed and unprimed seeds of *E. glaucus, N. pulchra,* and *P. secunda,* with the same protocols as the first trial, except there were three replicates for each species.

Field competition study

In March–July 2000, we carried out field experiments testing the effect of priming on establishment and competitive ability using the three native species (*N. pulchra, P. secunda,* and *E. glaucus*). We conducted these trials in University of California, Davis, agricultural research fields, 1 mile south of the campus in Yolo County. These field sites have flat topography, sandy loam soils, and have been in cultivation for research for several decades. No exotic grasses grew in the test fields at the time of our experiment.

Table 1. Percent mean (SE) total germination and mean (SE) germination speed (number of days to 50% of total germination [LD50]) for seeds of three exotic annual *Bromus* species and five native perennial species. For *B. diandrus, B. hordeaceus, B. madritensis, E. glaucus* (unprimed), *N. pulchra* (unprimed), and *P. secunda* (unprimed), means are across both growth chamber experiments.

Species	Percent Mean (SE) Total Germination	Mean Germination Speed (LD50)
Bromus diandrus	93.2 (4.2)	3.1 (0.2)
Bromus hordeaceus	99.2 (0.8)	2.3 (0.2)
Bromus madritensis	94.0 (1.4)	1.9 (0.2)
Elymus glaucus (unprimed)	97.6 (1.5)	3.5 (0.2)
Elymus glaucus (primed)	95.3 (3.7)	1.4 (0.03)
Nassella pulchra (unprimed)	90.0 (3.0)	6.8 (0.3)
Nassella pulchra (primed)	70.7 (5.2)	5.3 (0.4)
Poa secunda (unprimed)	51.6 (2.9)	8.6 (0.2)
Poa secunda (primed)	68.0 (2.3)	6.3 (0.1)
Elymus trachycaulus (unprimed)	97.0 (1.0)	5.6 (0.3)
Hordeum brachyantherum (unprimed)	7.0 (1.0)	8.4 (0.6)

SE = standard error

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We prepared the field site by plowing and disking the ground in February 2000. We divided the site into a grid of 0.5 m × 0.5 m plots. Each plot was separated from the adjacent plots by 0.5 m. We assigned each plot one of nine treatments in a random stratified manner such that each of 15 columns of the study grid had one replicate of each of nine treatments. For each of the three native grass species, one plot had the unprimed seeds planted alone, one had unprimed seeds planted with seeds of exotic annual grasses, and one had primed seeds planted with seeds of exotic annual grasses.

In each plot, we planted five native grass seeds in late March 2000, configured with one seed in the middle and four others near the corners of each plot. For those treatments with exotic annual grasses added, we sowed a 7:3 mixture of *B. madritensis:B. hordeaceus* evenly over the plot at a density of approximately 400 seeds per plot (equivalent to a density of 1,600 per m^2). We watered the plots evenly after planting, and irrigated them with an impact-type sprinkler every other day or more, as needed. We weeded all plots regularly to remove volunteer broadleaf weeds. There were no volunteer grasses. In late July, we located and measured each surviving native grass plant for height, number of culms, basal diameter, and degree of herbivory.

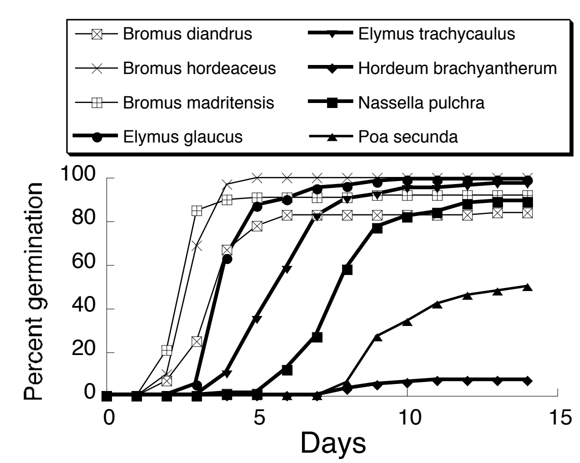

Fig. 1. Percent germination of five native perennial grasses and three exotic annual grasses (*Bromus*) in growth chamber conditions from the first trial (see "Methods"). The three annual species are represented by the thinner lines.

Statistical analysis

We analyzed data from both germination experiments with ANOVA to determine if significant differences existed between native and exotic species, and between primed and nonprimed seeds, using JMP statistical software (SAS Institute). When included, species was a nested effect within annual–perennial status. We analyzed field data to test differences in survivorship and size among the different experimental treatments.

Results

Germination trials

In both greenhouse trials, the three invasive annual grasses germinated significantly more quickly than the unprimed perennial grasses ($p < 0.0001$, Table 1, Figs. 1–2), with nearly 100% germination. *Bromus madritensis* was the fastest germinator of all tested species, with half of the seeds germinating in less than 48 hours. Of the unprimed native perennial grasses, *Elymus glaucus* and *E. trachycaulus* germinated quickly; both had high total germination. *Nassella pulchra* germinated relatively slowly but had high total germination. *Poa secunda* also germinated slowly and had relatively low total germination. Few *Hordeum brachyantherum* seeds germinated, and germination occurred slowly for this species.

In the second greenhouse trial, the primed seeds of the three native perennial species, *P. secunda, N. pulchra, E. glaucus,* germinated significantly faster ($p < 0.0001$) than the unprimed seeds of the same species (Table 1, Fig. 2). When each species was analyzed separately, each showed a significant increase in germination speed with priming (*P. secunda,* $p < 0.0001$; *N. pulchra,* $p = 0.03$; *E. glaucus,* $p < 0.0001$). The average germination speed for primed *E. glaucus* seeds was even faster than that of any of the three annual grasses. Total germination responses to priming differed among the native species (Table 1). Priming had no affect on total germination for *E. glaucus,* but *P. secunda* increased total germination by >15% when primed ($p = 0.008$), and *N. pulchra* had 20% lower total germination when primed ($p = 0.01$, Table 1).

Field competition study

Poa secunda did not establish sufficiently in the field study to be included in the analysis. The data for *N. pulchra* and *E. glaucus* were first analyzed together and showed significant ($p < 0.001$) differences between both species and treatment classes for establishment and size (culms per plant). Because significant interactions

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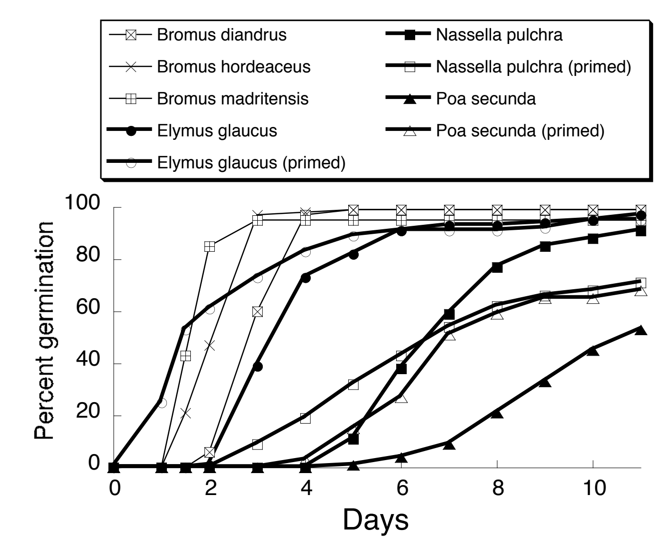

Fig. 2. Percent germination of five native perennial grasses and three exotic annual grasses in growth chamber conditions from the second trial (see "Methods"), including primed seed for three native perennial grasses. The three annual species are represented by the thinner lines.

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existed between species and treatment, the two species were analyzed separately.

For *N. pulchra,* establishment was approximately 45% in the two unprimed treatments, which were not significantly different. Priming reduced the establishment of this species to only 15%. The unprimed, no-weed treatment yielded plants with the highest number of culms (Fig. 3). Annual grasses reduced the number of culms by 50% in both the unprimed and primed treatments with annual grasses ($p < 0.01$).

For *E. glaucus,* the unprimed treatment with no annual grasses showed 60% establishment, whereas the survival rate for both the unprimed and primed *E. glaucus* growing with annual grasses was only about 30%. Competition with exotic annual grasses significantly reduced the number of culms in *E. glaucus* grown from unprimed seed ($p < 0.01$), but this difference became nonsignificant with primed seeds ($p = 0.12$), which produced plants with nearly as many culms as those grown without competition (Fig. 3).

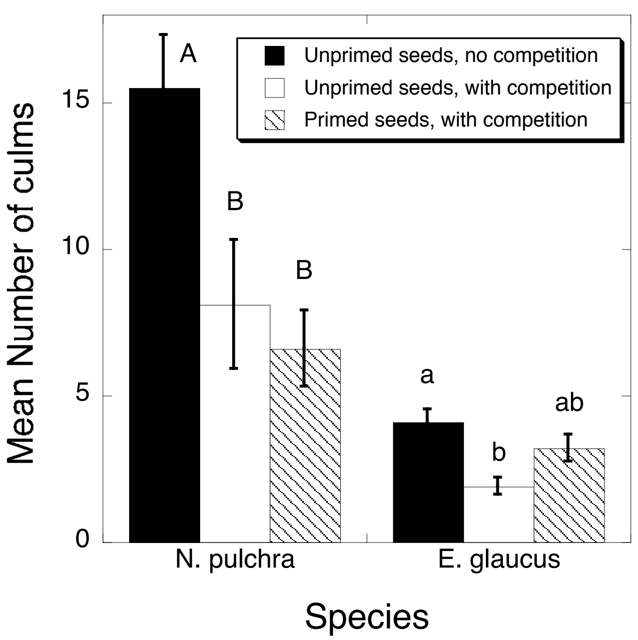

Fig. 3. Mean size of native grasses germinated and grown in a field experiment with exotic annual grasses. On the left, native grasses from unprimed seed grown alone; in the middle, native grasses from unprimed seed grown with exotic annual grasses; and on the right, native grasses from primed seed grown with exotic annual grasses. Error bars are 1 standard error.

Discussion

There are few published studies comparing germination speeds of perennial and annual grasses (Morgan 1998; Reynolds et al. 2001). The three annual *Bromus* species in this study germinated rapidly (Figs. 1–2). In contrast, the perennial grasses germinated an average of several days later, and over a period that was nearly twice as long as that of the annuals.

What evolutionary factors may have favored such differences in germination speeds between these annual and perennial grasses? The exotic annual grasses are early successional species that thrive in disturbed sites. Such sites favor species that are first to colonize and establish. By germinating rapidly, the exotic annuals are very effective competitors at the establishment stage, and once established they grow quickly (Jackson and Roy 1986). In addition, because annual species must germinate, flower, and set seed in a single season, individuals need to quickly germinate, establish, and reproduce before unfavorable environmental conditions develop (e.g., summer drought).

When competition is not severe, perennial species appear to have succeeded in the past, despite slow germination. The extended germination patterns of the perennial grass populations might be favored if conditions worsened after germination (e.g., dry weather), because there would be seeds left to germinate once favorable conditions returned.

Demonstrated differences between perennial and annual grass species in this study are in the context of two confounding factors: (1) the annuals in this study are of European origin, whereas the perennials are California natives, and (2) all the annuals were from a single genus (*Bromus*). The

Techniques that could increase the germination speeds of perennial grass seeds could potentially contribute to the restoration of grassland communities.

differences in germination patterns may reflect differences in the climates in which the two groups evolved (Jackson and Roy 1986; Jeffrey Clary, pers. comm.). There is a need to conduct similar experiments on other California native grasses as well as exotic grasses from genera other than *Bromus*.

Priming significantly increased the germination speeds of the three native perennial grass species tested (Fig. 2). However, increased germination speed of native species was accompanied by limited improvement in establishment or growth in the field when subjected to competition from annual grasses in the field experiment. When grown with annual competitors, *Elymus glaucus* from primed seed did show greater initial growth than *E. glaucus* from unprimed seeds (Fig. 3), suggesting that, for this species at least, some of the priority advantages of exotic annuals could be offset by priming.

Primed *Nassella pulchra* showed decreased germination in the greenhouse and decreased establishment in the field trials compared to unprimed *N. pulchra.* It is possible that fine-tuning the priming protocol for this species could reduce these effects, but perhaps *N. pulchra* is inherently less tolerant of priming. Another strategy would be to merely increase seeding densities for this species when using primed seed. However, both of these suggestions presuppose some competitive advantage to priming, which we were unable to demonstrate for *N. pulchra.*

Conclusion

This study demonstrated that the five native perennial grasses we examined do germinate more slowly than three exotic

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annual grasses, and that seed priming can greatly reduce this difference in some native species. Our field competition experiment revealed limited potential of priming for restoration purposes. However, further research with *Elymus glaucus* may be warranted, and other perennial species should be tested as well. Priming could also be coupled with techniques to control exotic annual grasses. Many restoration practitioners kill the first flush of annual grasses with herbicide, then immediately plant seeds of native species. Primed seeds could be used in such a scenario to get a head start on any weed seeds left in the seed bank. We hope this research will contribute to knowledge about seed priming and lead to further experimentation.

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Grass is the forgiveness of Nature — her constant benediction. Fields trampled with battle, saturated with blood, torn with the ruts of cannon, grow green again, and carnage is forgotten.

Streets abandoned by traffic become grass-grown like rural lanes and are obliterated. Forests decay, harvests perish, flowers vanish, but grass is immortal.

–John James Ingalls, 1827