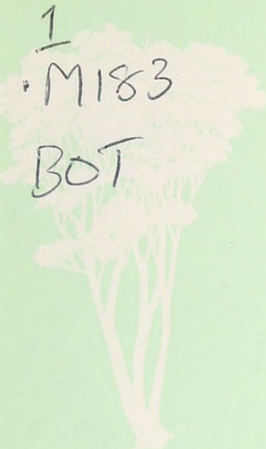

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INVASIVE EUROPEAN ANNUAL PLANTS IMPACT A RARE ENDEMIC SUNFLOWER

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ABSTRACT

Pentachaeta lyonii A. Gray is a state- and federally-listed endangered species, endemic to heavily invaded southern California grasslands. Recent population extirpations resulting in a decrease in range size have prompted investigation into the effects of invasive annual plants on this species. The goals of this study were (1) to examine the impacts of competition from non-native species from three different functional groups (annual grasses, early-season forbs, and late-season forbs) on *P. lyonii* success in the field and in pots, (2) to determine which non-native species/functional groups have the greatest competitive effect on *P. lyonii*, and (3) to evaluate the environmental conditions that contribute to the displacement of *P. lyonii* by non-native plants. In the field, at two sites over two years, control plots were paired with plots in which non-native competitors were clipped at the soil surface. In pots, individual *P. lyonii* plants were grown in competition with all three groups of non-native competitors at both high and low density. In both the field and in the pots, all three non-native plant groups had negative effects on *P. lyonii* reproductive potential, with *Centaurea melitensis* L. having the greatest effect. The effects on *P. lyonii* height were variable among non-native competitors and between years. Comparisons made of environmental features of sites where *P. lyonii* has been extirpated to those where it persists suggested that the presence of annual grass is associated with *P. lyonii* extirpation. Management of *P. lyonii* presents a challenge considering the tendency of this species to coexist with non-native annual plants due to their common disturbance-dependence, and the ubiquity of European annuals in *P. lyonii* habitat.

Key Words: California grassland, competition, conservation, endangered species, non-native invasive plants, *Pentachaeta lyonii*, rare plants, restoration.

Pentachaeta lyonii A. Gray (Asteraceae) is a state and federally listed endangered species endemic to southern California grasslands (Fotheringham and Keeley 1998). Following its extirpation at sites in the southern part of its range, *P. lyonii* became restricted to 21 populations in the Santa Monica Mountains and Simi Hills, persisting entirely within the increasingly suburban northern Los Angeles and southern Ventura counties. Historically, *P. lyonii* had a wider distribution in the Los Angeles basin, Santa Catalina Island, and San Diego (Hickman 1993), but as many as 15 populations have been extirpated within recent decades, and many of the remaining populations appear to be in decline (Brigham 2007). The U.S. Fish and Wildlife Service (1999) recovery plan for *P. lyonii* identifies competition from invasive non-native plants as a possible cause of the species' decline. In the case of a rare endemic such as *P. lyonii*, which has already lost at least 45% of its populations in recent decades, and with the remaining populations geographically isolated by fragmentation, competitive pressures could contribute to local declines and possibly to its ultimate extinction.

Annual surveys done by the National Park Service of both *P. lyonii* numbers and the presence of invasive species have indicated a possible relationship between invasion and declines, but no competition studies have been done previous to the present work. Invasive species do play an important role in native species diversity declines (Hobbs and Mooney 1998; Simberloff 2005). Impacts include the alteration of ecosystem functioning (Evans et al. 2001), altered disturbance regimes (Brooks et al. 2004) and competition for resources (Dyer and Rice 1997; Eliason and Allen 1997; Brooks 2000). Rare native plants can be particularly vulnerable to competition from invasive plants (Huenneke and Thomson 1995; Walck et al. 1999; Miller and Duncan 2003; Kingston et al. 2004; Thomson 2005; Corbin et al. 2007), especially those species

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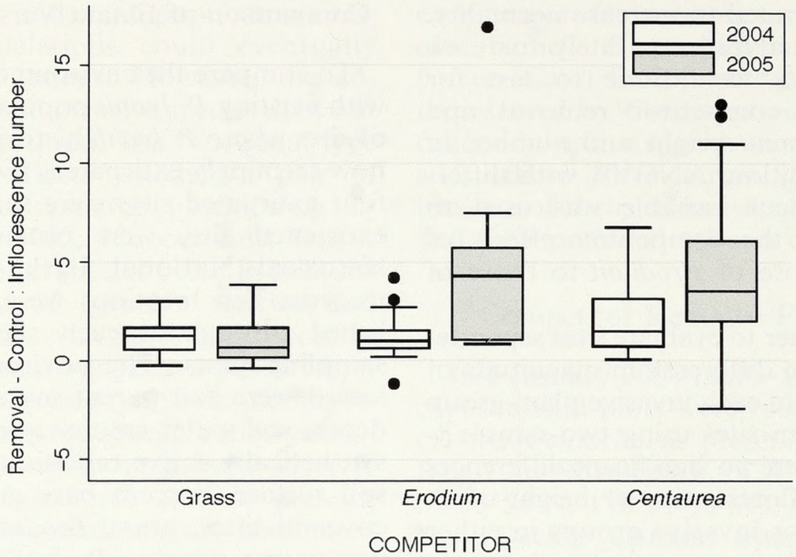

FIG. 1. Differences in number of inflorescences on *P. lyonii* plants between paired field plots. Pairs consisted of non-native competitors removed, and competitors present. Results are shown for two different seasons. Box plots are centered at the median, and whiskers indicate the octiles. Paired t-tests showed significant differences in all cases ($P < 0.01$).

Centaurea and grasses, ($P < 0.05$), but not significant between *Centaurea* and *Erodium* ($P = 0.5688$). Grasses and *Erodium* did not differ significantly in their competitive effects on *P. lyonii* inflorescence number ($P = 0.1426$).

Effects from competition on height of *P. lyonii* differed among the non-native functional groups and between years (Fig. 2). In four of the six cases, differences in height were not significant for competition vs. no-competition plants. Significant differences were found between treatments in *Erodium* plots in 2004, where those released from competition grew taller than those in control plots ($P = 0.01$, Fig. 2). In contrast, in 2005, plants competing with annual grasses grew taller than those in plots with competitors removed ($P < 0.01$, Fig. 2). In 2004, *P. lyonii* plants growing without competition from *Centaurea* were marginally taller than those in control plots ($P = 0.064$, Fig. 2). Annual grasses had a greater effect on *P. lyonii* height in the field than *Centaurea* or *Erodium* ($P < 0.05$).

Pot Competition Experiment

Under the more controlled research conditions of the pot experiment, competition from all non-native groups had a negative effect on *P. lyonii* reproductive potential. *Pentachaeta lyonii* plants produced significantly fewer inflorescences when

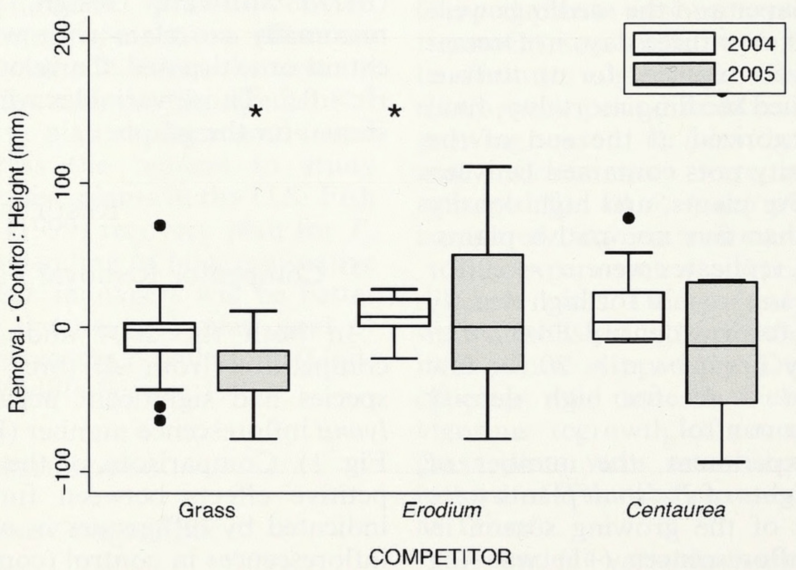

FIG. 2. Differences in height (mm) of *P. lyonii* plants between paired field plots. Pairs consisted of non-native competitors removed, and competitors present. Results are shown for two different seasons. Box plots are centered at the median, and whiskers indicate the octiles. Asterisks indicate cases in which paired t-tests showed significant differences between treatments.

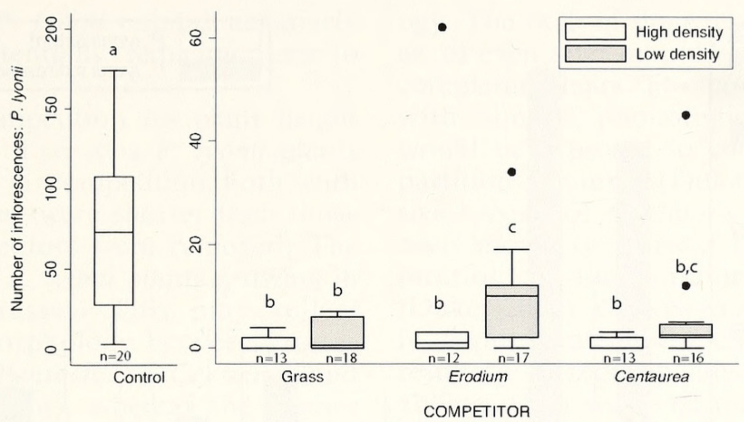

FIG. 3. Numbers of inflorescences on *P. lyonii* plants grown in pots with different non-native competitors growing at both high and low density, compared with *P. lyonii* plants grown in pots without competitors (control). Box plots are centered at the median, and whiskers indicate the octiles. Different letters above the plots indicate significant differences (Tukey HSD).

grown in pots with non-native competitors at both low and high densities compared with control plants grown without competition ($P < 0.001$, Fig. 3). *Pentachaeta lyonii* plants grown with *Erodium* or *Centaurea* at low density had more inflorescences than those growing with *Erodium* or *Centaurea* at high density, or those growing with annual grasses (Fig. 3). Similarly, *P. lyonii* plants growing without competition (control) were significantly taller than plants growing in competition with all three non-native species groups, both at high and low densities ($P < 0.001$, Fig. 4). With all three invasive competitors, *P. lyonii* plants competing in low-density pots were taller than those in high-density pots; however, these differences were only significant in the *Erodium* group (Fig. 4).

Comparison of Extant Versus Extirpated Sites

The logistic regressions suggested that high cover of litter, annual grasses, and non-native plants other than those in our target groups, as well as low cover of *Erodium* and bare ground were good predictors of *P. lyonii* extirpation ($P < 0.05$ in all cases, Fig. 5). Nonmetric multidimensional scaling yielded a final $stress_2$ of 0.33747. All of the environmental variables that were correlated with whether the population at a site was extant or extirpated had $r^2 > 0.2$ except for volumetric water content and percent cover of *Centaurea*. There was a clear separation of extant from extirpated sites (along the horizontal axis). The factors that were most positively correlated with sites supporting extant populations of *P. lyonii* were percent cover of *Erodium*, PAR and percent bare ground. Amount of litter and annual grasses were the most negatively correlated with sites with extant populations (Fig. 6).

DISCUSSION

This study addressed the direct effects of competition from three different functional groups of non-native plants on *P. lyonii*, and the factors possibly contributing to its extirpation. Competition from all three groups of non-native plants reduced the reproductive potential

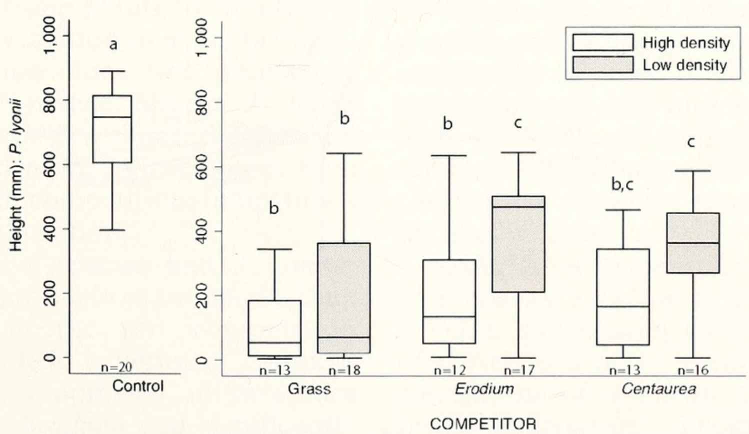

FIG. 4. Heights of *P. lyonii* plants grown in pots with different non-native competitors grown at both high and low density, compared with *P. lyonii* plants growing in pots without competitors (control). Box plots are centered at the median, and whiskers indicate the octiles. Different letters above the plots indicate significant differences (Tukey HSD).

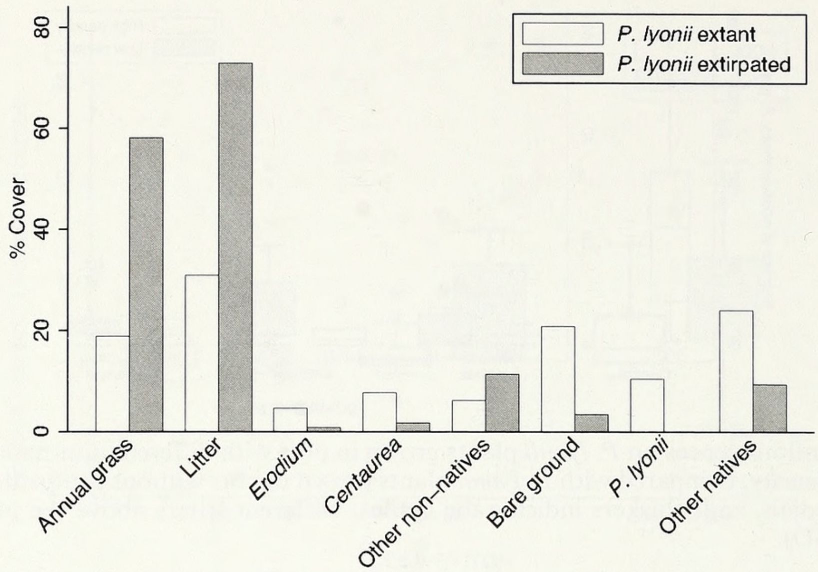

FIG. 5. Comparison of the composition of sites where *P. lyonii* is extant and sites where it is extirpated.

of *P. lyonii*, and the presence of annual grasses not only resulted in direct competitive interactions, but also was implicated as an indirect factor contributing to *P. lyonii* extirpation.

Direct Effects of Competition

The competitor removal experiment took place over two field seasons with very different environmental conditions (2003–2004 and 2004–2005), and examined two possible indicators of competitive effects on *P. lyonii*: number of inflorescences produced and plant height. Effects of competition on the number of inflorescences remained consistent over both field seasons for all three invasive plant groups, despite the large difference between years in available soil moisture. 2004–2005 was an exceptionally wet year (56 cm above average), with four times more rainfall than in 2003–2004. Even with an excess of a potentially limiting resource, competitive interference from non-native plants significantly reduced the reproductive output of *P. lyonii*. This indicated that these invasive plants have a superior ability to capture other important limiting resources (perhaps nutrients, space, and/or light). These results were corroborated in the pot competition study, where growing conditions were more controlled, and water was generously provided. The reduction in number of inflorescences across the board indicated that at least three non-native plant groups that

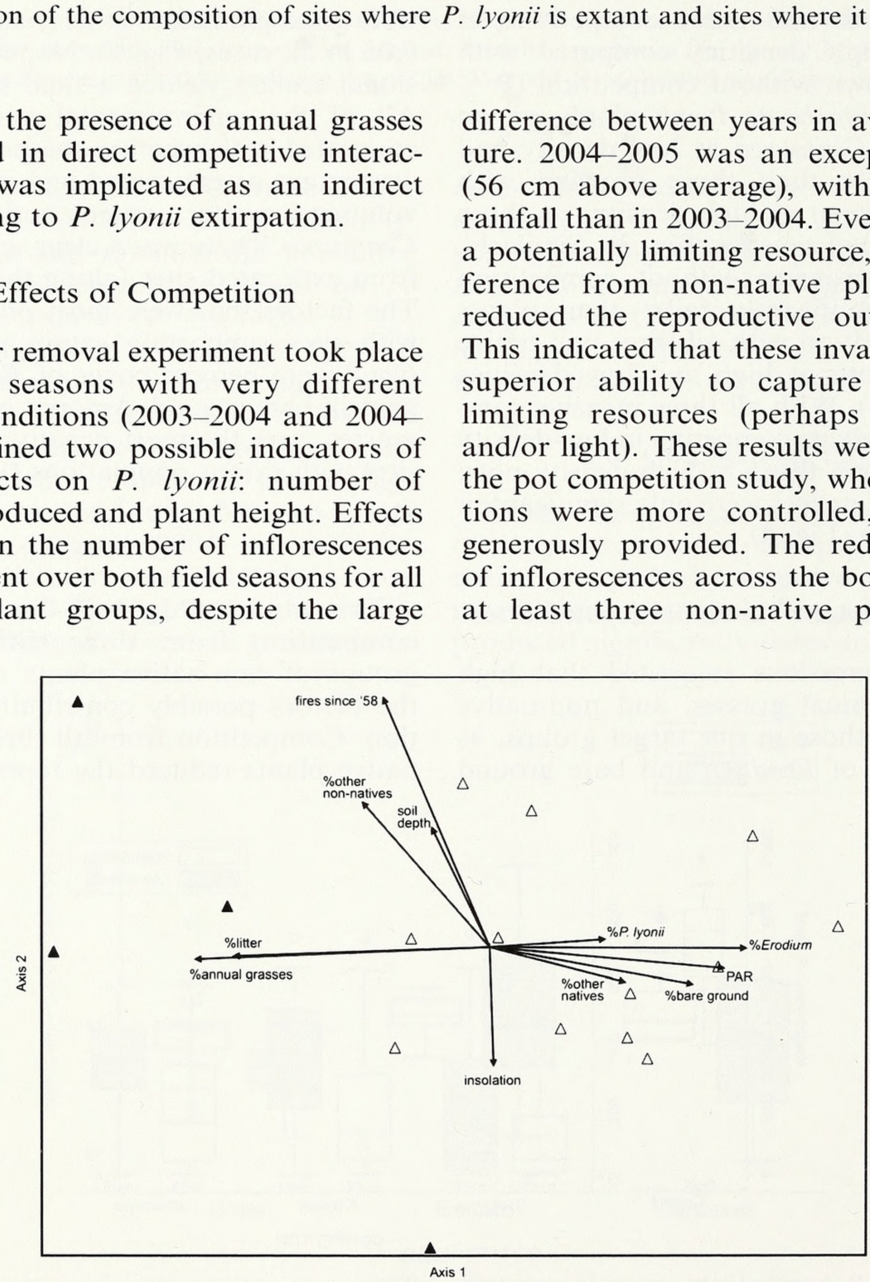

FIG. 6. Nonmetric multidimensional scaling of environmental variables. Ordination rotated so Axis 1 correlates maximally with extant (unfilled triangles) versus extirpated (filled triangles) sites. The lengths and directions of the vectors indicate the strengths and directions of the correlations with the axes.

commonly occur in *P. lyonii* habitat negatively impact fecundity, potentially reducing time to extinction.

The impacts of competition on plant height were less clear. In both seasons *P. lyonii* plants growing in the field in competition both with *Centaurea* and *Erodium* were shorter than those in plots where competitors were removed. The opposite was true for *P. lyonii* plants growing in competition with grasses. This may reflect differences in root morphology between grasses and forbs. The forbs, *Pentachaeta*, *Centaurea* and *Erodium*, possess taproots, whereas the grasses have fibrous root systems. These rooting differences may cause interspecific variation in the ability of plants to access below-ground resources and thereby affect aboveground growth and competitive dynamics (Gurevitch et al. 2006). They may also account for the difference in effects between wet and dry years. Height differences were greater in the forb groups in 2003–2004, when soil moisture was more limited, than in 2004–2005 when it was more abundant.

Functional group phenology may contribute to differences in height response between *P. lyonii* competing with forbs and *P. lyonii* competing with grasses. Both *Centaurea* and non-native grasses typically grow taller than *P. lyonii* (Hickman 1993), and can potentially reduce available light. However, the grasses gain height earlier in the season than *Centaurea*, which spends its first few months as a basal rosette and then matures later in the season. *Erodium* also grows rapidly early in the season, but it is generally of shorter stature than *P. lyonii* (Hickman 1993), and likely does not significantly reduce the light available to *P. lyonii* plants. The large height difference in grass plots between taller *P. lyonii* plants in control plots and shorter ones in plots from which competitors had been removed in 2004–2005 may have been due to the abundance of rainfall that year. Greater moisture availability likely resulted in exceptionally fast growth rates of grasses, causing *P. lyonii* plants to elongate to compensate for early reduction in available light. However, this response does not necessarily indicate superior performance. Shorter *P. lyonii* plants that were growing without competition from grasses produced more inflorescences than tall plants growing with competition, indicating a trade-off in resource allocation.

None of the invasive species had a greater effect on *P. lyonii* reproduction or height than any of the others in the pot competition experiment, but in the field experiment competition from *Centaurea* suppressed inflorescence production more than *Erodium* and significantly more than annual grasses did. *Centaurea melitensis* and *P. lyonii* are both late-season annuals with basal leaf rosettes and taproots, sharing functional traits in both phenology and morphology. The bulk of their reproductive efforts occur as, or even after, annual grasses and *Erodium* are completing theirs. Two co-occurring plant species with similar phenologies and morphologies would be expected to compete for, rather than partition resources (Dukes 2002). Another invasive species of *Centaurea* (*C. solstitialis* L.) has been shown to increase late-season evapotranspiration in the communities it has invaded (Dukes 2001). *Centaurea melitensis* may, similarly, deplete water more efficiently than *P. lyonii*, resulting in reduced late-season resource availability, when water becomes more limiting, and ultimately reduced reproductive capacity.

Differences in the phenologies of annual grasses, *Erodium*, and *Centaurea* could subject a *P. lyonii* individual to competition early in development (annual grasses and *Erodium*) as well as later during flowering (*Centaurea*). Depending on the species composition of the immediate neighborhood of a *P. lyonii* plant, competitive pressure could affect an individual plant throughout its life cycle.

Environmental Factors Associated with Extirpation

In the absence of outright destruction of habitat, it is difficult to be certain of the causes of local extinction of this species, but comparisons of sites with extant populations and sites with extirpated populations can identify environmental factors correlated with extirpation. The three variables that were the best predictors of extirpation were related. Percent cover of annual grasses, percent cover of litter, and low percent cover of bare ground are all associated with *P. lyonii* extirpation, and with annual grass invasion and dominance. The persistence of litter in some annual grass species can reduce open patches of bare ground through the winter rainy season, when germination of *P. lyonii* takes place. The light and moisture conditions at ground level can be drastically altered under a layer of grass litter, possibly precluding germination of *P. lyonii*. The association of these three variables suggest that grasses are not only important direct competitors with *P. lyonii*, as indicated in the competitor removal experiment, but also cause indirect competitive pressures strong enough to displace the species locally.

Aside from the implication of annual grass presence as a factor in local extirpation of *P. lyonii*, it is interesting to note the unexpected lack of correlation of *C. melitensis*, and the negative correlation of *Erodium* spp. presence with *P. lyonii* extirpation. The percent cover of *C. melitensis* was not correlated with sites with either extant or extirpated populations of *P. lyonii*. Considering the magnitude of this species' negative effect on *P. lyonii* reproduction, its co-occurrence with *P. lyonii* may not be as common as the co-occurrence of *P. lyonii* with annual grasses. It may be a much newer phenomenon, as the spread of *C. melitensis* in southern California wildlands has been increasing in recent years (Cal-IPC 2008). If this is the case, competition from *C. melitensis* has the potential to pose an even greater threat to *P. lyonii* populations in the future. The unexpected negative correlation of *Erodium* with *P. lyonii* extirpation suggested that it, like *Pentachaeta*, favors sites without extensive annual grass presence.

Management Implications

Conservation biology is a crisis discipline (Primack 2010). Because of the unprecedented rate of species extinctions, often managers are forced to take actions to attempt to preserve endangered species without thorough prior investigations into their ecological relationships. In the case of *P. lyonii*, little is known about its ecology. The disturbed grassland areas where *P. lyonii* occurs exhibit characteristics that promote invasion by non-native species, and non-native plants have dominated many of the sites with extant *P. lyonii* populations over a long period of time. In this study, non-native plants were removed individually by hand. These methods would be extremely labor-intensive and expensive for large-scale, long-term management of *P. lyonii*. However, they are the only methods to date shown to significantly improve reproductive potential for *P. lyonii*. Until alternative methods have been explored, hand-weeding should be implemented at least in the most threatened sites.

Alternative methods should be investigated to facilitate the feasibility of large scale, long-term restoration efforts. The use of monocot-specific herbicides early in the season to eliminate competition from annual grasses may be an option, but effects on the native community as a whole should be studied before implementation. The use of prescribed burning may also be an alternative. However, *P. lyonii's* ability to tolerate fire is poorly understood, and experiments to evaluate the effects of fire frequency, intensity, and seasonality on both *P. lyonii* and its associated community should be carried out prior to consideration as a restoration tool. Moreover, large-scale removal of invasive species in habitats where they are established members of the community can have unexpected and undesirable consequences for ecosystems (Zavaleta et al. 2001; Ogden and Rejmanek 2005).

Conservation and restoration research in California grassland ecosystems has focused primarily on the native perennial grass, *Nassella pulchra* (Hitchc.) Barkworth (Stromberg et al. 2007). However, annual forbs are increasingly recognized as a major native component of these systems (Keeley 1990; Schiffman 2000, 2007), contributing greatly to their biodiversity (Kimball and Schiffman 2003). In some heavily invaded grasslands, native forbs have been excluded from fertile sites, and persist only in marginal, relatively low-resource refugia, where non-native plants cannot invade (Seabloom et al. 2003). The resulting fragmentation of native forb populations and reduction of population size can potentially contribute to local extinction (Lande 1993). In order to preserve biodiversity in California grassland ecosystems, conservation research efforts must include annual forbs.

Although much work remains ahead for the conservation of *P. lyonii*, this study provides a foundation for the design of a sound conservation strategy for this endangered species, and serves as a starting point for further research. More broadly, the information gained here may be relevant to the conservation of other rare annual plants in other Mediterranean-type grassland ecosystems, which are under increasing pressure from the same non-native invaders.

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