Understanding Competitive Relationships as a Strategy for Restoring Crown Valley: Using the Rare Forb, *Erodium macrophyllum*, as a Model Species

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California grasslands have experienced one of the most dramatic biological invasions in North America; they have undergone an almost complete vegetation conversion from perennial to exotic annual species (Mooney et al. 1986; Mack 1989). Introduced grasses and forbs are responsible for a reduction in performance of many plant taxa native to the Mediterranean regions of California (Dyer and Rice 1997; Eliason and Allen 1997; Hamilton et al. 1999; Carlsen et al. 2000), while altered grazing regimes have magnified the severity of the invasion (Heady et al. 1992). Within grasslands there is temporal and spatial variation among dominant species (e.g. exotic grasses, exotic forbs and native forbs) and these dominants may form competitive hierarchies with different abilities to exclude rare native forbs (Keddy 1990).

Understanding competitive relationships may be especially important for restoring southern California annual grasslands because these areas are often comprised of a matrix of patches where the dominant species vary between the native *Amsinckia menziesii* and the invasive *Erodium* spp. and *Bromus* spp. (Gillespie unpublished data). Furthermore, restoration work done by Allen et al. (2003) () in southern California exotic annual grasslands has resulted in areas where the dominant species has shifted from exotic grasses to exotic forbs. If the competitive relationships were understood between the target species during restoration (e.g. native forbs or shrubs) and these dominant species, then restoration efforts could be appropriately aimed at seeding with natives in specific areas or after specific treatments. For example, if native forbs establish best in areas dominated by exotic *Erodium* spp., then restoration practices that result in increased *Erodium* spp. can be opportunistically seeded with native forbs. In contrast, if management practices result in increased dominance of *Bromus* spp. then seeding in such areas may result in poor restoration.

*Erodium macrophyllum* (Geraniaceae) is a rare, native annual California grassland forb. There are currently only 30 known extant populations of *E. macrophyllum* throughout its entire range (Gillespie unpublished data), but 105 total documented populations. We are chose *E. macrophyllum* as a model species because it was once more common (Gray 1876), it has a similar phenology to many other grassland forbs, it has several invasive congeners, and it is easily propagated in the greenhouse. Furthermore, previous research with *E. macrophyllum* has shown that its different life history stages are differentially impacted by different exotic species in different habitat
types (Gillespie, unpublished data), so it makes a good species to assess the impacts of invasive species on a rare native species.

We set up a field experiment in Crown Valley to better understand competitive relationships between native and exotic herbaceous species with the ultimate goal of furthering our ecological knowledge of how to restore Crown Valley. The field experiment lasted for three growing seasons, from fall 2000 until spring 2003. The funding from the Skinner-Shiply endowment supported the work for the 2002-2003 growing season, and previous years were supported by other grant sources. We tested the hypotheses that (1) *E. macrophyllum* will have a greater reproductive output in weeded plots versus non-weeded plots and (2) that *E. macrophyllum* will have a greater reproductive output when grown in plots dominated by *A. menziesii* as opposed to plots dominated by the exotic *Bromus* spp. or *E. brachycarpum*. To test these hypotheses we used a 2 by 3 randomized factorial design. To study competition between *E. macrophyllum* and the various matrix species (those listed above), 0.5 m² plots were set-up where each matrix species was dominant and sowed with approximately 200 seeds of *E. macrophyllum*. Additionally, each seeded, non-weeded plot was paired with a control plot where all vegetation was manually weeded during the first year of the study (fall 2000).

**Results**

The 2001-2002 growing season was very dry and no *E. macrophyllum* plants reproduced in any of the treatments. Because of this, we could not analyze fecundity data for *E. macrophyllum* and therefore, the rest of the results focus on data from the 2000-2001 and 2002-2003 growing seasons.

During the 2000-2001 *E. macrophyllum* plants growing in weeded plots produced more fruit than in the non-weeded plots (Figure 1). For non-weeded plots, *E. macrophyllum* had the greatest fecundity in the plots dominated by *Bromus*, but this difference was only marginally significant (P=0.08; Figure 1).

![Figure 1.](image)

During the 2002-2003 season, *E. macrophyllum* plants growing in the weeded plots again had the greatest fecundity, even though weeding took place two years earlier (Figure 2). There was also a matrix species effect, where *E. macrophyllum* plants growing in *Bromus* plots had the greatest fecundity (Figure 2).
We used a multiple regression to assess the relative effects of percent cover of different species groups on the fecundity of *E. macrophyllum*. The model accounted for approximately 58% of the variation ($F_{3,26}=12.21\; P<0.0001$). Native forbs had the largest negative effect on fecundity, followed by exotic forbs and finally exotic grass. Increasing percent cover of each matrix species contributed significantly to lower fecundity. In late winter of 2002, when seedlings of *E. macrophyllum* were small (~2-4 cm in diameter) we measured surrounding neighbor density and species and classified each seedling of *E. macrophyllum* as either healthy or wilting. We then used a logistic regression to assess the impacts of seedling density on seedling survival of *E. macrophyllum*. We found that density of the exotic, *Erodium brachycarpum*, had a significant effect on *E. macrophyllum* seedlings be classified as "wilting" ($P<0.001$). No other seedling densities (*Amsinckia* or *Bromus* had an effect on the likelihood that an *E. macrophyllum* seedling would wilt). A regression of *E. macrophyllum* fecundity against overall stem density in plots was also significant (Figure 3; $R^2_{adj}=0.41\; F=21.3\; P<0.0001$).
Plots that were weeded in fall of 2000 were not weeded again in fall 2002 so any plants growing in them represent natural re-establishment or “invasion” following removal of all species (except *E. macrophyllum*). We found that weeded plots did not achieve as great as cover for any one species group compared to non-weeded plots, although total cover was comparable (Figure 4).

Conclusions

Fecundity of *E. macrophyllum* was severely affected by competition from all three matrix species; for both years *E. macrophyllum* produced more fruits in weeded plots compared to non-weeded plots. However, density can also play an important role in affecting fecundity because less dense plots had greater fecundity. Exotic grasses are often the focus of many native vs. exotic competition studies e.g. (Dyer and Rice 1996; Hamilton et al. 1999), but our results suggest that at lower densities, the impact of *Bromus* on *E. macrophyllum* is not as great as either *Amsinckia* or *E. brachycarpum*. This is not as we hypothesized and it means that simply applying a restoration technique the reduces exotic grass cover may not be enough if it results in increased density of forbs.

Although *E. macrophyllum* apparently does well when competing with *Bromus*, there could be intrinsic properties of the *Bromus* plots aside from *Bromus* cover that allows *E. macrophyllum* to do well in these plots. This may be especially true because *E. macrophyllum* had the greatest fecundity in the weeded *Bromus* plots, suggesting that there is something about the *Bromus* plots even in the absence of *Bromus* that allows for *E. macrophyllum* to have high fecundity. We are still waiting for soil analyses from each of the plots which may help us understand what it is about *Bromus* plots that allow for the greatest reproductive output of *E. macrophyllum*. Additionally, *Bromus* density may have been especially low in 2002-2003 because they previous drought year they had poor seed reproduction.

The chances that *E. macrophyllum* seedlings would survive was related to the density of neighboring *E. brachycarpum* seedlings. *Erodium brachycarpum* may have
had the greatest effect on *E. macrophyllum* seedling death because they are closely related and may compete for the same resources in the same area of the soil profile.

The weeding treatment applied in fall 2000 had a similar effect on plant cover as some of the current restoration approaches currently being undertaken in Crown Valley (Allen unpublished data) in that exotic grass cover was reduced and native and exotic forb cover was increased. Although the total cover of weeded plots in 2003 surpassed total cover of some non-weeded plots, they remained less dense. And as mentioned earlier, plant density and not just cover is an important factor in determining reproductive output of *E. macrophyllum*.

Plant fitness is not just a function of fecundity, but also of establishment and subsequent survival. Seedling establishment can be affected by soil microsites and manually weeding plots altered soil microsites by removing litter. *Bromus* was very slow to re-colonize weeded plots. While it may be intuitive to think that when all competitors are removed (i.e. weeded the plots) *Bromus* returned with the lowest cover, therefore we relieved competitive suppression, this may be incorrect. It is quite likely that weeded plots were quickly re-colonized with native and exotic forbs because some of these species have increased germination on exposed soils (Rice 1985). Non-*Bromus* plots may have high density and cover of native and exotic forbs because the preferentially establish where there is not a dense buildup of litter.

**Literature Cited**


