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Restoration of *Danthonia californica*, *Elymus glaucus*, and *Nassella pulchra* at Elkhorn Slough National Estuarine Research Reserve

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AUTHOR AFFLIATION

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Abstract. California grasslands are one of the most invaded, endangered, and altered ecosystems in the world. Seven of the 10 million hectares of California's grasslands are now dominated by exotic annual grasses of Mediterranean origin, replacing the native perennial bunchgrasses. Of all California grasslands, coastal grasslands remain the most intact floral assemblages, in which native species dominate in remnant patches. Thus, coastal grasslands have high potential for restoration and conservation purposes. We designed an experiment to evaluate at which life stages native perennial bunchgrasses need the most assistance for survival when competing with exotic annual grass species. In addition, our experiment evaluated which native perennial bunchgrass species and treatment are the most appropriate for restoration efforts. We used three plots, three native perennial bunchgrass species (*Danthonia californica*, *Elymus glaucus*, and *Nassella pulchra*), and three treatment types (weeding, mulching, and initial clearing). The three bunchgrass species responded differently, with *D. californica* growing the largest in terms of basal area and *E. glaucus* growing the tallest. Species also differed in survival and reproduction, with *E. glaucus* having the highest percent survival and *D. californica* reproducing the least. Species responded differently to the three treatments; however; weeding led to better establishment for all three bunchgrass species.

INTRODUCTION

California grasslands are one of the most invaded, endangered, and altered ecosystems in the world. They have been ranked among the top ten most endangered ecosystems in the United States alongside the Florida everglades (Hayes 2004). Seven of the 10 million hectares of California's grasslands have been invaded and dominated by exotic annual grasses of Mediterranean origin (Heady *et al.*1992, Hamilton *et al.* 1999), replacing the native perennial bunchgrasses. Where native perennial bunchgrasses still exist in small remnant patches, they always occur with exotic annual grasses, and the exotics usually cover over eighty percent of the area (Hamilton *et al*. 1999). The conversion of California's grassland composition was probably due to the introduction of livestock, the invasion of exotic species of Mediterranean origin, consecutive years of drought, and suppression of fire beginning with the arrival of Europeans (Heady *et al.* 1992). Due to the heavy impact of European invasion, California's grasslands today inhabit an environment very different from that in which they evolved (Dyer & Rice 1997). The original extent and species composition of pre-settlement California grasslands is unknown (Heady 1977), however, perennial bunchgrasses, especially *Nassella pulchra*, were probably dominant (Heady 1977, Heady *et al*. 1992, Brown & Rice 2000).

California's Mediterranean grasslands are composed of two major vegetation types: the annual-dominated Valley Grassland and the Coastal Prairie (Hatch *et al*. 1999). Interior grasslands, or valley grasslands, occupy the hot and dry regions of the Coast Range, Central Valley, and Sierra Nevada foothills (Corbin & D'Antonio 2004). Coastal grasslands are located below an elevation of 1000 m and within the moderating effects of the ocean (< 100 km from the coast); (Hayes & Holl 2003). Grasslands along California's coast differ considerably from the annual-dominated interior grasslands (Hatch *et al*. 1999) because they still tend to be dominated by native perennial bunchgrasses in many areas (Heady *et al.* 1977, Heady *et al*. 1992, Hatch *et al*. 1999, Corbin & D'Antonio 2004). Characteristic coastal perennial bunchgrass species include *Calamagrostis nutkaensis, Danthonia californica, Deschampsia caespitosa, Festuca idahoensis,* and *F. rubra* (Heady *et al*. 1992). Little research has been done on coastal grasslands (Stromberg *et al*. 2001), even though they represent a valuable resource as remnant California grasslands (Hatch *et al*. 1999). Scattered remnant patches of native-dominated grassland in coastal California, in which exotic cover can be less than 10 percent, illustrate that under certain conditions native species are capable of resisting conversion to exotic dominance (Corbin & D'Antonio 2004). Despite the pressures of agriculture, urban development, invasion by exotic species, habitat fragmentation, and changes in disturbance regime, coastal grasslands remain the most intact floral assemblages of any California grassland (Hayes & Holl 2003). Thus, coastal grasslands have high potential for restoration and conservation purposes (Hatch *et al.* 1999).

The high densities of exotic grasses in California's grasslands have fundamentally altered growing conditions for native perennial bunchgrasses through interspecific competition (Dyer *et al.* 1996, Dyer & Rice 1997). In addition, attempts to restore native perennial grass populations within interior grasslands have achieved little success (Bartolome & Gemmill 1981, Dyer *et al.* 1996, Dyer & Rice 1997) unless populations of alien plants were reduced or eliminated (Dyer & Rice 1997). *N. pulchra* plants grown in interior grasslands without interspecific competition grew larger and produced more flowering stalks than plants grown with interspecific competition (Dyer & Rice 1997, 1999). In coastal grasslands, plots of native bunchgrasses alone are more than twice as productive than plots with mixed native and exotic grasses during the first growing season (Corbin & D'Antonio 2004). However, at the end of four growing seasons, the aboveground biomass of the native bunchgrasses *F. rubra* and *N. pulchra* did not differ between treatments, but they became increasingly dominant in the mixed plots. In addition, exotic productivity in the mixed plots was found to negatively correlate with native productivity (Corbin & D'Antonio 2004). Thus, native perennial bunchgrasses may be better at competing against exotic annuals than previously expected.

It has been shown that reproductive effort in native perennial bunchgrasses may be more sensitive than vegetative growth to interspecific competition (Dyer & Rice 1999). Flowering stalk production has been shown to be higher in plots that are continuously weeded (Dyer & Rice 1999). Fehmi *et al*. (2004) also found that reproductive output was poorly correlated with final basal area of the plant. These results together suggest that floral stalk production may be a critical resource use stage for the plant (Dyer *et al.* 1996). Since the initiation of flower stalks occurs before the period of maximum competition in the summer, native perennial bunchgrasses may retain too few reserves to survive the summer dry season when faced with interspecific competition from exotic annuals (Fehmi *et al*. 2004).

Evidence from both field and greenhouse studies indicate that native perennial grasses also have problems competing with exotic annuals during seed germination and seedling establishment (Bartolome & Gemmill 1981, Dyer *et al*. 1996, Brown & Rice 2000). In California, seedlings of *N. pulchra* often do not survive well. Dyer *et al*. (1996) found that only 1.1% of *N. pulchra* seeds planted in the field survived after emergence during the first year of growth. Bartolome and Gemmill (1981) found similar results in a greenhouse study where, *N. pulchra* seeds germinated more slowly and attained a lower density when competing with exotic grasses. One solution to outplanting seeds is to pregerminate and grow plants to seedling stage in a greenhouse. The release from competition in the greenhouse should increase the bunchgrass root size and give it an increased chance for survival once outplanted (Fehmi *et al*. 2004). The limited research on transplanted bunchgrasses has shown that they survive well in cleared and weeded sites, but have high mortality in untreated interior annual grasslands (Dyer & Rice 1997).

Perennial bunchgrass seedlings may be sensitive to interspecific competition, but are likely to survive well after their first year. Dyer and Rice (1999) found that vegetative growth in one-year old *N. pulchra* plants was not affected by interspecific competition after weeding was stopped. Thus, native perennial bunchgrasses may experience a reduction in competition as the plant matures, and even eventually suppress annual neighbors by interspecific competition or by simply occupying the area first (Ross & Harper 1972). An established perennial individual would be expected to have primary access to such resources as soil nutrients, water, and light, and thus could limit available space for germination of annual seeds, having a negative effect on annual seedlings (Corbin & D'Antonio 2004). Few studies have explicitly looked at changes in competition across all life-stages for native perennial bunchgrasses and exotic annual grasses, so it is not known if exotic annuals outcompete native perennial at all lifestages. Studies of this nature are important because the ability of perennial bunchgrass seedlings to survive may have no relationship to their ability to out-compete annuals as adults (Hamilton *et al.*1999).

To better understand the interactions between exotic annuals and native perennial bunchgrasses, an experiment was designed in February 2004 to address the following questions: (1) At which life-stage are native perennial bunchgrasses most affected by interspecific competition? (2) Among three treatments, which one will increase the survival, growth, and reproduction of native perennial bunchgrasses? (3) Among three native perennial bunchgrasses, which one is more likely to survive and be the most appropriate native perennial bunchgrass for restoration purposes? (4) Are native perennial bunchgrasses reproducing and does reproduction in the spring affect summer mortality?

MATERIALS AND METHODS

Study Species

Nassella pulchra (purple needlegrass) is a perennial bunchgrass native to California and occurs in oak woodland, chaparral, and grasslands below 1300 m (Hickman 1993). *N. pulchra* is thought to have once dominated the original California grasslands (Heady *et al*. 1992). *Elymus glaucus* (blue wildrye) is a perennial bunchgrass native to California and occurs in open areas, chaparral, woodlands, and forests throughout the state below 2500 m. *Danthonia californica* (California oatgrass) is a perennial bunchgrass native to California and occurs generally in moist, open sites in meadows and forests below 2200 m (Hickman 1993).

Study Site

The Elkhorn Slough National Estuarine Research Reserve (ESNERR) is located 145 kilometers south of San Francisco, California and 32 kilometers north of Monterey, California.

It includes 583 hectares of the Elkhorn Slough, which is a shallow estuary that extends inland east from Moss Landing Harbor (Caffrey *et al*. 2002). The climate at ESNERR is characterized as coastal Mediterranean with cool wet winters and dry, but foggy summers. The average air temperatures at ESNERR range between 5°C and 35°C on a seasonal basis, while the average rainfall occurs between October and May, with an average rainfall of 55.2 cm (Caffrey 2002).

The majority of the upper slough at ESNERR is covered with grasslands dominated by exotics. A few remnant patches of all three study species persist, as well as the native perennial bunchgrass, *Leymus triticoides* (creeping wild rye). Experimental plots were established on a hillside once thought to be covered by native grasses, but now dominated by *Phalaris aquatica* (Harding grass)*, Poa Annua* (annual bluegrass)*, Vulpia* spp.*,* and other invasive weeds (Andrea Woolfolk, pers. comm.).

Experimental Design

Three 2.7 x 3.0 m plots were cleared in February 2004. Each plot contained different initial vegetation: native (*L. triticoides* dominance), exotic (P. *aquatica* dominance), and mixed (a combination of native and exotic vegetation). Each plot contained different microclimate conditions because of variation in vegetation and moisture levels. The plots were cleared by hand using a scythe and hoe. After the plots were cleared, holes were placed in the ground 30 cm apart, with a 30 cm border around the edge of the plot. Each plot was planted with young seedlings of *N. pulchra*, *E. glaucus*, and *D. californica.* These plants were grown in a greenhouse from seeds collected within the reserve. Each species of grass was subjected to three treatments: clearing, mulching and weeding. The clearing treatment was cleared initially with a hoe then left alone. In the mulching treatment, mulch was placed 7.6 cm around the plants, 5.1 cm deep. In the weeding treatment, all ground cover 7.6 cm around each plant was removed by hand once a month for 1 year (February 2004 to February 2005). A total of 72 plants were randomly planted in each plot, consisting of eight replicates of each of the three species and three treatments. Each plant was measured for number of green blades, length of tallest green blade, and width and length at the base of the plant every month from February to June 2004 during the first growing season and from December 2004 to February 2005 during the second growing season. Plant mortality was checked in November 2004 during the beginning of the second growing season. During the first growing season flower stalks were collected from May to July 2004 to determine reproductive output.

Statistical Methods

Basal areas of *N. pulchra*, *E. glaucus*, and *D. californica* for February 2005 were found using $[(r_1/2 * r_2/2) * \pi]$, where r_1 equals the length of the plant at the base and r_2 equals the width of the plant at the base (Fehmi *et al.* 2004). Early relative growth rate was determined using, [(JuneArea04 – FebArea04)/FebArea04]. Perennial bunchgrass basal areas, heights, reproductive output, and early relative growth rate were log transformed. For reproductive output and early relative growth rate, (1) was added to the initial values before log transformation to eliminate negative numbers and zeros. Perennial bunchgrass basal areas, heights, reproductive output and early relative growth rate were compared using the factors: plot, species, treatment, plot*species, plot*treatment, species*treatment, and plot*species*treatment using an ANOVA in Systat v.10.2 (www. systat.com). If significance was found for a particular ANOVA factor, pairwise comparisons were done to determine which pairs of means differed significantly. Dead plants were removed from ANOVA analyses.

A repeated measures ANOVA was performed for each bunchgrass species for the factors: basal area, treatment, and area*treatment to analyze if time had an effect on growth. Dead plants were removed from the repeated measures ANOVA analysis.

Correlations were done between the logged transformed area, length, width, blade number and height for each species for February 2005. Correlations were also done between reproductive output and February 2005 area. A two-group t-test was used to analyze the relationship between Spring 2004 reproductive output and November 2004 survival. A two-group t-test was used to analyze the relationship between June 2004 basal area and November 2004 survival for each of the bunchgrass species. Dead plants were removed from all correlations and t-tests. A Kaplan Meier Truncated Survival Model was used to analyze the relationship among treatments in survival through time in JMP-IN ed. 3.2.1 (www.jmp.com).

RESULTS

Survival

Average percent survival after one year for *D. californica*, *E. glaucus*, and *N. pulchra* was 72.2%, 86.1%, and 61.1%, respectively (Fig.1A, 1B, & 1C). For all three species, highest mortality occurred during the summer dormancy period with a 20% increase for *D. californica* and *E. glaucus* and a 15% increase for *N. pulchra* (Fig. 2A, 2B, & 2C). The Kaplan Meier Truncated Survival Statistical Model revealed no significant difference among treatments in survival through time when lumped together (Wilcoxon p= 0.6947, Fig. 3). There were also no significant differences among treatments in survival through time when treated as separate species (Wilcoxon p = 0.323, 0.914, 0.337, respectively). A two-group t-test revealed no difference in basal area in June 2004 between those that did and did not survive until November

2004 for *D. californica* and *E. glaucus* (df = 67, t = -0.481, p = 0.632; df = 65, t = 0.779, p = 0.434, respectively). Due to insufficient data, this test could not be used for *N. pulchra*.

Growth

For all three species, basal area, length, width, and blade number were correlated with each other, but height was not correlated with any of the growth measurements (Table 1).

For plant area, there was a significant species by treatment interaction using an ANOVA (Table 2A). For all three species, the weeding treatment was the best, however, the effects of the mulching and clearing treatments varied among species. All three main effects (plot, species, and treatment) were also significant (Table 2A, Fig.4). Pairwise comparisons revealed that the native plot was significantly different from the mixed plot (p = 0.009). *D. californica* and *E. glaucus* were not different from each other, however, both were significantly different than *N. pulchra* ($p < 0.001$ for both). Clearing and mulching treatments showed no significant difference from each other, but both were significantly different from the weeding treatment ($p < 0.001$, p = 0.002, respectively).

For plant height, there was also a significant species by treatment interaction using an ANOVA (Table 2B). For all three species, the weeding and mulching treatments were comparable, except*, N. pulchra* was least productive when mulch was applied. Plot and species also had a significant effect on plant height, but treatment did not (Table 2B, Fig.5). The exotic plot was significantly different from the native and mixed plots (p = 0.067, 0.081, respectively), however, the native plot and mixed plot did not differ from each other. *E. glaucus* was significantly different from *D. californica* and *N. pulchra* in relation to plant height ($p < 0.001$ for both).

The repeated measures ANOVA showed a significant difference for the basal area by treatment interaction for all three species (Table 3 & 4). For all three species, the weeding treatment was the best. However, the effects of the mulching and clearing treatments varied among species. In addition, basal area growth was significant over the year for all three species with *D. californica* having the largest basal area (Table 3 & 4). Treatment interaction was also significantly different over the year for all three species with weeding always the best (Table 3 & 4).

For early relative growth rate, there was a species by plot interaction using an ANOVA. *D. californica* and *E. glaucus* did the best in the native plot, while, *N. pulchra* did better in the mixed plot. All three main effects (plot, species, and treatment) were also significant. (Table 5A, Fig.6). Pairwise comparisons revealed that the exotic plot was significantly different from the native and mixed plots ($p < 0.001$, for both), however, the native plot and mixed plots did not differ from each other. *D. californica* growth rate was significantly different from *E. glaucus* and *N. pulchra* ($p < 0.001$, for both). In addition, *E. glaucus* was significantly different from *N. pulchra* in relative growth rate ($p < 0.001$).

Reproduction

Reproductive output was positively correlated with second year basal area for *E. glaucus* and *N. pulchra* ($r = 0.609$, 0.604, respectively). Due to insufficient stalk production by *D. californica*, no data is available regarding the relationship between reproductive output and second year basal area.

An ANOVA of reproductive output revealed a significant species by plot interaction (Table 5B). *E. glaucus* had the highest reproductive output in the native plot, while *N. pulchra* had the highest reproductive in the exotic plot and *D. californica* reproductive output did not vary among plots. Species and plot were also significantly different in reproductive output, although there was not a significant effect of treatment, the weeding treatment produced more stalks than the other two treatments (Table 5B, Fig.7). *D. californica* was significantly different from *E. glaucus* and *N. pulchra* ($p < 0.001$, for both), but *E. glaucus* and *N. pulchra* did not differ in reproductive output. A two-group t-test revealed no difference in reproductive output between those that did and did not survive until November 2004 when all three species were lumped together ($df = 178$, $t = -1.942$, $p = 0.054$).

DISCUSSION

Few studies have looked at native perennial bunchgrass species response to interspecific competition across all lifestages. During the twelve months of our study, we found that the three native bunchgrass species experienced the highest mortality during the onset of summer and the summer dormancy period. *D. californica* and *E. glaucus* experienced a 20% increase in mortality, while *N. pulchra* experienced a 15% increase. In addition, removal of interspecific competition during the summer did not result in significantly higher survival for any of the three bunchgrasses species. Thus, native perennial bunchgrass species may be affected by water limitation during the summer, even when within the range of maritime influences. Soil water is the most important limiting resource in a Mediterranean environment, thus summer competition for soil moisture may reduce the survival of perennial bunchgrass seedlings (Dyer & Rice 1997). Hamilton *et al*. (1999) found that through the addition of water, densities of *N. pulchra* seedlings increased by 88%, and caused total aboveground *N. pulchra* biomass to increase by almost 90%. Further study is needed to verify that bunchgrass mortality was due to competition for water during the summer, since our study did not analyze soil moisture or bunchgrass water potential.

Despite, high mortality during the summer dormancy period, all three bunchgrass species had moderately high survival, with *E. glaucus* having the highest survival. Our data contrasts an earlier study by Dyer *et al.* (1996), which found a low survival during the first year of growth. In addition, our findings also contrast an earlier study by Hamilton *et al*. (1999) that found that there is “no safe size” for *N. pulchra* even after the first year of growth. Our data suggest that native perennial bunchgrasses are moderately competitive at a young age. In our experiment, pregerminated plugs were planted in the ground instead of seeds, which could have given the native bunchgrasses a competitive edge over the exotic species. Our data support an earlier study by Corbin and D’Antonio (2004), which found that survival of native bunchgrasses was high through three growing seasons despite the presence of interspecific competition when transplants were used.

Plant size was found not to influence survival through the summer dormancy period. Our study, found that plant size was relatively the same for plant’s that died and survived. In addition, plants of *E. glaucus* that died over the summer had the highest basal area in June 2004. Our results contrast an earlier study by Fehmi *et al.* 2004, which found that change in basal area had significant predictive power for mortality. However, our study was not able to include *N. pulchra* in the analysis due to insufficient data, which was the focal species for the previous study by Fehmi *et al.* 2004. Our results may also differ because of small sample size.

Using three treatments, our data suggest that treatment was not a significant factor for survival over time. Our results differ from a previous study by Dyer and Rice (1997), which found that plant mortality was significantly influenced by interspecific competition and that survival was greatest in weeded plots. Our results may contrast to Dyer and Rice (1997) because of small sample size or differences in duration of experiment. Although interspecific has been found to significantly influence plant mortality, other factors such as herbivory may also influence mortality. Dyer and Rice (1997) also found that gophers had a strong effect on *N. pulchra* survival and that gophers were more likely to kill plants in weeded plots. Even though, herbivory was not measured in this experiment, higher herbivory was seen on weeded plants (pers. obs.)

Interspecific competition was found to significantly influence basal diameter. Removal of interspecific competition through weeding promoted the most productive growth for all three native perennial bunchgrass species. These results suggest that interspecific competition by exotic annual grasses and forbs significantly impedes resource availability and productivity of native perennial bunchgrasses (Dyer & Rice 1997 & 1999). Early peak growth along with decreased root to shoot ratios of annual species result in rapid canopy cover and soil moisture depletion in upper soil layers (Dyer and Rice 1999; Seabloom *et al.* 2003; Corbin & D'Antonio 2004), which enables annual species to establish and deplete the resources available in an area before perennials. Our results suggest that interspecific competition has an effect on native bunchgrass growth independent of which native species is used. Previous studies have also found that *N. pulchra* basal area was two to three times greater than plants grown with interspecific competition (Dyer & Rice 1997 & 1999).

Although, treatment was not found to have a significant effect on reproductive output, the weeding treatment did, however, have the highest reproductive output of the three treatments. These results support previous work by Dyer and Rice (1999) and Hamilton *et al.* (1999), which had shown that reproductive effort was sensitive to interspecific competition.

Although, plot was not a focus of this study, two of the three native perennial bunchgrasses were found to be more productive in the native plot. In contrast *N. pulchra,* was more productive in the exotic plot. Besides lacking the dominant Harding grass (*Pharalis aquatica*), the native plot received moderate temperatures and moisture, which probably benefited *D. californica* and *E. glaucus*. The exotic plot, on the other hand, was partially dominated with *P. aquatica* and dry conditions. In previous studies, *N. pulchra* has been able to sustain and increase in frequency and abundance during dry conditions such as a drought (Hamilton *et al*. 1999). Other studies have also found that fewer annual seedlings occur in California grasslands in years with dry periods (Heady 1958). The exotic plot may have created a habitat that was too harsh for many non-native annuals and for *D. californica* and *E. glaucus*, while releasing resources *N. pulchra* could use to grow and survive. In addition, plot also had a significant effect on reproductive output, with the native and exotic plots both having higher reproductive output than the mixed plot. Further research is needed to determine if plot affects plant survival, growth, and reproduction, since each plot type was not replicated.

Virtually all other studies focusing on the interactions between native perennial bunchgrasses and exotic annuals have focused on the native perennial bunchgrass, *Nassella pulchra* (Corbin & D'Antonio 2004). We found that *D. californica* and *E. glaucus* were significantly more productive than *N. pulchra*. Our results correspond with a previous coastal grasslands study that showed that *N. pulchra* was consistently the smallest and least productive of the native perennial bunchgrass species used in the experiment (Corbin & D'Antonio 2004). In addition, Seabloom *et al.* (2003), also found that *N. pulchra* was the least productive native bunchgrass in an interior grassland, while, *E. glaucus* and *B. carinatus* rapidly colonized the area. Our results suggest that a broader range of native perennial bunchgrass species should be used for research and restoration purposes (Hatch *et al*. 1999, Seabloom *et al.* 2003, Corbin & D'Antonio 2004). The use of only *N. pulchra* in research could be misleading by generalizing conditions and attributes of native perennial bunchgrasses that are not true for all species (Seabloom *et al.* 2003).

For all three bunchgrass species, height was not correlated with basal area. Thus, different native perennial bunchgrass species may put more energy into height rather than basal area. *E. glaucus* was found to be significantly taller than the other two bunchgrass species. This may be due to different growth patterns of the three native bunchgrass species. As well as looking at different native bunchgrass species, researchers may need to include other growth measurements into their analysis to account for different growth patterns of native bunchgrasses.

Our study found that native perennial bunchgrasses are capable of reproducing in California's coastal grasslands. However, the three bunchgrass species studied varied in their reproductive output. *E. glaucus* had the highest reproductive output followed by *N. pulchra*. *D. californica* reproduced the least out of the three native grasses. The difference in reproductive output may be due to *D. californica* not being mature enough to reproduce during the first year of growth. The difference in reproductive output exemplifies the importance of using a variety of native bunchgrass species for restoration efforts to insure adequate seeds are deposited into the seed bank. Seabloom *et al.* (2003) found that low native seed recruitment is a probable cause of domination by exotic species in California grasslands.

Reproductive output was found not to have a significant effect on summer mortality. However, reproductive output was positively correlated with second year basal area, which does not support earlier work by Fehmi *et al.* (2004), where reproductive output was negatively correlated with final basal area. In addition, our data does not support the idea that reproductive output is the critical use point for the plant (Fehmi *et al.* 2004). The contrast in results may be due to the locality of both sites. Comparisons between our study in coastal grassland and ones in the interior suggest that native perennial bunchgrasses vary across grasslands within California. The coastal grassland that our study took place in is moderated during the summer by maritime influences (Corbin & D'Antonio 2004), while Fehmi's study, located in an inland California grassland, is not. The harsher summer conditions of inland grasslands may make reproductive output an extremely critical point for a plant.

Based on our results, restoration of native perennial bunchgrasses is a viable option in coastal California grasslands. The maritime influences may promote better survival than previously seen in inland grassland studies and help support native perennial bunchgrasses during the summer when plants are under more stress. Location of the restoration site, bunchgrass species, and treatment should all be taken into consideration, when planning a restoration project. Also, native bunchgrass seeds should be started in the greenhouse to ensure survival past the seedling stage. The location of the restoration site should be a combination of moist and dry areas that are sparsely populated with other natives or vegetation. A mixture of bunchgrass species would be optimal since each of our bunchgrass species contributed to the restoration of the plots in their own way (i.e., establishment, growth, and survival *D. californica* and *E. glaucus*, and reproduction *N. pulchra* and *E. glaucus*). In addition, a combination of mulching and weeding should be employed to promote growth and survival of native bunchgrass species through the first couple of growing seasons.

The overall success of our study supports earlier studies by Hatch *et al*. (1999) and Corbin and D'Antonio (2004), where native bunchgrass restoration was found to be successful within coastal California grasslands. Current grassland restoration efforts may need to shift towards restoration of coastal grasslands since they have higher potential for restoration and conservation (Hatch *et al.* 2004). This study gives hope and support to the major effort currently underway in California towards restoring California grasslands to their pre-European status.

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LITERATURE CITED

Bartolome, J.W., and B. Gemmill. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. *Madrono* **28**: 172-184.

Brown, C.S., and K.J. Rice. 2000. The Mark of Zorro: Effects of the Exotic Annual Grass *Vulpia myuros* on California Native Perennial Grasses. *Restoration Ecology* **8**: 10-21.

Caffrey, J. 2002. Climate. In J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein, eds., *Changes in a California Estuary: A Profile of Elkhorn Slough*. Moss Landing: Elkhorn Slough Foundation, pp. 25-28.

Caffrey, J., C.Zabin, M. Silberstein, and L. Strnad. 2002. Introduction. In J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein, eds. *Changes in a California Estuary: A Profile of Elkhorn Slough*. Moss Landing: Elkhorn Slough Foundation, pp. 1-14.

Corbin, J.D., and C.M. D'Antonio. 2004. Competition Between Native Perennial and Exotic Annual Grasses: Implications For A Historical Invasion. *Ecology* **85(5):** 1273-1283.

Dyer, A.R., H.C. Fossum, and J.W. Menke. 1996. Emergence and survival of *Nassella pulchra* in a California grassland. *Madrono* **43**: 316-333.

Dyer, A.R., and K.J. Rice. 1997. Intraspecific and diffuse competition: the response of *Nasella pulchra* in a California grassland. *Ecological Applications* **7**: 484-492.

Dyer, A.R., and K.J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* **80**: 2697-2710.

Fehmi, J.S., K.J. Rice, and E.A. Laca. 2004. Radial Dispersion of Neighbors and the Small-Scale Competitive Impact of Two Annual Grasses on a Native Perennial Grass. *Restoration Ecology* **12**: 63-71.

Hamilton, J.G., C. Holzapfel, and B.E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* **121**: 518-526.

Hatch, D.A., J.W. Bartolome, J.S. Fehmi, and D.S. Hillyard. 1999. Effects of Burning and Grazing on a Coastal California Grassland. *Restoration Ecology* **7(4)**: 376-381.

Hayes, G. 2004. Listening to California's Grasslands and Their Stewards. *Fremontia* **32(3)**: 12-16.

Hayes, G. F., and K.D. Holl. 2003. Cattle grazing impacts on annual forbs and vegetation composition of Mesic Grasslands in California. *Conservation Biology* **17(6)**: 1694-1702.

Heady, H.F. 1958. Vegetational changes in the California annual type. *Ecology* **39**: 402-416.

Heady, H.F. 1977. Valley grassland. In M.G. Barbour and J. Major, eds., *Terrestrial vegetation of California*, Special publication number 9. Sacramento: California Native Plant Society, pp.491-514.

Heady, H.F., J.W. Bartolome, M.D. Pitt, G.D. Savelle, and M.C. Stroud. 1992. California Prairie. In R.T. Coupland, ed., *Natural grasslands: introduction and western hemisphere*. New York: Elsevier, pp.313-332.

Hickman, J.C. 1993. *The Jepson manual: higher plants of California*. Berkeley, California: UC Press.

Ross, M.A., and J.L. Harper. 1972. Occupation of biological space during seedling establishment. *Journal of Ecology* **60**: 77-88.

Seabloom, E.W., W.S. Harpole, O.J. Reichman, D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *PNAS*. **100(23)**: 13384-13389.

Stromberg, M.R., P. Kephart, and V. Yadon. 2001. Composition, Invasibility, and Diversity in Coastal California Grasslands. *Madrono* **48(4)**: 236-252.

TABLES and FIGURES

Table 1. Pearson Correlations for Growth Measurements from February 2005 by Species

A. *Danthonia californica*

	AREA	LENGTH	WIDTH	BLADES	HEIGHT
AREA	1				
LENGTH	0.932	1			
WIDTH	0.936	0.745	1		
BLADES	0.875	0.802	0.852	1	
HEIGHT	0.418	0.315	0.464	0.289	1

B. *Elymus glaucus*

	AREA	LENGTH	WIDTH	BLADES	HEIGHT
AREA	1				
LENGTH	0.89	1			
WIDTH	0.896	0.596	1		
BLADES	0.835	0.724	0.768	1	
HEIGHT	0.141	0.08	0.171	0.091	1

C. *Nassella pulchra*

	AREA	LENGTH	WIDTH	BLADES	HEIGHT
AREA	1				
LENGTH	0.949	1			
WIDTH	0.941	0.786	1		
BLADES	0.81	0.775	0.756	1	
HEIGHT	0.606	0.54	0.608	0.443	1

Table 2. ANOVA Tables for Plant Growth

A. Area for February 2005

Source	df	Mean-Square	F-ratio	P-value
PLOT	2	1.889	4.564	0.012
SPECIES	2	15.852	38.288	0.000
TREATMENT	2	5.577	13.47	0.000
PLOT*SPECIES	4	0.460	1.112	0.354
PLOT*TREATMENT	4	0.386	0.933	0.447
SPECIES*TREATMENT	4	1.216	2.938	0.023
PLOT*SPECIES*TREATMENT	8	0.381	0.919	0.503
ERROR	131	0.414		

B. Height for February 2005

Source	df	Mean-Square	F-ratio	P-value
PLOT	2	0.395	3.721	0.027
SPECIES	2	9.603	90.529	0.000
TREATMENT	2	0.003	0.025	0.975
PLOT*SPECIES	4	0.083	0.785	0.537
PLOT*TREATMENT	4	0.045	0.428	0.789
SPECIES*TREATMENT	4	0.287	2.702	0.033
PLOT*SPECIES*TREATMENT	8	0.151	1.419	0.194
ERROR	131	0.106		

Table 3. Mean Values from Repeated Measure ANOVA: Changes Over Time with Respect to Area

A. *Danthonia californica* Mean Values for Area (mm^2)

FEBRUARY 04	MARCH 04	APRIL 04	MAY 04	JUNE 04
112.856	276.412	526.506	659.190	808.082
DECEMBER 04	JANUARY 05	FEBRUARY 05		
1022.442	1101.985	1443.363		

B. *Elymus glaucus* Mean Values for Area (mm^2)

FEBRUARY 04	MARCH 04	APRIL 04	MAY 04	JUNE 04
26.703	60.192	267.019	314.700	429.127
DECEMBER 04	JANUARY 05	FEBRUARY 05		
827.692	908.496	1057.55		

C. *Nassella pulchra* Mean Values for Area (mm^2)

FEBRUARY 04	MARCH 04	APRIL 04	MAY 04	JUNE 04
181.279	254.647	286.235	311.619	359.759
DECEMBER 04	JANUARY 05	FEBRUARY 05		
415.587	378.353	453.603		

Table 4. ANOVA Table for Repeated Measures ANOVA

A. *Danthonia californica*

BETWEEN SUBJECTS				
	df	Mean-Squares	F-ratio	P-value
TREATMENT	2	1.21076	15.406	0.000
ERROR	49	785924.38		
WITHIN SUBJECTS				
AREA	7	1.04997	65.652	0.000
AREA*TREATMENT	14	1252708.278	7.833	0.000
ERROR	343	159930.189		

B. *Elymus glaucus*

BETWEEN SUBJECTS				
	df	Mean-Squares	F-ratio	P-value
TREATMENT	2	2134422.553	4.865	0.011
ERROR	59	438713.279		
WITHIN SUBJECTS				
AREA	7	9237018.322	74.607	0.000
AREA*TREATMENT	14	318938.109	2.576	0.001
ERROR	413	123809.597		

C. *Nassella pulchra*

BETWEEN SUBJECTS				
	df	Mean-Squares	F-ratio	P-value
TREATMENT	2	1178198.474	6.331	0.004
ERROR	41	186111.566		
WITHIN SUBJECTS				
AREA	7	419083.203	6.835	0.000
AREA*TREATMENT	14	136177.908	2.221	0.007
ERROR	287	61318.43		

Table 5. ANOVA Tables for Early Relative Growth Rate and Reproductive Output

A. Early Relative Growth Rate

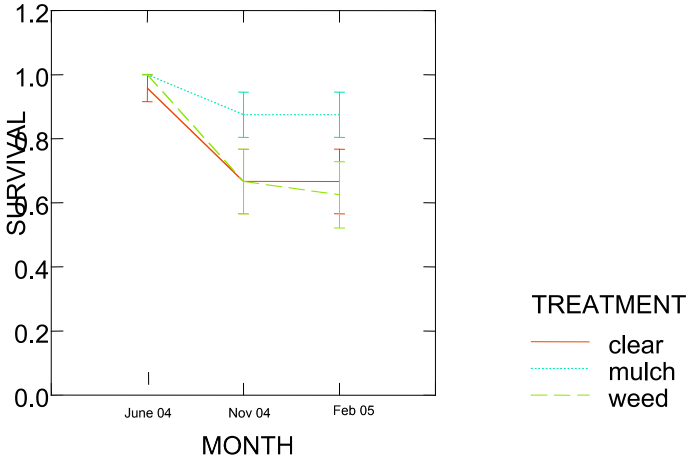
Source	df	Mean-Square	F-ratio	P-value
PLOT	2	21.577	17.384	0.000
SPECIES	2	48.914	39.410	0.000
TREATMENT	2	9.288	7.483	0.001
PLOT*SPECIES	4	3.524	2.839	0.026
PLOT*TREATMENT	4	1.001	0.807	0.523
SPECIES*TREATMENT	4	1.167	0.940	0.443
PLOT*SPECIES*TREATMENT	8	1.272	1.025	0.420
ERROR	153	1.241		

B. Reproductive Output 2004

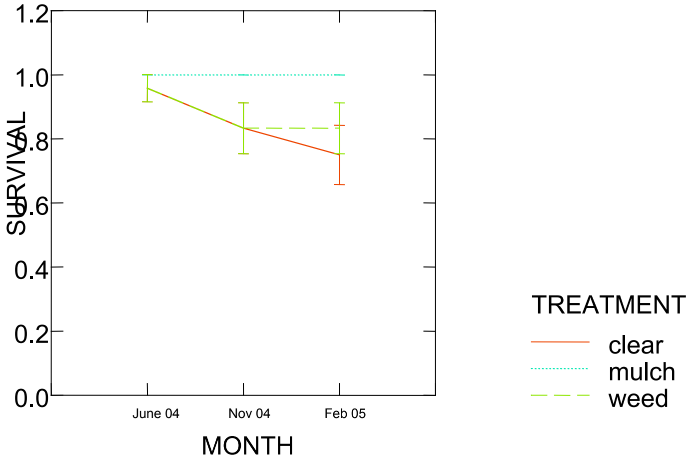
Source	df	Mean-Square	F-ratio	P-value
PLOT	2	1.644	8.832	0.000
SPECIES	2	5.758	30.925	0.000
TREATMENT	2	0.159	0.852	0.429
PLOT*SPECIES	4	1.083	5.818	0.000
PLOT*TREATMENT	4	0.121	0.648	0.629
SPECIES*TREATMENT	4	0.344	1.847	0.123
PLOT*SPECIES*TREATMENT	8	0.151	0.813	0.529
ERROR	153	0.186		

Figure 1**.** Percent Survival by Species

A. Percent Survival for *Danthonia californica*, with ± one standard error



B. Percent Survival for *Elymus glaucus*, with ± one standard error



C. Percent Survival for *Nassella pulchra*, with ± one standard error

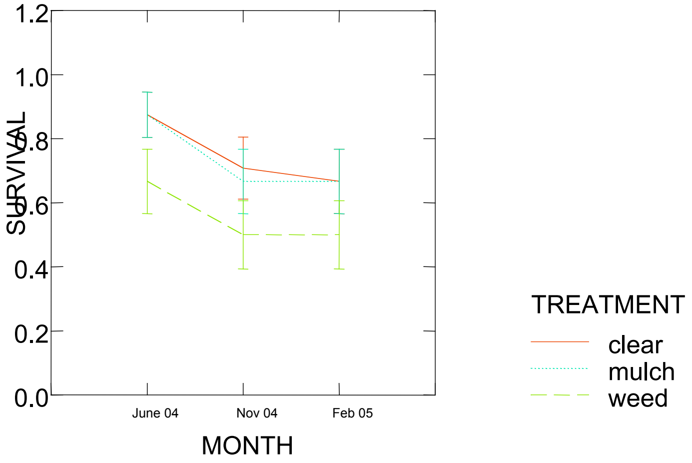
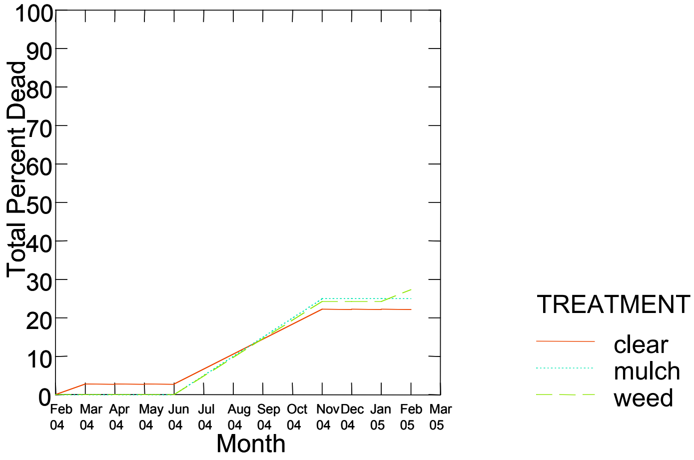
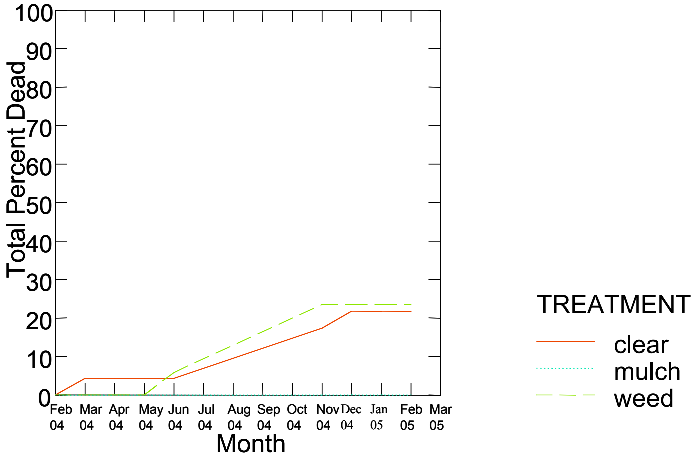


Figure 2. Percent Mortality by Species

A. Percent Mortality for *Danthonia californica*



B. Percent Mortality for *Elymus glaucus*



C. Percent Mortality for *Nassella pulchra*

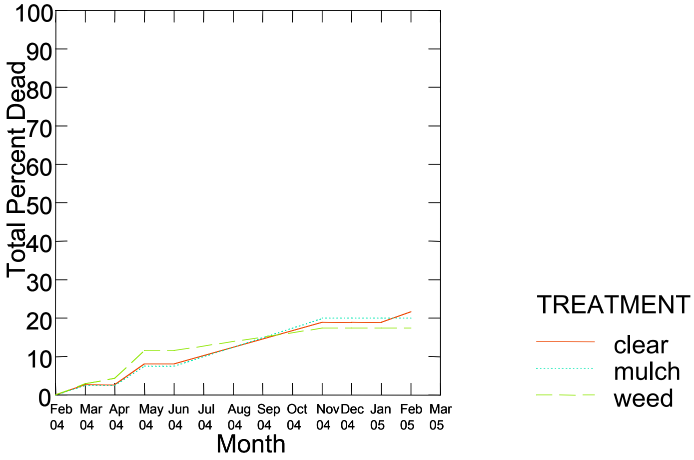


Figure 3. Kaplan Meier Truncated Survival Analysis with All Species Combined

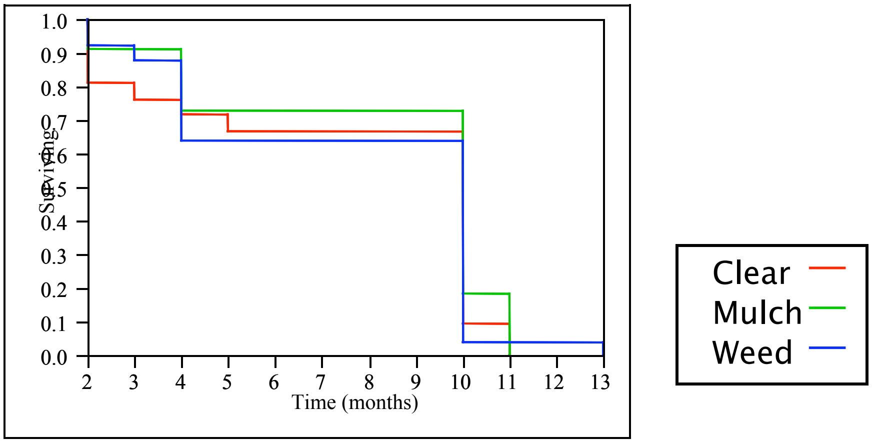


Figure 4. Plant Area (mm^2) for February 2005, with one standard deviation

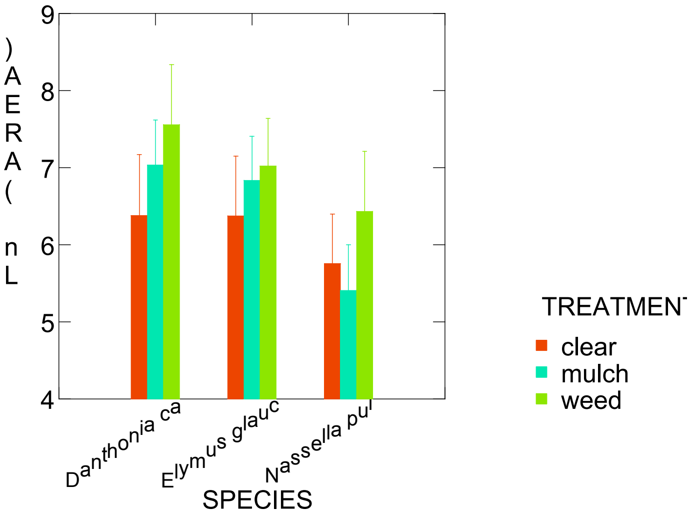


Figure 5. Plant Height (cm) for February 2005, with one standard deviation

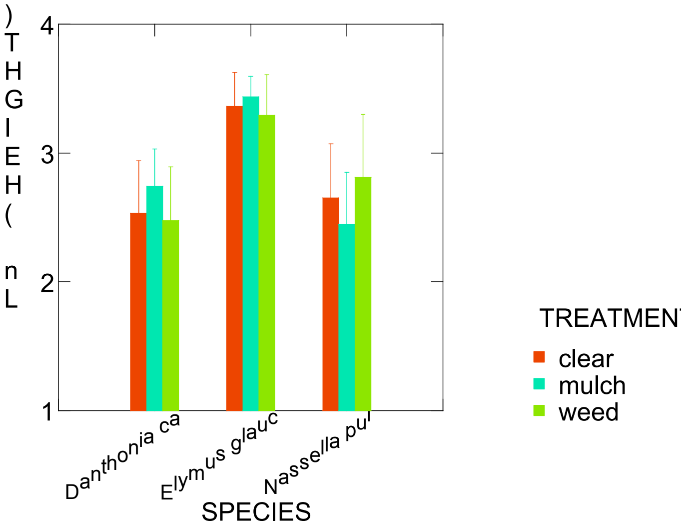


Figure 6. Early Relative Growth Rate (February 2004 – June 2004), with one standard deviation

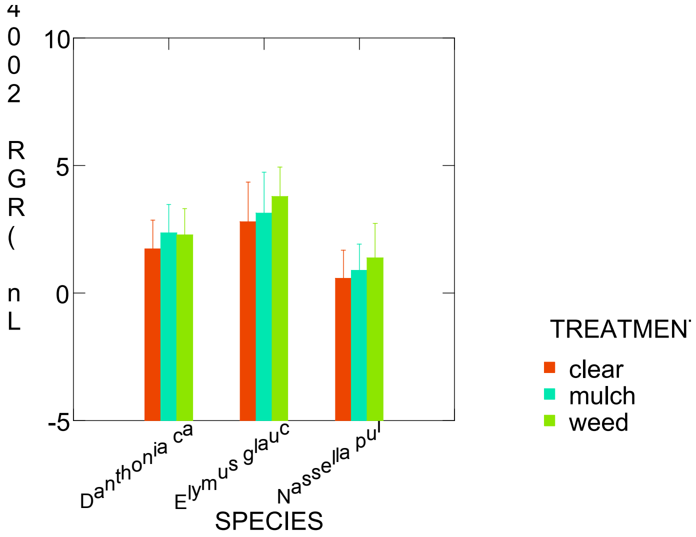


Figure 7. Reproductive Output 2004, with one standard deviation