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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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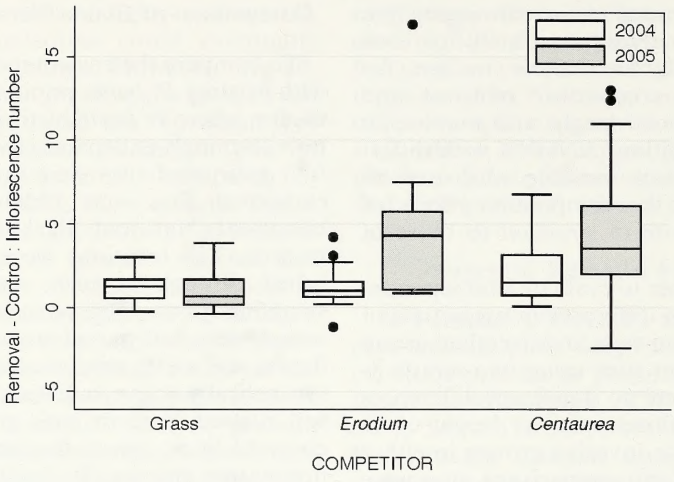

FIG. 1. Differences in number of inflorescences on *P. lyonii* plants between paired field plots. Pairs consisted of non-native competitors removed, and competitors present. Results are shown for two different seasons. Box plots are centered at the median, and whiskers indicate the octiles. Paired t-tests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

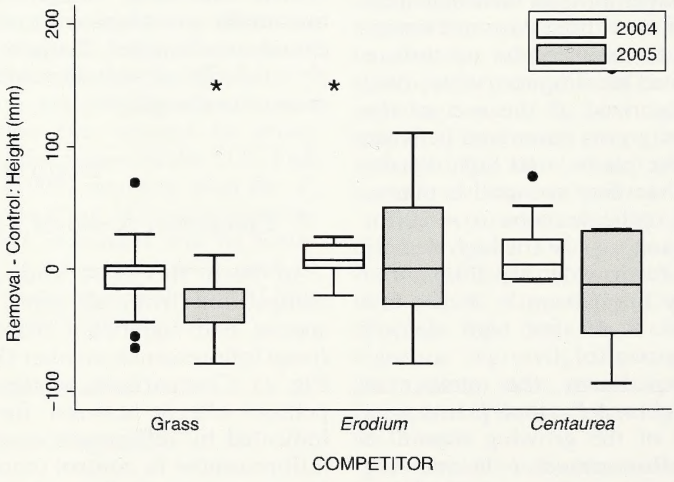

FIG. 2. Differences in height (mm) of *P. lyonii* plants between paired field plots. Pairs consisted of non-native competitors removed, and competitors present. Results are shown for two different seasons. Box plots are centered at the median, and whiskers indicate the octiles. Asterisks indicate cases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

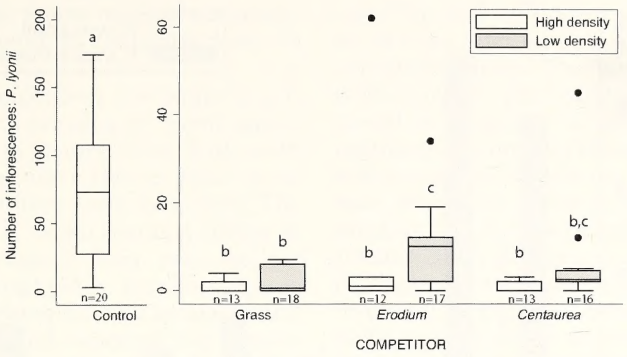

FIG. 3. Numbers of inflorescences on *P. lyonii* plants grown in pots with different non-native competitors growing at both high and low density, compared with *P. lyonii* plants grown in pots without competitors (control). Box plots are centered at the median, and whiskers indicate the octiles. Different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

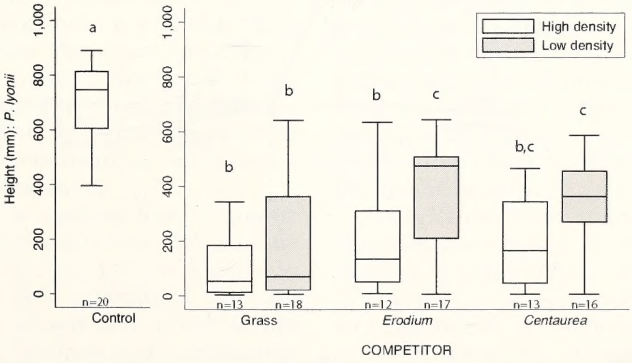

FIG. 4. Heights of *P. lyonii* plants grown in pots with different non-native competitors grown at both high and low density, compared with *P. lyonii* plants growing in pots without competitors (control). Box plots are centered at the median, and whiskers indicate the octiles. Different letters above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

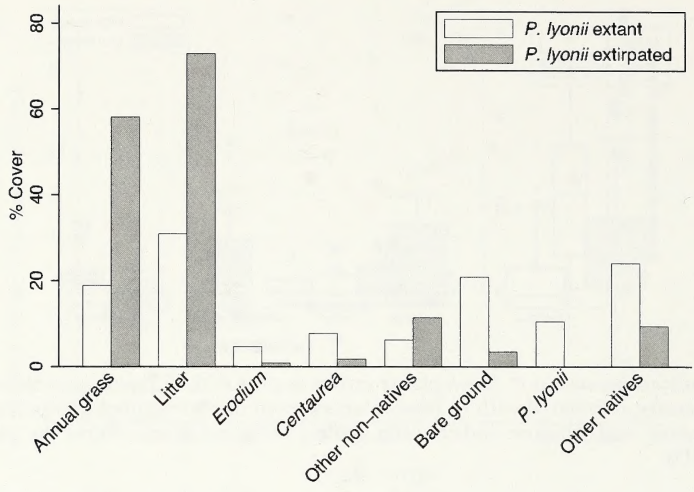

FIG. 5. Comparison of the composition of sites where *P. lyonii* is extant and sites where it is extirpated.

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

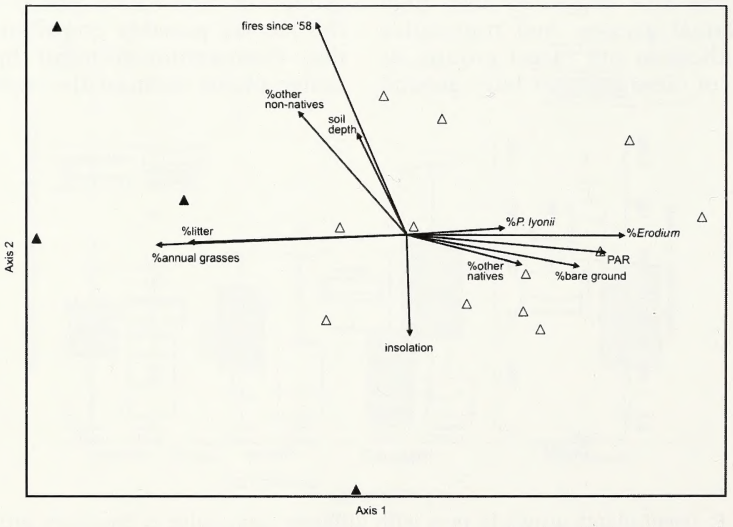

FIG. 6. Nonmetric multidimensional scaling of environmental variables. Ordination rotated so Axis 1 correlates maximally with extant (unfilled triangles) versus extirpated (filled triangles) sites. The lengths and directions of the vectors indicate the strengths and directions of the correlations with 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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POLLEN SIRING SUCCESS IN THE CALIFORNIA WILDFLOWER *CLARKIA UNGUICULATA* (ONAGRACEAE)

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ABSTRACT

Cryptic self-incompatibility (CSI) is a type of non-random mating observed in self-compatible plants in which outcross pollen sires proportionally more seeds than self pollen when both pollen types are available on the stigma. Levels of CSI are known to vary among individuals and populations. We conducted competitive pollinations consisting of mixtures of self and outcross pollen to investigate reports of CSI in certain populations of *Clarkia unguiculata* Lindl. We also investigated how the order of self and outcross pollen deposition on the stigma influences the degree of nonrandom mating. Finally, we looked at whether the source population of outcross pollen affected the ability of outcross pollen to outcompete self pollen. We utilized recessive (white-petaled) maternal (and self pollen donor) plants from a locality near Morro Bay, California, and dominant (pink-petaled) outcross pollen donor plants from 17 localities widespread through the species range in California. Progenies from pollinations made with equal mixtures of self and cross pollen included significantly more outcross-pollinated than self-pollinated offspring in 10 of the 17 cross-pollen donor populations. However six populations showed no significant difference between self- and outcross-pollinated offspring, and one population yielded a majority of progeny sired by self pollen. Progenies from sequential self pollen followed by outcross pollinations included significantly more self offspring in 12 of the donor populations, no significant difference between outcross and self offspring in four donor populations and significantly more outcross offspring in one donor population. Progenies from sequential outcross pollen followed by self pollinations included significantly more outcross offspring in 15 donor populations and no significant difference between outcross and self offspring in two donor populations. Our results confirm the occurrence of non-random mating in *C. unguiculata*, and demonstrate that the degree of non-random mating can depend on the order of self vs. outcross pollen deposition and the source population of outcross pollen. This non-random mating can influence the proportion of self and outcross progeny in sequential pollinations.

Key Words: *Clarkia unguiculata*, cryptic self-incompatibility, geitonogamy, non-random mating, sexual conflict.

Cryptic self-incompatibility is essentially a case of non-random mating in which normal seed set occurs upon self pollination in the absence of competitive outcross pollen. However, with mixtures of self and outcross pollen, weak self rejection reactions promote preferential fertilization by outcross pollen (Bateman 1956; Weller and Ornduff 1977; Eckert and Allen 1997; Kruszewski and Galloway 2006).

Nonrandom mating in plants is not limited to examples of CSI but also occurs in mixtures of outcross pollen from several donors, as in *Raphanus sativus* L. (Marshall and Ellstrand 1986; Marshall 1991, 1998). Of particular interest in these cases is the observation that pollen donors may differ significantly in their ability to sire seed, and the rank order of their siring ability can be consistent across several maternal plants (Marshall 1998). This fact suggests that the source of outcross pollen is likely to affect the degree of non-random mating due to CSI.

Self-incompatibility may evolve in outcrossing populations in response to inbreeding depression. If a normally outcrossing population carries a genetic load, self-incompatibility could confer a fitness advantage to maternal plants if they produce more outcross progeny than selfed progeny in mixed pollinations. In contrast to "complete" self-incompatibility, plants exhibiting CSI maintain the ability to produce progeny through self-fertilization. This ability should confer the fitness advantage of reproductive assurance to annual plants that grow where access to pollinators or mates is limited. During growing seasons when pollinators and other resources are plentiful, non-random mating by favoring outcross pollen allows maternal plants to increase fitness by increasing the proportion of outcross progeny they produce. During less optimal growing seasons, when resources and

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pollinators are limiting, maternal fitness is enhanced through self-pollination.

Another important consideration is the role that non-random mating by favoring outcross pollen might play in promoting outcross pollination in plants with varied patterns of pollen deposition. The number of pollen grains deposited on the stigma in natural populations of *Clarkia unguiculata* Lindl. increases with time (Nemeth and Smith-Huerta 2003), indicating that pollinators make multiple visits to flowers, depositing loads of pollen sequentially over time. These loads of pollen are likely to vary in composition from mixtures of outcross pollen to loads of self pollen. Geitonogamous self pollination is possible since *C. unguiculata* is strongly protandrous (Vasek 1968, 1977; Vasek et al. 1987). A pollinator could visit a flower in the male phase and then visit another flower on the same plant in the female phase resulting in self pollination. It is possible that CSI could promote outcross pollination in cases where the stigma of a flower first receives a load of self pollen and soon after receives a load of outcross pollen. In fact, although geitonogamy is possible (and probable) in *C. unguiculata*, outcrossing rates in a natural population have been measured at greater than 90% (Vasek 1965). Non-random mating by favoring outcross pollen (CSI) may well have contributed to these high outcrossing rates. In fact, CSI is known to occur in at least one population of *C. unguiculata* (Bowman 1987) and in one population of *C. gracilis* A. Nelson and J. F.Macbr.(Jones 1994). Interestingly, CSI was reported to be completely absent from another population of *C. unguiculata* (Travers and Mazer 2000). This suggests that the strength and nature and of non-random mating could vary from population to population and also with the source of outcross pollen.

The purpose of our investigation was to examine a single population of *C. unguiculata* maternal plants to determine whether the order that self and outcross pollen is deposited on the stigma affects non-random mating. Furthermore, we examined if the source population of outcross pollen affects levels of CSI. This closer examination of non-random mating in *C. unguiculata* is important given the possibility of sequential and geitonogamous pollination in *C. unguiculata* (Vasek 1968, 1977; Vasek et al. 1987; Nemeth and Smith-Huerta 2003), the variation in levels of CSI documented previously in two different populations of *C. unguiculata* (Bowman 1987; Travers and Mazer 2000), and that pollen donors may differ significantly in their ability to sire seed (Marshall 1998).

Materials and Methods

Mixed-donor pollinations were employed to determine the relative frequency of fertilization by self vs. cross pollen. Test plants were genetically marked for petal color. Flower color in *C. unguiculata* varies from white to red or purple but most populations are characterized by pink or lavender-pink flowers. White flowers are conditioned by a single recessive allele and pink or red flowers are conditioned by a dominant allele at the same locus (Rasmuson 1920; Vasek 1965, plus extensive unpublished data; Bowman 1984). Plants with pink flowers contain malvidin 3, 5-diglucoside in their flowers, leaves, stems and seedlings (Bowman 1987) whereas plants with white flowers lack this and other anthocyanins. Consequently, flower color can be determined in the seedling stage merely by scoring seedlings as green (non-anthocyanous) or red (anthocyanous) because green seedlings grow up to produce white flowers and red seedlings grow up to produce pink flowers (Bowman 1987; Vasek 1965).

Organization of Experiments

Ten white-flowered families were developed from available stocks from a natural population near Morro Bay, California because they were available and we knew they were fully self-fertile (Vasek 1986). Each family consisted of approximately 6–8 siblings (homozygous for white petal) and was used as a line of maternal test plants, and simultaneously as self-pollen donors.

Seventeen pink-flowered families were developed from available stocks from Morro Bay and 16 widespread localities in California (Table 1). Each family consisted of about 6–8 siblings and was used as a line of cross pollen donors. These plants were homozygous for pink flowers because they were grown from selected, available stocks known to have produced only pink-flowered progeny.

Seeds from the source localities were sown on vermiculite in December, 1987 in a University of California greenhouse in Riverside, California. Subsequently, seedlings were transplanted to 6 inch pots of standard UC soil mix, irrigated as needed, fertilized weekly with half strength Hoagland's solution and grown to maturity in the same greenhouse. Experimental pollinations were made during a period of about two months in the spring of 1988.

Mixed-Donor Pollinations

All experimental pollinations utilized pollen from a pink-flowered cross-pollen donor and pollen from a white-flowered self pollen donor. The self pollen donor was also the seed parent. Pollen was always applied to stigmas which were 1–2 days old as judged by the degree of stigma expansion not greater than 180 degrees (see figure 2 in Smith-Huerta and Vasek 1984).

TABLE 1. SEED COLLECTION LOCALITIES (ALL IN CALIFORNIA) FOR CROSS-POLLEN DONOR PLANTS. DIR = direction from Morro Bay: S = Coast Ranges to the south; N = Coast Ranges to the north; E = Sierra Nevada to the East; DIS = approximate linear distance in km from Morro Bay.

Population	Locality	County	DIR	DIS
15	Morro Bay - Atascadero Rd	San Luis Obispo	—	00
4	Santa Maria	Santa Barbara	S	58
5	Pinnacles Natl. Monument	San Benito	N	126
11	Rancheria Rd	Kern	E	185
6	Kern River	Kern	E	188
13	Caliente Hills, Low Canyon,	Kern	E	189
17	Caliente Hills, High Canyon	Kern	E	190
8	Santa Paula	Ventura	S	193
7	Sequoia	Tulare	E	220
9	Bouquet Canyon	Los Angeles	S	238
14	Laurel Canyon	Los Angeles	S	260
2	Jackson	Amador	E	330
3	Riverside -Fairmount Park	Riverside	S	350
10	San Luis Rey	San Diego	S	398
16	Old Castle Rd	San Diego	S	406
1	Clear Lake	Lake	N	430
12	Feather River, North Fork	Butte	E	485

One protocol (MIX) followed the methodology used by Bowman (1987). Cross pollen and self pollen were mixed together in equal amounts and then applied to the stigma of the maternal test plant, which was also the self-pollen donor. In the second protocol (S/X), self pollen was applied first followed immediately by cross pollen. In the third protocol (X/S), cross pollen was applied first, followed immediately by self pollen.

We pollinated 246 flowers in 82 competitive pollinations. Each pollination included one pollination by each of the three protocols described above. Several siblings of each cross pollen donor population were used, for a total of 47 pollen donors from the 17 cross-pollen donor lines. Thus, the actual competitive comparisons involved closely related siblings rather than identical individuals.

Following competitive pollinations, the resulting capsules were harvested at maturity, the seeds were then separated, counted, weighed and stored over the summer.

Data Harvest

Beginning in October 1988, seeds were sown on vermiculite in small plastic pots and put in a temperature controlled chamber. Temperatures were approximately 20 degrees C with a 12 h day 12 h night lighting schedule. Two weeks after germination, seedlings were moved to a greenhouse for continued development because space in the temperature controlled chamber was limited. Red pigments in stems and along leaf veins develop well with cool temperatures and bright daylight. Our greenhouse conditions were not always optimum for red pigment development (e.g., warm weather). Consequently, if any seedlings were not clearly red or not clearly green they were grown to maturity for direct scoring of flower color.

Analysis

We expect the progeny from competitive (MIX) pollinations to include half pink-flowered outcrosses if mating is non-random. However, preferential functioning of either cross or self pollen will yield ratios of white to pink progeny significantly different from 1:1. The frequency of outcrosses in each resulting progeny was multiplied by 100 and expressed as a percent. The progeny of (S/X) pollinations should include significantly more self pollinated white than pink progeny if mating is random. We expect the first pollen grains on a receptive stigma should interfere with the normal germination of pollen arriving later. The progeny of (X/S) pollinations should include significantly more pink than white progeny.

Each of the 246 progenies from MIX, S/X and X/S pollinations was tested for significant departure from an expected 1:1 ratio of outcrosses to selfs by a G-test (Zar 1984). A Bonferroni P-value correction was applied to avoid inflated type-I error (avoid high risk of false positive results) across the multiple tests (Zar 1984). Progenies from all of the competitive pollinations within the 17 populations were also tested for significant departure from an expected 1:1 ratio of outcross to selfs by a G-test (Zar 1984).

RESULTS

Both the order of pollen deposition and source of outcross pollen had variable affects on the degree of non-random mating due to CSI in our competitive pollinations (Table 2, Fig. 1). In the

TABLE 2. G-TEST VALUES FOR ALL PROGENY PRODUCED IN COMPETITIVE POLLINATIONS. The symbols "*," "**," "***," and "ns" indicate significant difference from a 1:1 ratio of self to outcross progeny at the 5%, 1%, and 0.1% levels, and not significantly different, respectively.

Population	MIX	S/X	X/S
1	68.219***	48.753***	61.926***
2	16.934***	0.134 ns	9.150**
3	34.464***	1.590 ns	51.451***
4	17.357***	0.0055 ns	71.653***
5	32.142***	19.534***	55.477***
6	12.659***	29.500***	46.019***
7	9.419**	11.027***	16.933***
8	14.710***	37.016***	42.659***
9	7.905**	80.327***	2.987 ns
10	7.266**	12.162***	14.009***
11	1.697 ns	29.354***	30.372***
12	2.337 ns	7.703**	24.856***
13	0.032 ns	26.640***	23.774***
14	0.643 ns	9.550**	25.641***
15	0.0303 ns	144.658***	3.412 ns
16	0.024 ns	0.468 ns	13.832***
17	11.512***	106.878***	9.662***

MIX competitive pollinations, 10 of the 17 cross pollen donor populations exhibited CSI, yielding progenies that significantly favored outcross pollen (Table 2, Fig. 1). However six of the 17 pollen donor populations did not exhibit CSI, and one population yielded a majority of progeny sired by self pollen (Table 2, Fig. 1).

In the S/X competitive pollinations, one of the 17 cross pollen donor populations yielded progenies that significantly favored outcross pollen, 12 pollen donor populations significantly favored self pollen, and four of the donor populations did not differ significantly from a 1:1 ratio (Table 2, Fig. 1).

Fifteen of the pollen donor populations in X/S competitive pollinations significantly favored outcross pollen, and two donor populations did not differ significantly from a 1:1 ratio (Table 2, Fig. 1).

DISCUSSION

Overall, the results of our MIX pollinations confirm the occurrence of CSI and non-random mating in *Clarkia unguiculata*. More than half of the competitive MIX pollinations yielded progenies that significantly favored outcross pollen, and approximately 20% of competitive pollinations yielded progenies with significantly more offspring produced by self pollen. Only about 23% of competitive pollinations yielded progenies that did not differ from a 1:1 ratio. Our investigation differs in detail and scope from previous studies of CSI and non-random mating in *Clarkia* (Bowman 1987; Jones 1994; Travers and Mazer 2000), and may help to explain their variable results. Previous studies were conducted within single populations of plants (Jones 1994; Travers and Mazer 2000) or used a commercial seed source (Bowman 1987). Our study included maternal plants derived from one population and outcross pollen plants derived from 17 populations distributed throughout California. In the present study, competitive pollinations made with pollen from 10 of the 17 populations yielded results similar to those found by Bowman (1987) and Jones (1994) with a majority of pollinations favoring outcross pollen. Competitive pollinations with outcross pollen derived from six of the populations yielded results similar to those found by Travers and Mazer (2000), with outcross pollen favored in fewer than half the pollinations. In contrast to all of the previous studies, competitive pollinations made with outcross pollen derived from 1 of our study populations yielded a majority of progenies in which self pollen was favored significantly over outcross pollen.

Non-random mating when outcross pollen is favored over self pollen has the potential to reduce the negative effects of inbreeding depression in populations through the increased production of outcross progeny, at the same time preserving the ability of individuals to produce offspring by selfing. Inbreeding depression has been documented in several populations of *C. tembloriensis* Vasek (Holtsford and Ellstrand 1990) and the magnitude of this inbreeding depression was shown to vary between populations. It is possible that populations of *C. unguiculata* could vary with respect to genetic load, and selective pressure promoting non-random mating favoring self pollen might vary between populations. This could account for the variation observed in non-random mating in previous studies (Bowman 1987; Jones 1994; Travers and Mazer 2000).

As stated above, non-random mating by favoring outcross pollen not only promotes the production of outcross progeny, but also preserves the ability of a plant to produce offspring through self pollination. This provides reproductive assurance to annual plants that grow where access to mates may be limiting. Numbers of individuals in populations of *C. unguiculata* can vary from only a few plants to thousands of individuals (Lewis and Lewis 1955; Vasek 1964) and those growing in more marginal areas of the species range may experience large seasonal fluctuations in population size (Lewis and Lewis 1955). During seasons when plant populations are small, pollinators are rare, and access to mates limited, fitness might be enhanced by the production of self progeny.

Our sequential pollinations address the question of whether non-random mating by favoring outcross pollen can somehow mitigate the effects of geitonogamy when self pollen arrives first on

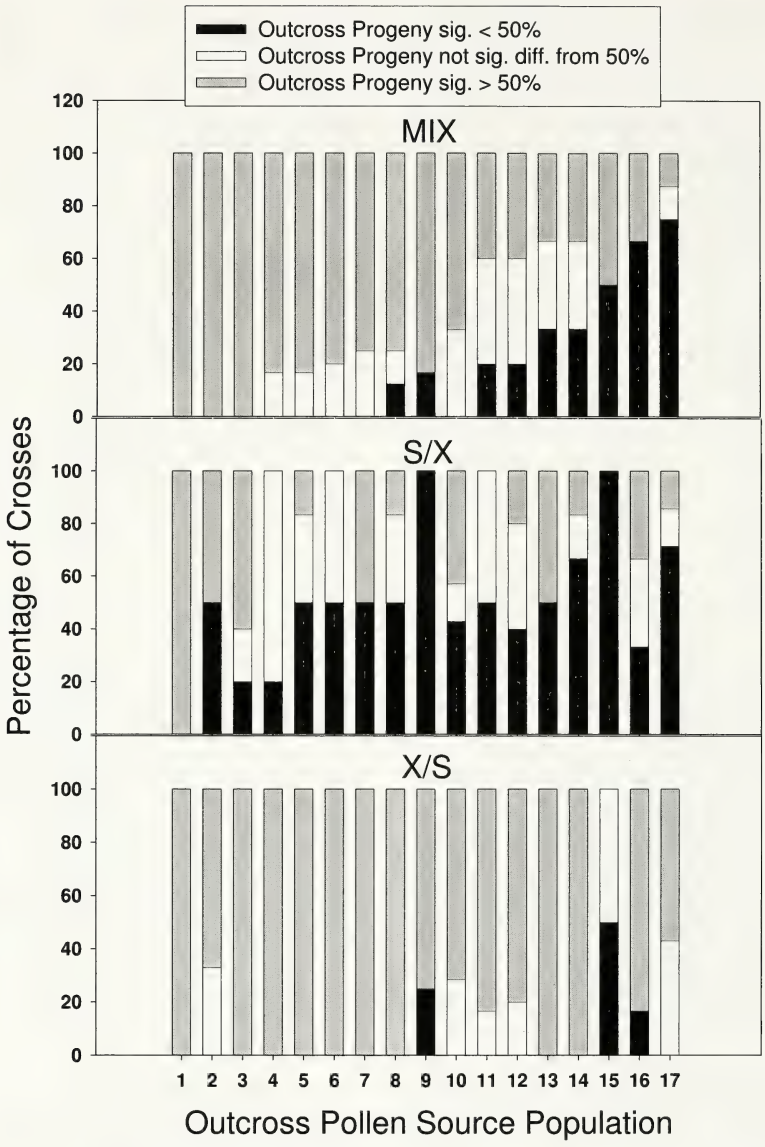

FIG. 1. Percent of total competitive pollinations within each of 17 cross pollen donor populations that yielded outcross progenies either significantly more or significantly less than expected by chance, or yielded outcross progeny not significantly different from chance expectations. For the MIX treatment, cross and self pollen were mixed together in equal amounts and then applied to the stigma of the maternal test plant, which was also the self-pollen donor. For S/X, self pollen was applied first followed immediately by cross pollen. For X/S, cross pollen was applied first, followed immediately by self pollen.

the stigma followed by outcross pollen. Rates of geitonogamy are influenced by the number of flowers that are open simultaneously on a plant (Karron et al. 2004). *Clarkia unguiculata* is strongly protandrous (anthers shed pollen before the stigma becomes receptive), and may have as many as 12 open flowers per spike (Vasek 1968, 1977; Vasek et al. 1987). Anthers of individual flowers shed pollen for up to 11 days before the stigma becomes receptive (Vasek 1968, 1977; Vasek et al. 1987). If pollinators visit more than one flower per plant, geitonogamous self pollination is likely. Geitonogamy does not provide reproductive assurance and is considered to be "an unavoidable by-product of selection for outcrossing success" in plants that have numerous flowers that are open simultaneously in an inflorescence (Goodwillie et al. 2005). It is possible that non-random mating by favoring outcross pollen could mitigate the unavoidable selfing that occurs when pollinators visit more that one flower per plant in *C. unguiculata*, and our S/X sequential pollinations were designed to explore this idea. If mating is random, S/X

pollinations (outcross pollen grains deposited immediately after self pollen grains) should yield progenies with significantly more self than outcross offspring. Twelve of the donor populations did yield progenies that significantly favored self pollen, even though six of these populations displayed non-random mating in MIX pollinations. In these cases, the documented presence of non-random mating did not appear to mitigate the effects of geitonogamy. In contrast, S/X sequential pollinations in five of the donor populations did not favor self progeny. Of these, four of the populations produced progeny that did not differ from a 1:1 ratio of self to outcross, and one population significantly favored outcross pollen. With one exception (population 16), these were the donor populations that displayed the strongest non-random mating by favoring outcross pollen in MIX pollinations. It appears that strong non-random mating by favoring outcross pollen has the potential to mitigate the effects of geitonogamy when self pollen arrives first on the stigma followed by outcross pollen.

Our X/S pollinations explored further the interactions of non-random mating and geitonogamy in *Clarkia*. The X/S pollinations were expected to produce significantly more outcross than self progeny in all pollinations, since the advantage of outcross pollen arriving first on the stigma should be enhanced by non-random mating. This proved to be the case in all but two of the donor populations which showed no significant difference between the number of self and outcross progeny produced. Interestingly, these two donor populations were the only populations in which self pollen was significantly favored in all of their sequential S/X pollinations.

The physical mechanism responsible for differential siring success in non-random mating and CSI has been investigated in other studies (Hessing 1989; Weller and Ornduff 1989; Aizen et al. 1990; Eckert and Allen 1997; Kruszewski and Galloway 2006; Figueroa-Castro and Holtsford 2009). In all of the above investigations, with one exception, outcross pollen germinated faster on the stigma and grew faster through the style than self pollen. The single exception occurred in *Campanulastrum americanum* Small in which pollen tube growth rates did not differ between self and outcross pollen (Kruszewski and Galloway 2006). Although we did not measure pollen germination and tube growth rates in the present study, this was the focus of previous studies in both *C. unguiculata* (Nemeth and Smith-Huerta 2002; Smith-Huerta et al. 2007) and *C. temblorensis* (Smith-Huerta 1996; Kerwin and Smith-Huerta 2000). Similar to *Campanulastrum americanum* (Kruszewski and Galloway 2006), no difference in percent germination or rate of pollen tube growth was observed between self and outcross pollen in single donor pollinations in these two *Clarkia* species (Smith-Huerta 1996; Kerwin and Smith-Huerta 2000; Nemeth and Smith-Huerta 2002). It is possible that self and outcross pollen must be present together on the stigma and in the style for the non-random mating of CSI to occur. This appears to be the case in *Clarkia*. Pollen germination was significantly reduced in two donor pollinations of self + outcross pollen and in outcross + outcross pollen (from two different donors) in *C. unguiculata* (Nemeth and Smith-Huerta 2002). Further, germination of pollen decreased with increasing contact between pollen grains (Nemeth and Smith-Huerta 2002). Pollen-pollen interactions, mediated by the stigma, might provide a possible mechanism to explain the differences in the relative success of self and outcross pollen observed in reported non-random mating and CSI in *Clarkia*.

The present investigation goes beyond an examination of self vs. outcross pollen performance within a single population, and examines the performance of outcross pollen derived from foreign populations. These outcross pollen source populations occur from 58 to 485 km from the maternal (self pollen) population. Clearly, the maternal plants in our study would not normally encounter outcross pollen from these populations. Interestingly, the Morro Bay population, which provided all of our maternal plants, did not show CSI in MIX crosses when Morro Bay plants were the source of outcross pollen. In contrast, levels of CSI could be very high when pollen from foreign populations was used. This great difference in outcross pollen donor success suggests that pollen-pistil interaction may evolve differently in each population of *C. unguiculata*, as a result of sexual conflict between male and female function. In plants, sexual conflict occurs when optimal reproductive fitness strategies for pollen differ from those of the maternal plant. The trait of CSI has the potential to enhance the fitness of ovules but not of pollen, thus creating a male-female sexual conflict. Although sexual conflict has been studied mostly in animals, several recent studies have examined the occurrence of sexual conflict in plants (Prasad and Bedhomme 2006; Lankinen and Larsson 2009; Madjidian and Lankinen 2009). In one instance, similar to the present study, male-female interactions were investigated in cross pollinations between plants derived from 4 different populations of *Collinsia heterophylla* Graham (Madjidian and Lankinen 2009). In this plant, the onset of stigma receptivity may be affected by both the source and recipient of the pollen, with early receptivity and fertilization resulting in the production of fewer seeds than late receptivity. In experimental cross pollinations, it was found that pollen donors from foreign populations were

more successful at inducing stigma receptivity than pollen donors derived from the same population (Madjidian and Lankinen 2009). These results may be interpreted to suggest that there is "sexually antagonistic coevolution" between maternal plants and pollen within populations of *C. heterophylla* (Madjidian and Lankinen 2009). It appears that when maternal plants receive pollen from foreign populations they are somehow "released from the cost of local pollen" (Madjidian and Lankinen 2009). In the present study, CSI and non-random mating varied extensively depending on the population source of outcross pollen. It is possible that this reflects a similar "release from the cost of local pollen" in our experiments.

In sum, we document the occurrence of non-random mating and CSI in crosses between different populations of *Clarkia unguiculata,* and demonstrate that this non-random mating can also influence the proportion of self and outcross progeny in sequential pollinations. The non-random mating observed in CSI may promote outcrossing in protandrous plants subject to geitonogamous pollination and contribute to reproductive assurance when access to mates is limited. Finally, the fact that levels of CSI vary between sources of pollen donors suggests that sexual conflict between pollen and maternal plants may result in coevolution unique to each population of *C. unguiculata.*

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SMALLER *OLEA EUROPAEA* FRUITS HAVE MORE POTENTIAL DISPERSERS: IMPLICATIONS FOR OLIVE INVASIVENESS IN CALIFORNIA

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Abstract

Olea europaea (European olive) is invasive in Australia and widely planted in California. Vertebrates, particularly birds, mediate *Olea* seed dispersal. Fruits are large, but their sizes range widely. We measured fruit widths from 12 study stands in California and constructed esophageal probes in diameters spanning the resulting size range. We then obtained whole-bird frugivorous bird carcasses and used the probes to determine the fruit sizes that each bird species would be anatomically capable of swallowing. This allowed us to develop lists of potential dispersers for each study stand. Even stands with the largest measured fruits had several potential disperser species, but the list of species expanded greatly as fruit sizes decreased. Feral *Olea* stands with remarkably small fruits have been observed in California and Australia. An increase in the incidence of such stands might augment the regional spread rate for the species.

Key Words: Bird-mediated dispersal, European olive, gape width, invasion, museum specimens, *Olea europaea*.

A variety of invasive, or potentially invasive, woody species are dispersed by birds (Richardson et al. 2000; Aslan and Rejmánek 2010). Among these is *Olea europaea* L. (Oleaceae) (European olive, hereafter, *Olea*), an upland species native to the Mediterranean. *Olea* is widely cultivated in California, as well as in other regions similar in climate, as a crop and landscaping species. *Olea* has become invasive in natural areas in Australia, where its fruits are bird-dispersed (Spennemann and Allen 2000b). Field observations have confirmed that birds consume *Olea* fruits in California, as well (Aslan 2010). Since (a) the climate is appropriate for *Olea* establishment, and (b) the species demonstrates dispersal mutualisms with resident birds, a potential incipient invasion by *Olea* in California appears possible.

Effective dispersal of *Olea* (and, by extension, the likelihood of invasion) may be dictated by fruit sizes. *Olea* fruit sizes range enormously (e.g., from a minimum of 5.6 mm to a maximum of 28.2 mm in width for fruits we collected from studied Californian populations). In general, however, the species is large-fruited and seed mass is positively correlated with fruit size (Alcántara 1995), making vertebrate-mediated dispersal necessary for removal of seeds from parental locations. Since the species is cultivated primarily for human food, artificial selection for large fruits has been imposed on *Olea* strains (Rey and Gutiérrez 1996). However, fruit size may constrain seed dispersal. Particularly large fruits of *Olea* and other species are often pecked rather than swallowed whole by birds (Rey and Gutiérrez 1996). This strategy is necessitated by gape width limitations, but appears energetically costly for birds, which prefer to swallow fruits whole when they are able to do so (Rey and Gutiérrez 1996). Fruit pecking transforms a mutualistic relationship into seed predation by rarely promoting effective dispersal beyond the stand canopy (Rey et al. 1997). Among wild olives, therefore, gape width limitations of potential dispersers appear to counteract selective pressures favoring large seeds (e.g., enhanced germination success and greater seedling vigor) and likely dictate seed size maxima (Alcántara and Rey 2003).

Olea was introduced to Australia in 1800 and planted in many locations over the next two centuries, but its profitability as a crop species was generally low, and most olive stands were abandoned (Hartmann 1962; Spennemann and Allen 2000b). Fruit and seed sizes in feral *Olea* populations in Australia are reportedly smaller than those of cultivated orchards (Spennemann and Allen 2000a). Size reduction in self-seeded populations that are geographically separated from any parent stand may result from one of two mechanisms: lack of anthropogenic cultivation and care in the early stages of stand establishment, or selection of smaller fruits by birds. Care (in the form of irrigation, pruning, fruit harvesting, or fertilization) is no longer provided in abandoned olive stands in Australia nor in our study stands in California, all of which are old and established as hedgerows rather than orchards; however, at least some irrigation was likely performed at initial planting in both countries. The phenomenon of fruit size reduction following disperser-mediated selection has been observed for palm seeds following toucan

TABLE 1. *OLEA EUROPAEA* STUDY STANDS AND RELEVANT CHARACTERISTICS.

Study stand (ranked by minimum fruit size)	Location	Land-use type	Varietal	Feral
1	Chico	Semi-natural	Mission	Yes
2	Chico	Semi-natural	Mission	No
3	Chico	Urban	Mission	No
4	BCCER	Semi-natural	Mission	No
5	PC	Agricultural	Manzanillo	No
6	Davis	Agricultural	Manzanillo	No
7	PC	Agricultural	Manzanillo	No
8	Davis	Agricultural	Manzanillo	No
9	BCCER	Semi-natural	Mission	No
10	Davis	Urban	Manzanillo	No
11	PC	Agricultural	Manzanillo	No
12	Davis	Urban	Manzanillo	No

exclusion (Galetti et al. 2010), while birds in a Spanish woodland selected *Prunus mahaleb* L. fruits that were significantly smaller on average than the mean size of available fruits (Jordano 1995). Furthermore, minimum fruit size was found to be more predictive of dispersal interactions than was average fruit size in a network of frugivores and large-seeded fruit in New Zealand (Kelly et al. 2010), implying that fruits small enough for ingestion were attractive even when they were surrounded by larger seeds. Logically, fruit size is likely to decrease following these selective pressures, and the suites of vertebrate species able to potentially disperse olive seeds may grow as a result (Spennemann and Allen 2000a). Theoretically, then, rates of dispersal and invasion may escalate as feralization continues.

In California, spontaneous spread of *Olea* is presently rare; we know of only two completely feral and reproductive populations of *Olea* at this time. Since *Olea* stands in California exhibit a range of fruit and seed sizes, we expect that the bird-mediated dispersal potential of different stands varies according to those sizes. Most *Olea* individuals, cultivated in orchards, have large fruits and receive irrigation, fertilizer, and pruning. Outside of orchards, many trees in old hedgerows that receive little care today but were likely irrigated at planting also exhibit large fruits. We hypothesize that dispersal of seeds from such trees is possible for only a limited number of bird species and is therefore relatively rare. We have, however, identified several *Olea* stands (generally planted for landscaping rather than crop purposes) with fruits that are quite small. We hypothesize that a wider diversity of bird species are capable of dispersing these fruits.

As a general rule, decreasing bird body size shows a slight but significant correlation with increasing population density across species (Juanes 1986). As olive fruits shrink and birds of smaller body size are capable of consuming them, the number of individual birds capable of dispersing fruits should increase at a greater rate than the number of disperser species. Correspondingly, dispersal potential itself will grow at an accelerating rate.

Due to both of these increases (increased diversity and increased population sizes) among disperser birds, we consider it likely that expanded suites of potential dispersers will result in greater dispersal, possibly creating small-seeded and small-fruited feral populations as has likely occurred in Australia (Spennemann and Allen 2000b). The appearance and multiplication of such feral populations in California might signify the beginning of a large-scale invasion by this species.

Here, we used esophageal probes and Californian bird carcasses to identify the suites of bird species that are likely capable of swallowing *Olea* fruits of varying sizes. We compare the diversity of birds comprising each suite and discuss the probable implications of fruit size reduction for *Olea* invasiveness.

METHODS

Study Species: *Olea europaea*

In California, *Olea* occurs in at least 27 counties (Calflora 2010) and is valued at more than $86 million as an agricultural commodity (CDFA 2008). For this study, we examined fruits from *Olea* stands in Yolo and Butte Counties in north-central California. Among the 12 focal stands, three were located in urban areas (Chico 3, Davis 3, and Davis 4), five in agricultural areas (Davis 1, Davis 2, PC 1, PC 2, and PC 3), and four in semi-natural areas (an abandoned homestead (BCCER 1 and 2), a municipal protected area (Chico 2) and one completely feral population in a previously-grazed, protected canyon (Chico 1) (Table 1). None of the study stands currently receive irrigation or fertilization.

Esophageal Fruit Passage Assessment

In January, 2009, we collected 10 ripe olives from each of up to 12 trees per study stand, for a

total of 60–120 olives from each of the 12 study stands. We used digimatic (Mitutoyo America Corporation, Aurora, IL) calipers to measure the width of each olive to the tenth of a millimeter. We calculated the mean, minimum, and maximum fruit widths for each population. Transverse diameter (width) was utilized because it is likely to be the limiting dimension determining the maximum size of fruits that can be swallowed whole (Wheelwright 1985). We examined the relationship between fruit sizes and land use type using ANOVA.

We then constructed gape width probes to determine which bird species are likely physically capable of swallowing average- and minimum-sized olives from each stand. Each probe consisted of an ellipsoid made of Teflon plumbing tape attached to one end of a wooden dowel. A total of 9 probes were created. The probes were measured to the tenth of a millimeter using digimatic calipers and created to incrementally span the range of average fruit sizes from the study stands. Because we used Teflon tape instead of a rigid or brittle substance, the probes had a smooth and slightly flexible surface, which to the touch resembled the surface of ripe *Olea* fruits and yielded similarly (slightly) when squeezed in the hand. We wrapped the Teflon tape as tightly as possible to create surface tension, mimicking the firmness of a full, ripe fruit.

We obtained previously-frozen, whole frugivorous bird carcasses from the University of California, Davis, Wildlife Museum. Once they had thawed, all carcasses were in good condition; we used none that had dried or otherwise stiffened, and all had mouths and esophagi that were open and unobstructed. The use of such carcasses instead of dried, prepared skins with closed mouths enabled us to both (a) reduce the risk of skin shrinkage that would alter measurements and mislead our conclusions, and (b) verify the ability of each bird to pass olives all the way through the esophagus and into the stomach. For each carcass, we measured the external bill gape width (bill width at the commissures) and the external maximum bill height (from the top to the bottom of the bill at its base). We then inserted each of the nine probes into each carcass's mouth to determine whether it could pass through the full esophagus to the stomach. We repeated this for up to 10 carcasses per bird species (depending upon availability). These trials generated a list of the stands containing fruits that could morphologically be dispersed by each tested bird species.

When all available carcasses (representing 18 species) had been tested, a few bird species remained that we believed to be candidates for olive dispersal (i.e., frugivorous in habit and occurring in olive stand sites) but that were not available as whole carcasses. These species included American crow (*Corvus brachyrhynchos*), California quail (*Callipepla californica*), northern mockingbird (*Mimus polyglottos*), spotted towhee (*Pipilo maculatus*), western meadowlark (*Sturnella neglecta*), and wild turkey (*Meleagris gallopavo*). Through logistic regression, we ascertained that external bill gape width was predictive of successful esophageal passage of all probes ($P < 0.0001$). We thus measured external gape width of prepared museum specimens of the remaining candidate bird species to determine which stands they are capable of dispersing. We used 10 museum specimens each for these species except when fewer than 10 were available (the museum owned only four turkey specimens, and all were used). All measurements were taken at the commissures and therefore relevant to the hard bill dimensions rather than skin dimensions; nevertheless, some drying and shrinkage could occur on study skins during their preparation. In light of our hypotheses (that a greater number of bird species should feasibly disperse fruits of smaller size), any shrinkage that may have led us to falsely conclude a negative (that a given bird species could not disperse a given fruit size) would lead us to underestimate the number of species capable of dispersal, making our approach conservative.

In winter, 2008–2009, we conducted bird counts at 70 points in each of the four study sites. Each count lasted seven minutes. At each point, all birds detected by sight or sound were recorded by species and number of individuals. To compare population densities among birds of smaller and larger body size, we examined point count results truncated at 25 m from the point (i.e., only birds detected within a 25-m radius of the point, or an area of 1963.5 m^2, were included in analyses). We calculated the density of detections (number of individuals per hectare) for each of the 22 potential disperser species identified by the esophageal probes and logistic regression. We then performed two linear regressions: first, we regressed the number of potential dispersers on the minimum fruit width to determine whether there was a significant increase in the size of potential disperser suites as minimum olive size decreased across stands. Second, we regressed the total density of detections of potential disperser species on the minimum fruit width to determine whether the density of total potential dispersers, across all species, increased more rapidly than did the diversity of dispersers as minimum olive size decreased. To compare slopes between the two regressions, we used proportional values, angular-transformed to meet regression assumptions, and graphed them together in the same space.

All statistical analyses were performed in JMP 5.0 (SAS Institute Inc., Cary, NC). Significance was accepted at $P \leq 0.05$.

TABLE 2. BIRD SPECIES CAPABLE OF SWALLOWING *OLEA EUROPAEA* FRUITS FROM EACH STUDY STAND, BASED ON AVERAGE GAPE WIDTH MEASUREMENTS, GAPE WIDTH PROBES, AND AVERAGE OLIVE WIDTHS. Ave. olive widths are means (mm) ±1 SE. Min. olive widths are minimum widths (mm) obtained in a random selection of 30 olives per stand. Gape width probes were used on frozen, whole carcasses to test esophageal passage of various fruit sizes for most bird species. For six bird species (AMCR, CAQU, NOMO, SPTO, WEME, WITU), no whole carcasses were available; stand list is based instead on external measurements and logistic regression results ($P < 0.0001$). [a]Bird abbreviations: AMCR = American crow; AMRO = American robin; CAQU = California quail; CEWA = cedar waxwing; EUST = European starling; GCSP = golden-crowned sparrow; HETH = hermit thrush; HOFI = house finch; HOSP = house sparrow; MODO = mourning dove; NOFL = northern flicker; NOMO = northern mockingbird; SPTO = spotted towhee; STJA = Stellar's jay; SWTH = Swainson's thrush; VATH = varied thrush; WCSP = white-crowned sparrow; WEBL = western bluebird; WEME = western meadowlark; WITU = wild turkey; WSJA = western-scrub jay; YBMA = yellow-billed magpie.

Study stand	Ave. width	Min. width	Potential dispersers[a] (average olive)	Potential dispersers[a] (minimum olive)
1	9.68 ± 0.21	5.61	AMCR, AMRO, CAQU, CEWA, HETH, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WEBL, WEME, WITU, WSJA, YBMA	AMCR, AMRO, CAQU, CEWA, EUST, GCSP, HETH, HOFI, HOSP, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WCSP, WEBL, WEME, WITU, WSJA, YBMA
2	9.93 ± 0.11	6.52	AMCR, AMRO, NOFL, SPTO, STJA, VATH, WEME, WITU, YBMA	AMCR, AMRO, CAQU, CEWA, EUST, HETH, HOFI, HOSP, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WEBL, WEME, WITU, WSJA, YBMA
3	12.19 ± 0.56	7.60	AMCR, AMRO, EUST, NOFL, STJA, VATH, WEME, WITU, YBMA	AMCR, AMRO, CAQU, CEWA, EUST, HETH, HOFI, HOSP, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WEBL, WEME, WITU, WSJA, YBMA
4	15.15 ± 0.41	9.13	AMCR, EUST, YBMA, WITU	AMCR, AMRO, CAQU, CEWA, EUST, HETH, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WEBL, WEME, WITU, WSJA, YBMA
5	14.07 ± 0.49	9.14	AMCR, WITU	AMCR, AMRO, CAQU, CEWA, EUST, HETH, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WEBL, WEME, WITU, WSJA, YBMA
6	14.50 ± 0.19	10.24	AMCR, EUST, WITU, YBMA	AMCR, AMRO, EUST, NOFL, SPTO, STJA, VATH, WEME, WITU, YBMA
7	17.79 ± 0.23	11.12	AMCR, WITU	AMCR, AMRO, EUST, NOFL, SPTO, STJA, VATH, WEME, WITU, YBMA
8	15.45 ± 0.17	11.39	AMCR, EUST, WITU, YBMA	AMCR, AMRO, EUST, NOFL, SPTO, STJA, VATH, WEME, WITU, YBMA
9	16.10 ± 0.26	11.50	AMCR, WITU	AMCR, AMRO, EUST, NOFL, SPTO, STJA, VATH, WEME, WITU, YBMA
10	18.57 ± 0.36	12.29	AMCR, WITU	AMCR, AMRO, EUST, NOFL, STJA, VATH, WEME, WITU, YBMA
11	17.37 ± 0.26	12.72	AMCR, WITU	AMCR, EUST, WITU, YBMA
12	20.28 ± 0.51	13.02	AMCR, WITU	AMCR, EUST, WITU, YBMA

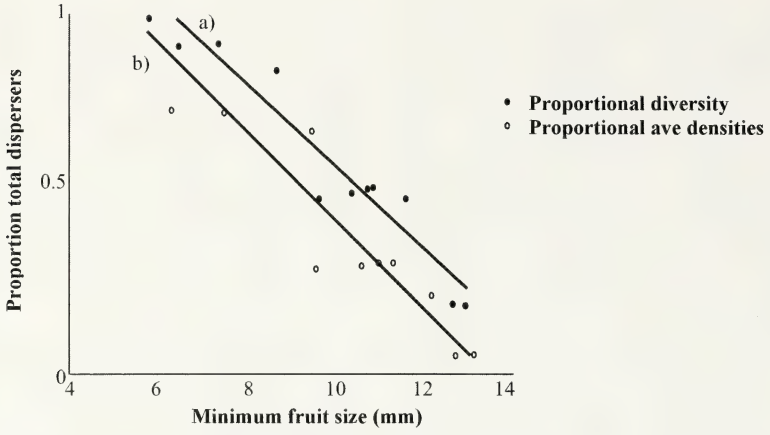

FIG. 1. Graph comparing the slopes of regressions between (a) proportion of total disperser species and minimum fruit width, and (b) proportion of average total disperser densities and minimum fruit width. Original data values are presented here, but arcsine-transformed values were used in statistical analysis. Average total number of disperser individuals accumulates at a slightly greater rate as fruit width decreases than does the total number of disperser species. However, the slopes between the two regressions are not significantly different.

Results

From esophageal probes and gape width measurements, we developed a list of birds that are anatomically capable of swallowing average- and minimum-sized *Olea* fruits from each study stand (Table 2). Only two species (American crow and wild turkey) are likely capable of dispersing average fruits from the largest-fruited stands, but additional species would be capable of consuming the smallest fruits from even these stands (Table 2).

There was no significant relationship between land use type and fruit size ($P = 0.19$). The smallest fruit sizes (both average and minimum) were found in the only feral population we were able to study. Across study stands, those with the smallest fruits and correspondingly greatest number of potential dispersers occurred in semi-natural or urban locations. The maximum number of potential dispersers for any stand was 17 bird species likely capable of swallowing average-sized fruits and 22 species capable of swallowing minimum-sized fruits (Table 2). Two bird species (golden-crowned sparrow, *Zonotrichia atricapilla*, and white-crowned sparrow, *Zonotrichia leucophrys*) were capable of swallowing only fruits of the smallest-fruited stand. When stands are ranked by their fruit sizes, a threshold can be observed between stands 3 and 4: twelve bird species capable of swallowing fruits from the three smallest-fruited stands have gape widths too small to accommodate fruits from the remaining nine stands (Table 2). Only 10 bird species appear capable of consuming fruits from those larger-fruited stands.

By linear regression, the relationship between number of potential disperser species and minimum olive size was highly significant ($R^2 = 0.90$; $P < 0.0001$) and negative, confirming that disperser suites become larger as olive sizes shrink. The regression between average density of potential disperser species and minimum olive size was also highly significant ($R^2 = 0.92$; $P < 0.0001$). The slope of the density regression was slightly steeper than that of the richness regression (ratio of slopes = 1.09) (Fig. 1). However, the slopes were not significantly different.

Discussion

In *Olea europaea*'s native range, birds shift from swallowing fruits to pecking them when gape width limits whole fruit ingestion (Rey and Gutiérrez 1996; Rey et al. 1997). We frequently observed western meadowlarks, European starlings (*Sturnus vulgaris*), and American robins (*Turdus migratorius*) selecting fruits on the ground beneath olive trees and attempting to swallow them by repeatedly grasping them in the beak and dropping them before resorting to pecking or moving on to swallow a smaller fruit. Logically, small-fruited feral populations resulting from bird selection may be facilitated by both this disproportionate selection of smaller fruits among larger ones and by increased visitation to small-fruited stands relative to large-fruited stands.

Our results demonstrated that smaller probes could pass through the esophagi of a wider diversity of bird species. This illustrates the anatomical mechanism enabling larger suites of potential dispersers for small-fruited populations. The only truly feral stand we examined (Stand 1) did indeed have the smallest fruits of all of our observed stands. This feral stand is located in Chico, Butte Co., CA, in a zone approximately 1 km^2 in area where *Olea* individuals are visibly spreading up-canyon from a century-old population cultivated at the edge of a municipal golf

course. Individuals in this feral stand are clustered beneath perch sites such as larger trees and power lines. Birds thus appear to be mediators of this localized invasion.

Our results are not sufficient to conclude that bird-mediated dispersal in California directly results in small-fruited feral *Olea* populations because we were unable to replicate this work in multiple feral stands due to their rarity and land jurisdictions. Instead, our study demonstrates the higher potential for bird-mediated dispersal of small *Olea* fruits relative to large fruits. Land managers in California should be alert to the establishment of feral *Olea* trees with small fruits, since these have a higher probability of becoming sources of species spread than would large-fruited conspecifics. Whether such small fruits result from lack of care, irrigation, and cultivation or from bird-mediated selection, a wider variety of birds and a greater number of birds may be expected to visit such stands and to disperse fruits than occurs for large-fruited trees.

A dramatic decrease in the diversity of potential dispersers can be seen when comparing study stands 1 through 3 with the remaining stands. Evidently, the minimum fruit size increase between stands 3 and 4 represents the crossing of a size threshold. Fruits smaller than this threshold have more than twice the dispersal potential (in terms of the number of species able to carry out dispersal) of fruits larger than this threshold. If small *Olea* fruits become more common in California as a result of feralization, we expect that a greater rate of bird-mediated dispersal is likely to manifest in the region. As long as no other factors (e.g., unsuitable soils, herbivory, or competition) serve as barriers to establishment, such a marked boost to a spread mechanism could propel *Olea* out of a lag phase and into overt regional invasiveness.

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SYSTEMATICS, PHYLOGENY, AND EVOLUTION OF *PAPAVER CALIFORNICUM* AND *STYLOMECON HETEROPHYLLA* (PAPAVERACEAE)

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ABSTRACT

We present a detailed comparison of *Papaver californicum* and *Stylomecon heterophylla*, which earlier were found to be sister species and most closely related to *Meconopsis cambrica* + *Papaver s.str.* from western Eurasia. The two species of winter annuals differ mainly in the shape of their distal cauline leaves, coloration of petals and staminal filaments, and most notably morphology of the gynoecium and capsule, with *Papaver californicum* having a sessile stigmatic disc and *Stylomecon heterophylla* having a distinct style. They were earlier found to differ in ploidy, with chromosome numbers of $2n = 28$ (*Papaver californicum*) and $2n = 56$ (*Stylomecon heterophylla*). Mapped distributions of the two species indicate that the range of *S. heterophylla* encompasses and exceeds that of *P. californicum*; both are known only from the California Floristic Province except for one collection of *S. heterophylla* from central Baja California. Whereas *Papaver californicum* is most commonly found in burn localities in the first wet season after fire, *Stylomecon heterophylla* is active under a broader range of environmenal conditions and often occurs in habitats that appear to be somewhat more mesic. Both species are self-compatible and autonomously self-pollinating. Experimental hybridization resulted in well-developed but entirely sterile hybrids; no hybrids are known from nature. Based on these and earlier findings, we conclude that *Stylomecon heterophylla* is best treated in *Papaver*, as *P. heterophyllum*.

Key Words: *Papaver*, *Meconopsis*, *Stylomecon*, fire poppy, wind poppy, breeding system, capsule morphology, hybridization.

In the native flora of California, Papaveraceae *s.str.* (i.e., excl. Fumariaceae and Pteridophyllaceae, see Stevens 2001 onwards) are represented by two subfamilies, i.e., subf. Eschscholzioideae, with *Dendromecon* Benth. and *Eschscholzia* Cham., and subf. Papaveroideae, with *Arctomecon* Torr. & Frém., *Argemone* L., *Canbya* Parry ex A. Gray, *Hesperomecon* Greene, *Meconella* Nutt., *Papaver* L., *Platystemon* Benth., *Romneya* Harv., and *Stylomecon* G. Taylor. Whereas Eschscholzioideae are endemic to western North America (the third genus of the subfamily, *Hunnemannia* Sweet, is distributed in Mexico), the genera of subf. Papaveroideae fall into an Old World clade and a New World clade, respectively (Schwarzbach and Kadereit 1995). Of the genera of subf. Papaveroideae in California, *Papaver*, with the fire poppy, *P. californicum* A. Gray [syn. *P. lemmonii* Greene], as its only native species, and the monotypic *Stylomecon*, with only the wind poppy, *S. heterophylla* (Benth.) G. Taylor [basionym *Meconopsis heterophylla* Benth., syn. *Papaver heterophyllum* (Benth.) Greene], are part of the Old World clade (Schwarzbach and Kadereit 1995), which in addition to *Papaver* and *Stylomecon* contains the Old World genera *Meconopsis* Vig. and *Roemeria* Medik.

A close relationship between *Papaver californicum* and *Stylomecon heterophylla*, first suggested by Gray (1887), based on vegetative and reproductive characters, and by Greene (1888), upon combination of (at that time) *Meconopsis heterophylla* into *Papaver*, was also suspected by Ernst (1962) in view of the close vegetative similarity of the two species. A sister-species relationship between the two was first shown by Kadereit et al. (1997) using chloroplast DNA (cpDNA) restriction site data, and was confirmed by Carolan et al. (2006) using nuclear ribosomal DNA internal transcribed spacer (ITS) and cpDNA sequence data. Considering gynoecium and fruit morphology, however, the close relationship between the two species was unexpected. *Papaver californicum* has a gynoecium with a sessile stigmatic disc, and the capsules open by small valves (Fig. 1) below this stigmatic disc. Both of these characteristics are typical for *Papaver* in its traditional circumscription (Kadereit 1993). In contrast, the gynoecium of *S. heterophylla* has a distinct style on top of a flattened ovary roof, and the capsules open by pores below that roof (Fig. 1). Within Old World Papaveroideae, gynoecia with a style are typical for most species of *Meconopsis*, and this charac-

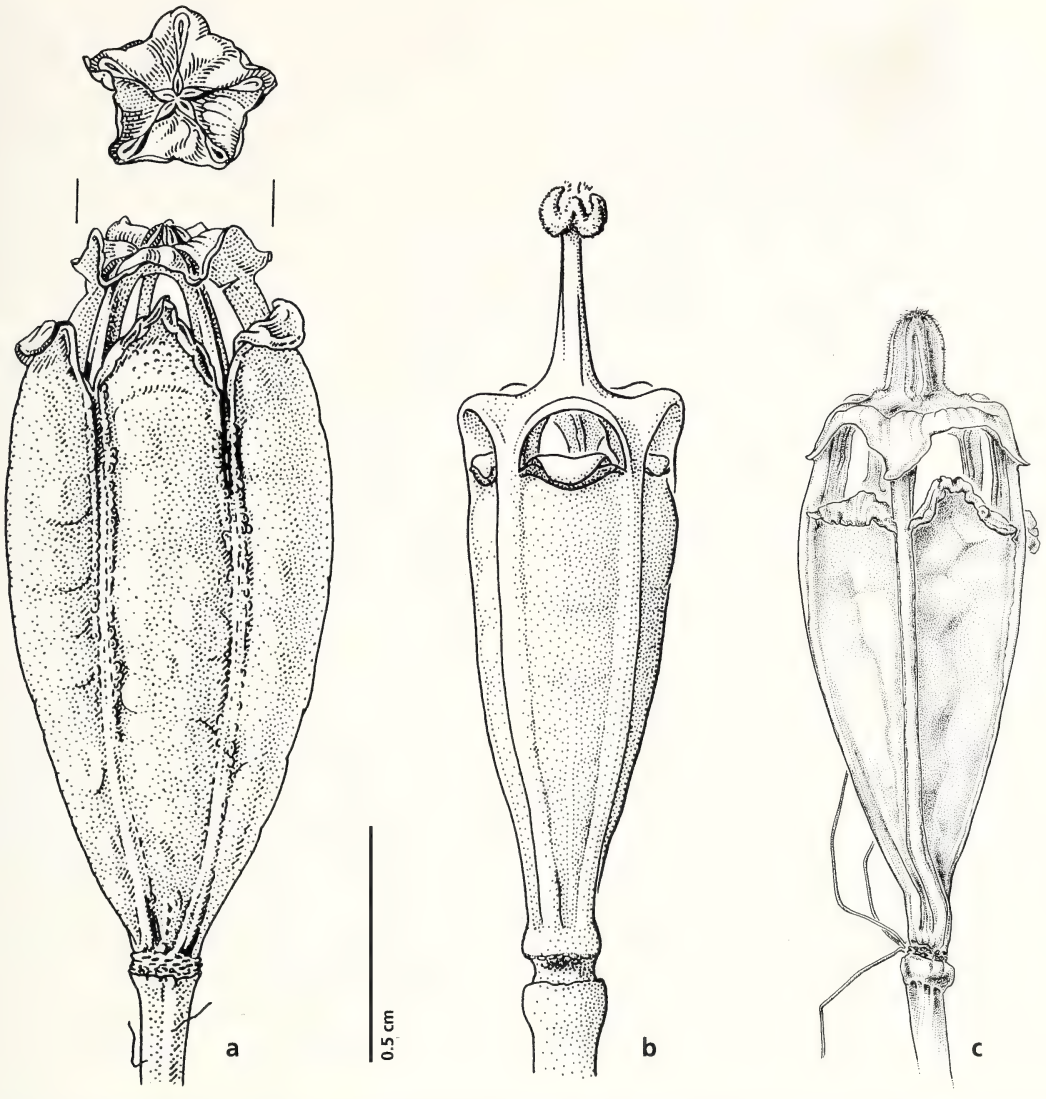

FIG. 1. Mature capsules of (a) *Papaver californicum*, (b) *Papaver heterophyllum* [*Stylomecon heterophylla*], and (c) their F_1 hybrid (*P. heterophyllum* × *P. californicum Rebman* 15166).

teristic led Bentham (1835) to originally describe *S. heterophylla* as a species of *Meconopsis*.

From the perspective of the close relationship but morphological distinctness of *Papaver californicum* and *Stylomecon heterophylla*, we here set out to present a detailed comparison of the two species. Whereas a recent taxonomic account is available for *P. californicum* (Kadereit 1988), no such account exists for *S. heterophylla*, although *P. californicum* and *S. heterophylla* were briefly compared by Kadereit et al. (1997). In particular, we compare the two species in terms of morphology, karyology, and breeding system, and describe their geographical distributions and ecology. Finally, we briefly discuss their morphological evolution and the disjunction between these two species and their closest relatives in the Old World.

METHODS

Sources and Cultivation of Living Material

Bulk seed was collected in California from one population of *Stylomecon heterophylla* (Contra Costa Co., Mt. Diablo, *S.J. Bainbridge s.n.* [JEPS], 2009) and two populations of *Papaver californicum* (San Diego Co., [1] Hellhole Canyon Open Space Preserve, E of Valley Center and NE of Lake Wohlford, 33.2256°N, 116.9443°W, 465 m. elevation, on mostly granitic substrates, *Rebman 15166* [SD], 14 May 2008, [2] Del Dios

Highlands County Preserve, SW of Escondido, NW of Lake Hodges and NE of Olivehain Reservoir, 33.0817°N, 117.1269°W, 242 m. elevation, granite and clay soils, *Rebman 15264* [SD], 23 May 2008).

Seeds were sown on moist filter paper in petri dishes and kept in a refrigerator at 5°C for about 14 days. Germination occurred readily in *Stylomecon heterophylla*, but required addition of 0.02% gibberellic acid in *Papaver californicum*. Seedlings or seeds were transplanted into pots and plants were cultivated in the experimental greenhouse at the Botanic Garden of Mainz University.

Breeding System and Hybridization

For the determination of breeding system, buds were bagged before opening, and seed set was checked at the time of capsule maturity. Four buds of *Stylomecon heterophylla* and seven buds of *Papaver californicum* were treated in this way. For interspecific hybridization, plants were emasculated before their anthers opened, and pollen of the crossing partner was applied to the stigmata once they became receptive. After pollination, the gynoecia were bagged and seed set was checked at capsule maturity. Twelve flowers of *S. heterophylla* and six flowers of *P. californicum* were used as female parents. Nine hybrid individuals were used in self-pollinations and inter-hybrid crosses.

Herbarium Material and Seed Morphology

All material of *Papaver californicum* and *Stylomecon heterophylla* in the University and Jepson Herbaria (UC/JEPS) was examined. For the distribution map of the two species, specimens in the Consortium of California Herbaria and, for Baja California, in UC and the San Diego Natural History Museum herbarium (SD) were used. The observations and descriptions presented below were based on both the cultivated and herbarium material. Scanning electron microscope pictures of gold-coated seeds were taken on an XL30 ESEM Philips (Philips Electron Optics, The Netherlands) microscope.

Results

Morphology

Papaver californicum and *Stylomecon heterophylla* differ from each other in both vegetative and reproductive (flower and fruit) morphology. Both species are short-lived annuals with a flowering peak in March and April, but plants have been found flowering as early as February and as late as May. In cultivation at Mainz, Germany during late spring/early summer they required between 6 and 9 weeks to reach the onset of flowering from time of seed germination.

Although Ernst (1962) stated that "(t)heir seedling stages are identical, and even the adult plants are so similar in appearance that determinations cannot be made without the gynoecia", *Papaver californicum* and *Stylomecon heterophylla* can be easily distinguished by leaf morphology. The rosette and proximal cauline leaves of the two species indeed are very similar in appearance; however, the middle and distal cauline leaves of *S. heterophylla* are distinguished by their fine dissection (Fig. 2). The rather abrupt transition between proximal and middle cauline leaf margins and shapes in wind poppy probably account for Bentham's (1835) choice of the specific epithet 'heterophylla'.

The two species are conspicuously different in flower and fruit morphology. First, the flowers differ in coloration. The petals of *Papaver californicum* are pale orange with a distinct but small whitish to greenish and sharply delimited spot at the petal bases, and the staminal filaments are white to pale yellow; in contrast, the petals of *Stylomecon heterophylla* are bright orange with a small, dark red and distally fading spot at the petal bases, and the staminal filaments are dark red to almost black. Often the petals of *S. heterophylla* also are substantially larger than those of *P. californicum*, which often has very small, narrow, and sometimes irregularly laciniate petals. Second, the number of stamens, at least in the plants cultivated for this study, is greater in *S. heterophylla* than in *P. californicum*. These latter two differences, petal size and stamen number, may be associated with a slight difference between the two species in breeding system (see below). We also note that the flowers of our cultivated material of *S. heterophylla* were slightly zygomorphic: in the slightly nodding flowers, a distinctly larger number of stamens was displaced to the upper than to the lower side of the flower. Third, and most conspicuously, the two species differ in gynoecium and fruit morphology. Whereas *P. californicum* has a gynoecium with a sessile stigmatic disc, and capsules that open by small valves below this stigmatic disc (Fig. 1), the gynoecium of *S. heterophylla* has a distinct style on top of a flattened ovary roof, and the capsules open by pores below that roof (Fig. 1). Finally, the two species differ in seed size, at least in the material cultivated for this study. The seeds of *P. californicum* ranged from 607 to 649 μm in length; those of *S. heterophylla* had a mean length of 803 μm. Seed surface morphology is very similar in the two species, but surface microsculpturing is coarser in *P. californicum* than in *S. heterophylla* (Fig. 3).

Karyology

Ernst (1962) reported a chromosome number of $2n = 28$ for *Papaver californicum* and of $2n =$

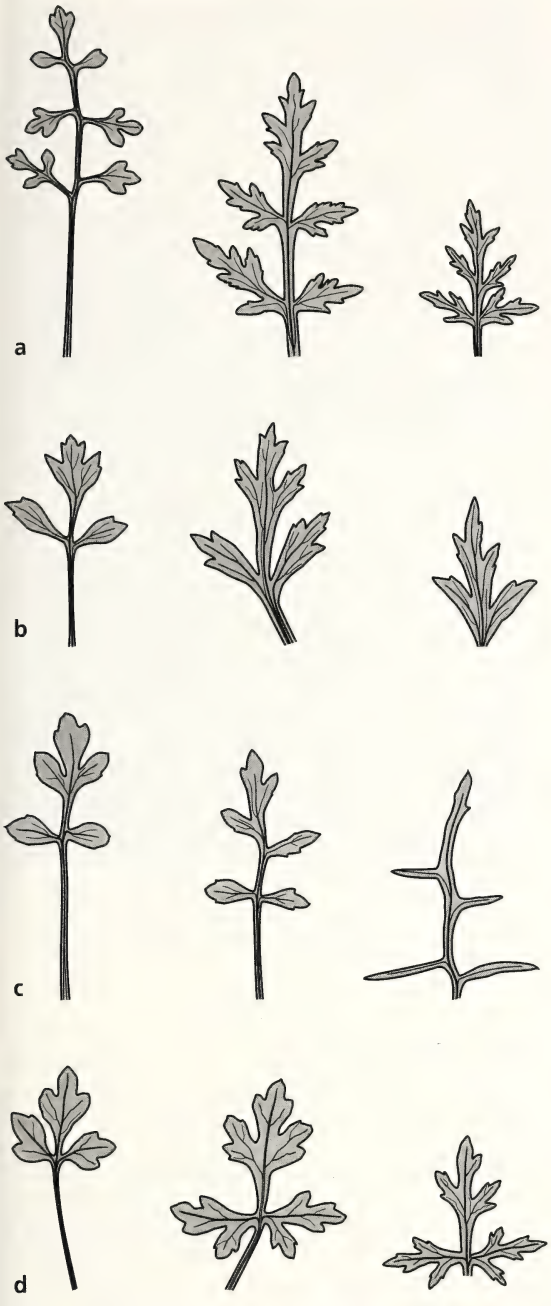

FIG. 2. Leaf shapes of (a, b) *Papaver californicum* (a: *Rebman 15166*, b: *Rebman 15264*), (c) *Papaver heterophyllum* [*Stylomecon heterophylla*], and (d) their F_1 hybrid (*P. heterophyllum* × *P. californicum Rebman 15166*). Left to right: rosette, proximal cauline, and distal cauline leaves.

56 for *Stylomecon heterophylla*. Considering that $x = 6$ and 7 are the lowest chromosome numbers found in *Papaver* and relatives (Kadereit 1993), *P. californicum* is interpreted here as tetraploid and *S. heterophylla* as octoploid.

Distribution

The geographic distribution of the two species is shown in Fig. 4. *Papaver californicum* is endemic to the western California Floristic Province (CA-FP) and known from the San Francisco Bay Area (Mt. Tamalpais vicinity and Mt. Diablo) of Central Western California south to northwestern Baja California, Mexico, with populations on Santa Cruz and Santa Rosa islands. Most known occurrences of fire poppy are documented from the South Coast, Transverse, and Peninsular ranges of California and from California's Central and South Coast, at elevations up to ca. 1220 m. The distribution of *S. heterophylla* encompasses the range of *P. californicum* and extends further north, south, and east, at elevations up to ca. 1500 m., with one record from outside the CA-FP, in the Vizcaino Desert of Baja California. Wind poppy also is known from all of the Channel Islands except San Nicolas Island and from near-shore Pacific islands of Baja California (Islas Los Coronados, Isla San Martin, and Isla Todos Santos). Wind poppy has been collected more extensively than fire poppy in Central Western California and northwestern Baja California, and is documented from the central and southern Sierra Nevada foothills, Tehachapi Mountains, and North Inner Coast Ranges (near Clear Lake), well outside the known range of fire poppy. The actual distribution of *P. californicum* is likely underrepresented by collections based on the infrequent appearance of plants, usually in the year immediately after fires (see below).

Ecology

Papaver californicum, as implied by its vernacular name, fire poppy, is most commonly found in burn localities in the first wet season after fire. However, the species occasionally also grows in otherwise disturbed or open sites (e.g., on cleared ground, *Brandegee 3372* [UC]; mesic openings in chaparral, *S. Boyd et al. 6736* [UC]; dry open ridge, *I.W. Clokey & B. Templeton 4464* [UC]; south facing boulder creek bed, *R. Ornduff & R.L. Taylor 4389* [UC]; along newly-made truck trail, *R. Bacigalupi 2876* [UC]).

The habitat of *Stylomecon heterophylla* is often but not exclusively described as moist and shady, and the species sometimes is found growing along streams. Soils are often described as loamy (e.g., soft sandy loam, clay loam, sandstone-derived clay-loam soil, leaf mold loam). In general, the habitat of this species often appears to be somewhat more mesic than that of *Papaver californicum*, although the ecological range of wind poppy extends into drier settings, as well (e.g., in Baja California). One specimen of *S. heterophylla* (*M.L. Bowerman 1410* [UC]) origi-

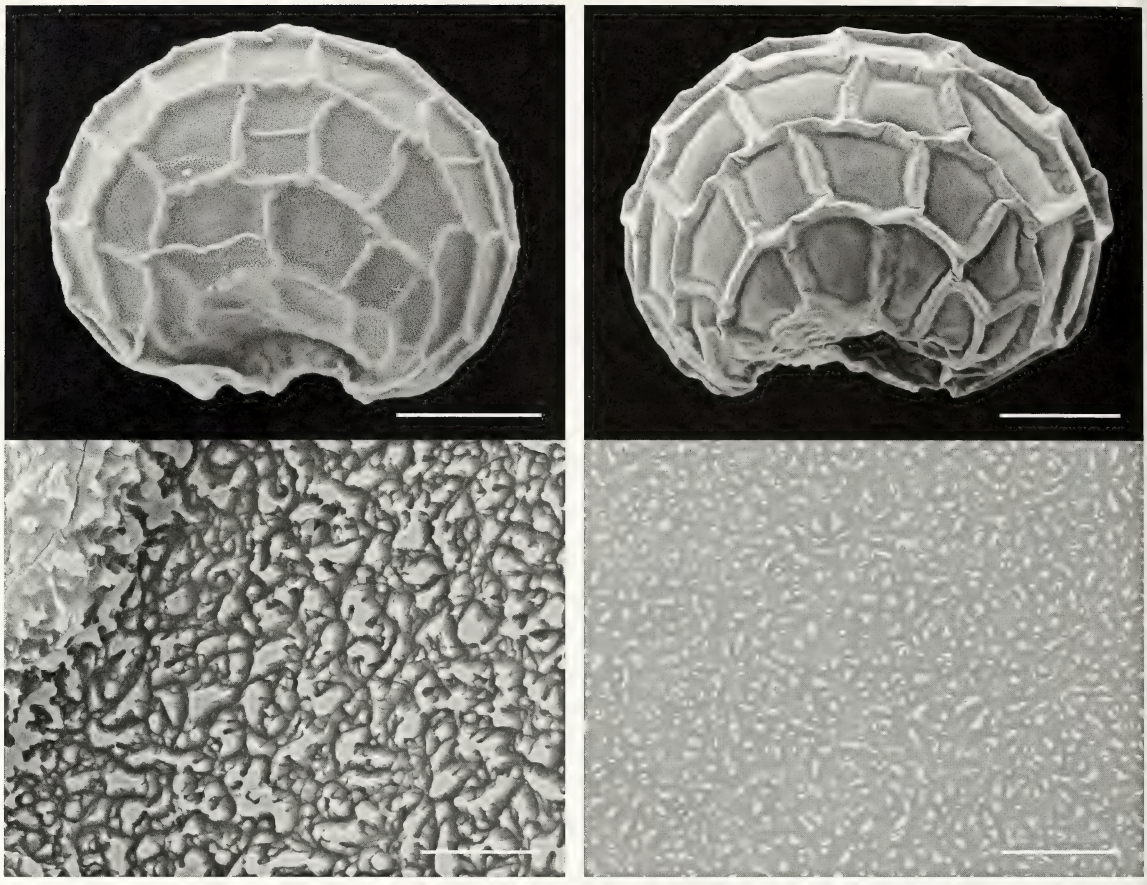

FIG. 3. SEM photographs of seeds (scale bars: 200 μm) and seed surface details (scale bars: 10 μm) of (a) *Papaver californicum* (*Rebman 15264*) and (b) *Papaver heterophyllum* [*Stylomecon heterophylla*].

nated from a site swept by fire in the previous year.

Breeding System

In the breeding-system experiment, all bagged flowers showed good seed set. Both species were thus determined to be self-compatible and autonomously self-pollinating. Their late floral development was found to differ, however. In *Papaver californicum*, stamens exceeded the gynoecium, anthers always opened in bud, and pollen was found on the stigmatic rays when the buds opened, although at that time the stigmatic rays appeared not to be receptive, as judged from the later appearance of stigmatic papillae. In *Stylomecon heterophylla*, the stigmata — elevated by the style — do not overtop the anthers in but are located at roughly the same level. The anthers were still closed when flower buds began to open. During opening of the anthers, some pollen is deposited on the stigmata, which, as in *P. californicum*, appeared not to be receptive at this stage.

Hybridization

Hybridization between *Papaver californicum* and *Stylomecon heterophylla* was successful only when *S. heterophylla* was the female parent, and all 12 crosses made in that direction resulted in seed set. Hybrid individuals developed normally but produced no seed when selfed or crossed with other hybrid plants. A hybrid capsule is shown in Fig. 1.

DISCUSSION

Phylogenetic Relationships, Evolution, and Biogeographical History of *Papaver californicum* and *Stylomecon heterophylla*

In their restriction site analysis of cpDNA, Kadereit et al. (1997) found *Papaver californicum* + *Stylomecon heterophylla* to be part of a polytomy with (1) the South African *P. aculeatum* Thunb., (2) a clade of *Papaver* sect. *Argemonidium* Spach + *Roemeria* Medik. as sister to *Papaver* sect. *Meconella* Spach, and (3) a clade

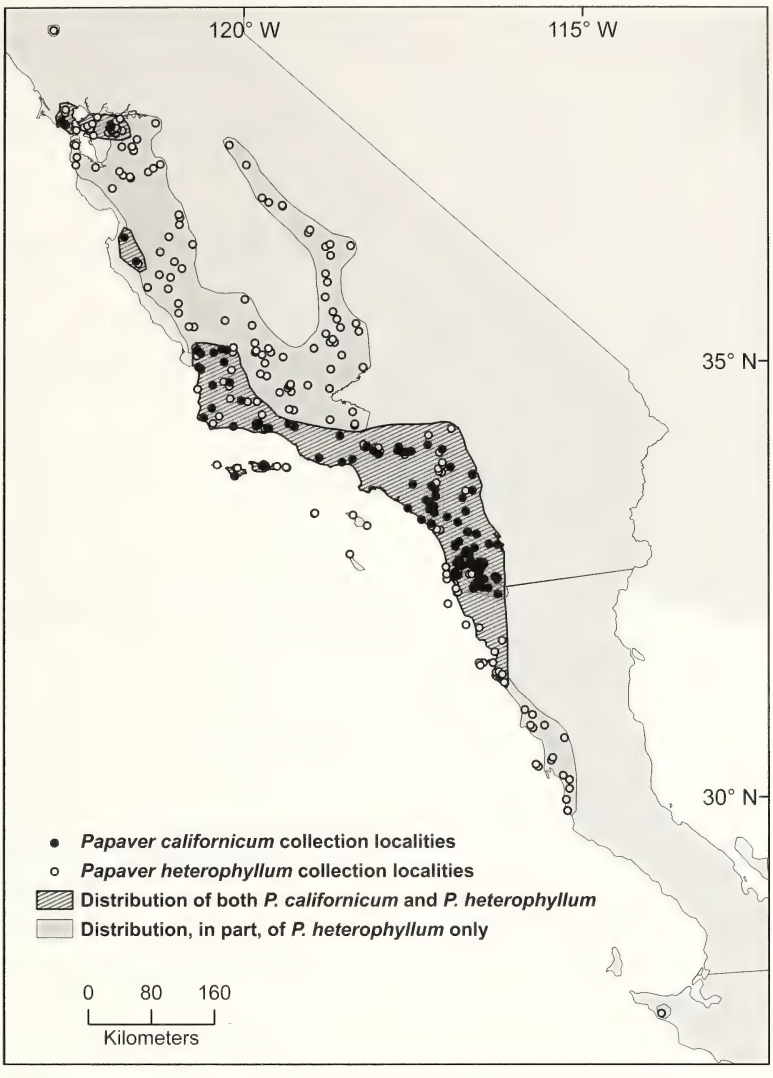

FIG. 4. Geographical distribution of *Papaver californicum* and *P. heterophyllum* [*Stylomecon heterophylla*].

of the western European *Meconopsis cambrica* (L.)Vig. as sister to *Papaver sensu* stricto (*s.str.*) as defined by Kadereit et al. (1997). Two lineages of Asian *Meconopsis* were successive sister groups to this polytomy, although without much support. In their analysis of ITS and cpDNA (*trn*L-F) sequence data, Carolan et al. (2006) recovered *P. californicum* + *S. heterophylla* as sister to *M. cambrica* + *Papaver s.str.* The remainder of those lineages listed above were found to be basally divergent to this clade. The sister-group relationship between the Californian *P. californicum* + *S. heterophylla* and the largely western Eurasian *M. cambrica* + *Papaver s.str.*, and the more basally divergent position of the remaining lineages was confirmed in an analysis of an enlarged ITS dataset by F. J. Valtueña Sánchez and J.W. Kadereit (unpublished). Phylogenetic relationships in Old World Papaveroideae as found by Kadereit et al. (1997) and Carolan et al. (2006) are summarized in Fig. 5. A close relationship of *P. californicum* + *S. heterophylla* to *M. cambrica* + *Papaver s.str.* had already been suspected by Ernst (1962). When discussing the results of their phylogenetic analysis, Kadereit et al. (1997) hypothesized that *Meconopsis*, as a genus of mostly mesic habitats, is best interpreted as paraphyletic in relation to several lineages of a polyphyletic *Papaver* (including *Roemeria* and *Stylomecon*). Except for the arctic-alpine *Papaver* sect. *Meconella*, all of these lineages grow in semi-arid to arid habitats.

The above phylogenetic interpretation, which is consistent with the results of Carolan et al. (2006) and F. J. Valtueña Sánchez and J.W. Kadereit (unpublished), has several implications for the morphological evolution of the Californian *Papaver californicum* + *Stylomecon heterophylla* lineage. First, the annual habit of this

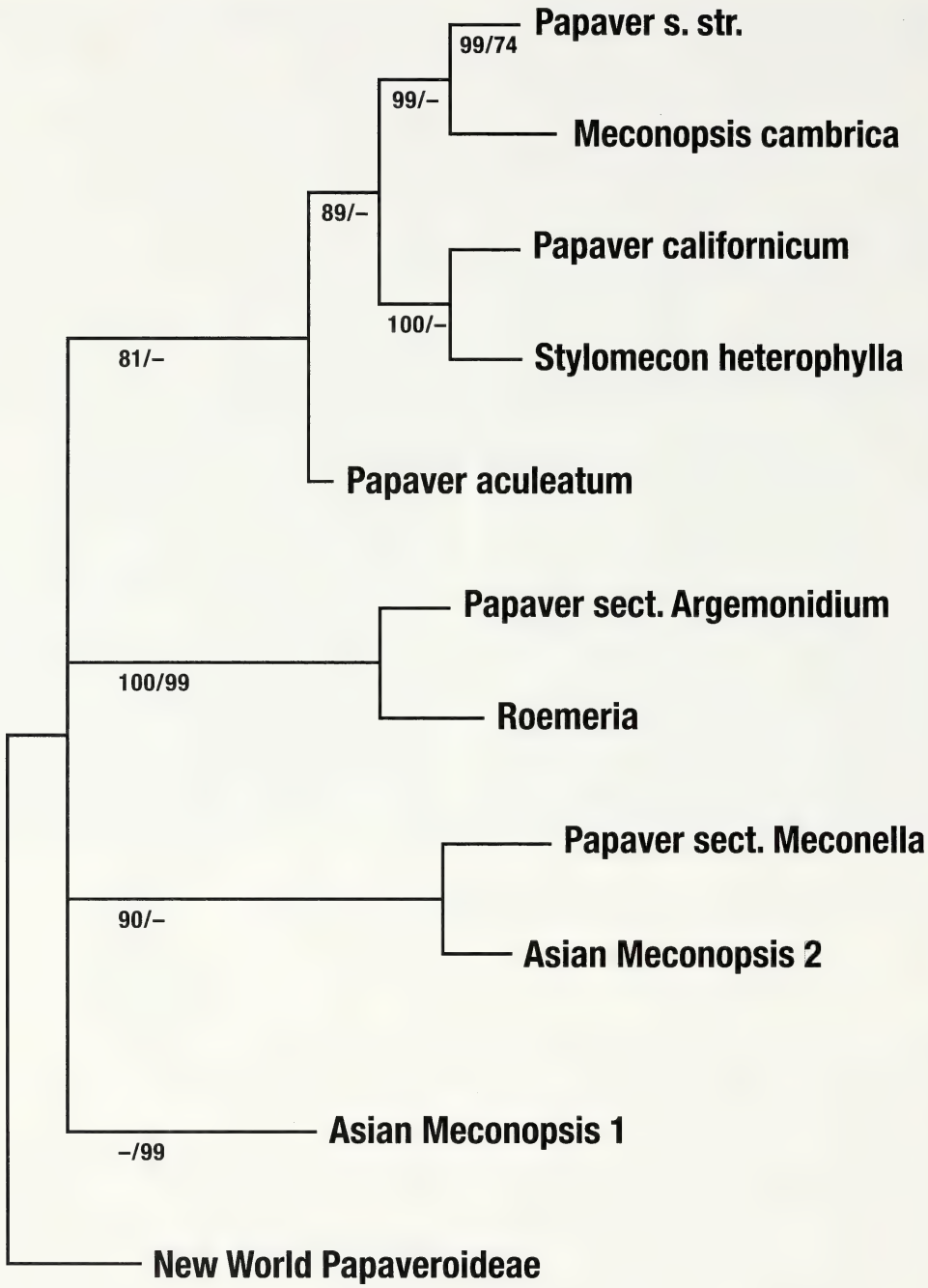

FIG. 5. Simplified phylogeny of Old World Papaveroideae based on Kadereit et al. (1997) and Carolan et al. (2006). Figures along branches represent bootstrap support found by Carolan et. al. (2006)/Kadereit et al. (1997).

lineage was likely derived from an ancestrally perennial condition, as found in *Meconopsis*, including *M. cambrica*, and large parts of *Papaver*. Second, the dark pigmentation of the filaments of *S. heterophylla* evolved independently from the similar coloration of filaments found in essentially all annual lineages of *Papaver s.str.*, in the perennial *Papaver* sect. *Macrantha* Elkan, and in the annual *Papaver* sect. *Argemonidium* + *Roemeria*—filaments are light in much of *Meconopsis*, including *M. cambrica*, and all biennial and perennial sections of *Papaver s.str.* except sect. *Macrantha* (Kadereit et al. 1997). Third, a distinct style, as present in *S. heterophylla*, is found only in some species of *Meconopsis*, including *M. cambrica*, and may not be strictly homologous across all of these taxa. Capsules with a stigmatic disc, as present in *P. californi-*

cum, are only found in the various lineages of *Papaver* discussed above. It is unclear from phylogenetic relationships alone whether the stigmatic disc of *P. californicum* arose in parallel to that of *Papaver s.str.*, or whether the style of *S. heterophylla* arose in parallel to that found in some members of *Meconopsis*, including *M. cambrica*. However, studies of gynoecium development (Kadereit and Erbar in press) support Ernst's (1962) conclusion that a distinct style may have arisen independently in different lineages of subf. Papaveroideae. Ernst (1962) questioned homology of gynoecium/capsule morphology in *Meconopsis*, including *M. cambrica*, and *Stylomecon*, particularly in light of capsule venation (see Kadereit et al. 1997 for detailed discussion). Accordingly, it seems most likely that the style of *S. heterophylla* arose from a structure similar to the stigmatic disc of *P. californicum*. The transition between gynoecia with and without styles results from the activity of a ring primordium located between the placentae and the carpel tips. Prolonged activity of this ring primordium results in the formation of a style (Kadereit and Erbar in press). As noted above, elevation of the stigmata by the style in *S. heterophylla* does not result in herkogamy and is not obviously associated with other floral characteristics of *S. heterophylla* that differ from those of *P. californicum* in ways that may indicate a stronger tendency toward outcrossing in wind poppies, with anthers not opening in bud and with generally larger petals and more stamens than in *P. californicum*.

The interpretation of *Meconopsis* as a paraphyletic grade basal to a polyphyletic *Papaver* (including *Roemeria* and *Stylomecon*) also has biogeographical implications. We hypothesize that the Californian lineage of *P. californicum* and *S. heterophylla* arose from an ancestral lineage of primarily mesic ecology and widespread northern hemisphere distribution. Based on a fossil-calibrated Bayesian analysis of divergence times, under a relaxed clock, using BEAST (Drummond and Rambaud 2007) with a large ITS data-set of Old World Papaveroideae, the split between *P. californicum* + *S. heterophylla* and *M. cambrica* + *Papaver s.str.* was dated to 18.3 (26.3 to 10.8) million years ago (mya) and the split between *P. californicum* and *S. heterophylla* to 13.4 (21.9 to 5.6) mya (F. J. Valtueña Sánchez and J.W. Kadereit unpublished). The disjunction between Old World and New World Papaveroideae would thus represent the geographical tail-ends of a formerly widespread northern hemisphere lineage, as found in several other flowering plant lineages (Kadereit and Baldwin in press). However, this hypothesis and an alternative hypothesis of long-distance dispersal as explanations for the disjunction between *S. heterophylla*/*P. californicum* and their Old World sister group (*M. cambrica*/*Papaver s.str.*) cannot be tested further in the absence of fossil evidence.

Considering the estimated ancient timing of the split between *Papaver californicum* and *Stylomecon heterophylla*, it is remarkable that we obtained viable hybrids between these two species. Attempts at such hybridization by Ernst (1962) were not successful. Hybrid plants were morphologically distinctive, with intermediate gynoecium and capsule morphology (Fig. 1), although they resembled *P. californicum* in leaf shape (Fig. 2) and filament and petal coloration. No such plants were seen among all herbarium specimens investigated in this study. In nature, hybridization between the two species probably is limited by their different ecological requirements, either prezygotically, through lack of crossing opportunities, or postzygotically, through lack of survival of hybrids under field conditions. The extent to which their different ploidy levels, as opposed to other genetic or chromosomal factors (e.g., lack of chromosomal pairing) are responsible for sterility of hybrids between them, and thus strong postzygotic reproductive isolation, remains to be studied.

Taxonomic Consequences

Considering the well-supported sister-group relationship of *P. californicum* + *S. heterophylla* to *Meconopsis cambrica* + *Papaver s.str.* (Kadereit et al. 1997; Carolan et al. 2006; Fig. 5), the generic assignment of either *P. californicum* or *S. heterophylla* needs to be revised in order to achieve monophyletic taxa. Two options for accomplishing this goal are readily apparent. First, *P. californicum* could be combined into *Stylomecon*. Considering phylogenetic relationships in Old World Papaveroideae (Kadereit et al. 1997; Carolan et al. 2006; Fig. 5), this approach would require a) establishing a new genus for the South African *P. aculeatum*, b) including *Papaver* sect. *Argemonidium* in *Roemeria*, c) establishing a new genus for *Papaver* sect. *Meconella* or including this section of *Papaver* into part of Asian *Meconopsis*, and d) treating Asian *Meconopsis* as generically distinct (possibly in two genera) from the phylogenetically isolated, European *M. cambrica*, the type species of *Meconopsis*. Second, *S. heterophylla* could be combined into *Papaver*. This approach would require the treatment of *M. cambrica* in *Papaver* — the species was originally described as *P. cambricum* by Linnaeus — but would allow *P. aculeatum* to remain in *Papaver*. Treatment of the remaining lineages listed above (i.e., *P.* sect. *Argemonidium*, *P.* sect. *Meconella*, Asian *Meconopsis*, and *Roemeria*) would depend on their exact relationships to *Papaver s.str.* (including *M. cambrica* and *S. heterophylla*), which have not yet been

resolved with high support (Kadereit et al. 1997; Carolan et al. 2006). Both taxonomic options would result in genera with heterogeneous capsule morphology and probably also in genera that cannot easily be diagnosed morphologically. Based on evidence that the stylar capsules of *M. cambrica* and *S. heterophylla* evolved independently and probably from ancestors with a *Papaver*-like stigmatic disc (Ernst 1962; Kadereit and Erbar in press) and on desirability of minimizing nomenclatural changes, we here follow the second option outlined above and treat *S. heterophylla* in *Papaver*, as *P. heterophyllum* (Benth.) Greene.

Acknowledgments

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MORPHOLOGICAL COMPARISONS OF WHITE FIR AND RED FIR DWARF MISTLETOES IN THE SIERRA NEVADA AND SOUTHERN CASCADE MOUNTAINS

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Abstract

Fir dwarf mistletoe (*Arceuthobium abietinum*, Viscaceae) is a common parasite of California white fir (*Abies lowiana*) and red fir (*Abies magnifica*) in California. Based on its host specificity, fir dwarf mistletoe consists of two special forms: *A. abietinum* formae specialis *concoloris* on California white fir and *A. abietinum* f. sp. *magnificae* on red fir. I sampled 17 populations of each special form in the Sierra Nevada and extreme southern Cascade Mountains (Mt. Lassen area) and completed additional morphological measurements of male and female plants, flowers, and fruits. As reported by previous studies, my results demonstrated that these special forms are morphologically similar. No significant differences were detected between the plant, flower, or fruit dimensions measured. The plant color of white fir and red fir dwarf mistletoe was also similar for both male and female plants, but some plants of red fir dwarf mistletoe are more brown-green than white fir dwarf mistletoe, particularly in the northern end of its geographic range. Based on the results of this study no change in the taxonomic status of the special forms of fir dwarf mistletoe was recommended.

Key Words: *Abies lowiana*, *Abies magnifica*, *Arceuthobium*, dwarf mistletoe.

Resumen

El muérdago enano del abeto (*Arceuthobium abietinum*, Viscaceae) es un parásito común del abeto blanco californiano (*Abies lowiana*) y del abeto rojo (*Abies magnifica*) en California. Basado en las especificidades de sus hospederos, el muérdago enano del abeto consiste de dos formas especiales: *A. abietinum* formae specialis *concoloris* en el abeto blanco californiano y *A. abietinum* f. sp. *magnificae* en el abeto rojo. Se muestrearon 17 poblaciones de cada forma especial en la Sierra nevada y en las Cascadas Montañosas extremas del sur (área de las montañas Lassen) y se completaron mediciones morfológicas adicionales de plantas femeninas y masculinas, flores y frutos. Como se ha reportado en estudios previos, los resultados demuestran que esas formas especiales son morfológicamente similares. No se encontraron diferencias significativas entre las dimensiones medidas de la planta, flor o fruto. El color de la planta de ambas formas de muérdago enano fue también similar para las plantas femeninas y masculinas, pero algunas plantas del muérdago enano del abeto rojo son más café verdosas que el muérdago enano del abeto blanco, particularmente en la parte norte de su rango geográfico. Basado en los resultados de este estudio, no se recomienda ningún cambio taxonómico en las formas especiales del muérdago enano del abeto.

Fir dwarf mistletoe (*Arceuthobium abietinum* Engelm. ex Munz) is a common parasite of California white fir (*Abies lowiana* (Gordon) A. Murray bis) (Hunt 1993) and red fir (*Abies magnifica* A. Murray bis) in California (Hawksworth and Wiens 1996). However, fir dwarf mistletoe populations that parasitize California white fir in the Sierra Nevada Mountains (SNM) do not infect red fir, while the fir dwarf mistletoe populations infecting red fir do not infect California white fir. Parmeter and Scharpf (1963) were the first to report this extreme host specificity of fir dwarf mistletoe populations in the SNM based on their field observations in mixed red and California white fir stands and cross inoculation studies. Based on additional field observations in mixed red fir and California white fir stands in the SNM, Hawksworth and Wiens (1972, 1996) confirmed the host specificity of fir dwarf mistletoe reported by Parmeter and Scharpf (1963). However, Hawksworth and Wiens (1972) reported that they did not find any morphological differences and only minor phenological differences between the fir dwarf mistletoe populations parasitizing California white fir and red fir in the SNM. Due to the economic impact that these dwarf mistletoes have on true firs in California, Hawksworth and Wiens (1972, 1996) argued that since the host affinities of the white fir and red fir dwarf mistletoes were so distinct, they deserved taxonomic recognition and designated them as formae speciales (f. sp.) in accordance with recommendation 4B of the International Code of Botanical Nomenclature: *A. abietinum* Engelm. ex Munz f. sp. *concoloris* Hawksworth & Wiens (white fir dwarf mistletoe) and *Arceuthobium abietinum* Engelm. ex Munz f. sp. *magnificae* Hawksworth & Wiens (red fir dwarf mistletoe).

During studies of fir dwarf mistletoe populations parasitizing Brewer spruce (*Picea breweriana* S. Watson) in northwestern California and southwestern Oregon, it was discovered that these mistletoe populations were also parasitizing red fir and to a lesser extent, white fir (Mathiasen and Daugherty 2009). Based on their analysis of morphological characters and host susceptibility differences for the fir dwarf mistletoe populations infecting Brewer spruce in the Klamath-Siskiyou Mountains, Mathiasen and Daugherty (2009) described these populations as a new subspecies of fir dwarf mistletoe: *A. abietinum* Engelm. ex Munz subsp. *wiensii* Mathiasen and C. Daugherty (Wiens' dwarf mistletoe). They also reported that their analysis of the morphological characteristics of the fir dwarf mistletoe populations on California white fir and red fir in the SNM confirmed the morphological similarity of the fir dwarf mistletoe populations described by Hawksworth and Wiens (1972, 1996). Furthermore, they substantiated the host preferences of these fir dwarf mistletoe populations for either white fir or red fir in the SNM based on their field observations in mixed conifer stands there. However, Mathiasen and Daugherty (2009) only sampled four populations of white fir dwarf mistletoe and five populations of red fir dwarf mistletoe from the SNM. Therefore, from 2009–2010 I sampled several additional populations of fir dwarf mistletoe from the SNM. In addition, I also sampled additional populations in the extreme southern end of the Cascade Mountains near Mount Lassen. I then combined this data with that used by Mathiasen and Daugherty (2009) for the same geographic area and compared the morphological characteristics of white fir and red fir dwarf mistletoes using this much larger sample.

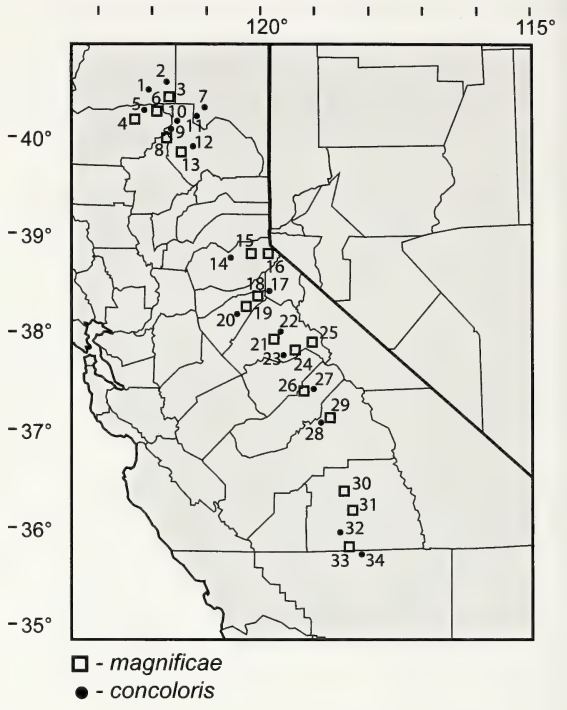

FIG. 1. Approximate locations of populations sampled for *Arceuthobium abietinum* f. sp. *magnificae* and *A. abietinum* f. sp. *concoloris* in California. Open squares represent f. sp. *magnificae* and closed circles represent f. sp. *concoloris*. Population numbers correspond with those in Appendix 1.

METHODS

Eleven populations each of white fir and red fir dwarf mistletoes (22 total populations) were sampled in 2009–2010. These were combined with six populations of each dwarf mistletoe collected by Mathiasen and Daugherty (2009) (12 populations), bringing the total number of populations sampled for this study to 34 (17 for each mistletoe; Fig. 1; Appendix 1). A combined dataset of well over 200 measurements for each character considered was made for comparing the special forms of fir dwarf mistletoe. Collections of male and female plants from each population were deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff (ASC), or at the University of Arizona Herbarium, Tucson (ARIZ). From each population, 10 to 20 infections were collected and the dominant shoot from each infection was used for morphological measurements. The dwarf mistletoe plant characters measured were those used by Hawksworth and Wiens (1996) for taxonomic classification. The following morphological characters were measured: height, basal diameter, third internode length and width, and color of the tallest male and female shoot from each infection collected; mature fruit length, width, and color; seed length, width and color; staminate flower diameter; number, length and width of staminate perianth lobes; and anther diameter and anther distance from the perianth lobe tip. Plants were measured within 24 hours after collection and were measured using a digital caliper, a dissecting microscope with a micrometer, or with a Bausch and Lomb 7× hand lens equipped with a micrometer. A one-way analysis of variance (ANOVA, $P \leq 0.05$) was used to determine if there were statistical differences between the means of the morphological characters measured.

RESULTS AND DISCUSSION

Plants of white fir and red fir dwarf mistletoes were morphologically similar as reported by Hawksworth and Wiens (1972, 1996) and Mathiasen and Daugherty (2009). Male and female plants of both special forms were consistently about the same size (Table 1). Differences

TABLE 1. MORPHOLOGICAL MEASUREMENT RESULTS FOR WHITE FIR DWARF MISTLETOE (*ARCEUTHOBIUM ABIETINUM* F. SP. *CONCOLORIS*) AND RED FIR DWARF MISTLETOE (F. SP. *MAGNIFICAE*) IN THE SIERRA NEVADA AND SOUTHERN CASCADE MOUNTAINS. Data is presented as **mean** [S_n](range)[n]. Plant heights in cm; all other measurements in mm. [1] – Distance of anther from the tip of the perianth lobe.

Character	White fir dwarf mistletoe	Red fir dwarf mistletoe
Female plants		
Height	**12.3** [2.9](6.4–24.5) [310]	**12.0** [3.0](5.6–22.2) [240]
Basal diameter	**3.6** [0.8](2.3–6.2) [310]	**3.7** [0.8](2.4–7.6) [240]
Third internode length	**16.0** [3.8](8.2–37.2) [310]	**15.7** [3.7](8.1–31.3) [240]
Third internode width	**2.2** [0.4](1.5–3.6) [310]	**2.2** [0.4](1.4–3.6) [240]
Color	Yellow-green/yellow	Yellow-green/yellow/green-brown
Male plants		
Height	**12.1** [3.4](5.2–20.5) [310]	**11.9** [3.2](6.2–19.2) [270]
Basal diameter	**3.5** [0.8](2.0–5.9) [310]	**3.5** [0.7](2.1–6.1) [270]
Third internode length	**15.5** [4.1](6.8–31.0) [310]	**15.2** [3.8](7.6–25.2) [270]
Third internode width	**2.3** [0.4](1.5–3.7) [310]	**2.2** [0.4](1.6–3.2) [270]
Color	yellow-green/yellow	yellow-green/yellow/green-brown
Staminate flowers		
Diameter - 3-merous	**2.7** [0.3](2.1–3.5) [260]	**2.6** [0.3](2.2–3.7) [270]
Diameter - 4-merous	**3.7** [0.4](2.7–4.8) [260]	**3.6** [0.4](2.6–5.0) [270]
Perianth lobe length	**1.4** [0.2](0.9–2.0) [520]	**1.5** [0.2](0.9–2.0) [540]
Perianth lobe width	**1.2** [0.2](0.8–1.6) [520]	**1.2** [0.2](0.8–1.7) [540]
Anther diameter	**0.6** [0.1](0.2–0.9) [520]	**0.6** [0.1](0.3–0.9) [540]
Anther distance[1]	**0.5** [0.1](0.2–1.1) [520]	**0.5** [0.1](0.2–1.0) [540]
Mature fruits		
Length	**4.8** [0.5](3.3–6.1) [270]	**4.7** [0.5](3.4–5.9) [260]
Width	**3.1** [0.3](2.2–3.8) [270]	**3.1** [0.3](2.2–3.9) [260]
Color	green, slightly glaucous	green, slightly glaucous
Mature seed		
Length	**2.5** [0.3](1.9–3.2) [270]	**2.5** [0.3](1.8–3.3) [260]
Width	**1.2** [0.1](0.8–1.6) [270]	**1.2** [0.1](0.8–1.6) [260]
Color	dark green	dark green

in plant height, basal diameter, and third internode dimensions were not statistically different between the special forms of *A. abietinum*. In addition, the color of plants of both special forms was typically yellow-green, or yellow as described by Hawksworth and Wiens (1972, 1996). However, occasionally the female plants, and rarely the male plants of red fir dwarf mistletoe were green-brown, particularly at the northern end of its geographic range.

Staminate flowers (both 3- and 4-merous flowers) of f. sp. *concoloris* and f. sp. *magnificae* were similar (Table 1) and the diameters and sizes of other characters were not significantly different. Hawksworth and Wiens (1972, 1996) reported that staminate flower diameter of fir dwarf mistletoe (for both special forms) was 2.5 mm and this must have been for 3-merous flowers because my measurements of 3-merous flower diameters averaged 2.7 and 2.6 mm for white fir and red fir dwarf mistletoe, respectively. Hawksworth and Wiens did not report flower diameters for 4-merous flowers, but I found that the average diameter of 4-merous flowers was 3.7 and 3.6 mm for white fir and red fir dwarf mistletoe, respectively. Mathiasen and Daugherty (2009) reported similar diameters for both 3- and 4-merous flowers, but they reported diameters for 4-merous flowers that were slightly less (3.5 mm for both special forms) than reported here.

Fruits of the special forms were similar also (Table 1) and their lengths and widths were not statistically different. The mean fruit lengths reported here for each special form were only slightly larger (0.1 mm) than reported by Mathiasen and Daugherty (2009), but their results and mine demonstrated that mean fruit length and width (approx. 4.7 × 3.1 mm) of fir dwarf mistletoe was larger than that reported by Hawksworth and Wiens (1972, 1996) (4.0 × 2.0 mm). Seed dimensions reported here and by Mathiasen and Daugherty (2.5 × 1.2 mm) were slightly smaller than reported by Hawksworth and Wiens (2.8 × 1.2 mm).

My results provide further confirmation that the special forms of fir dwarf mistletoe are morphologically similar. Although many of the sizes for plants, flowers, and fruits I report here were slightly larger than those reported by Mathiasen and Daugherty (2009) for both special forms of fir dwarf mistletoe, none of the differences were statistically different based on a

statistical analysis comparing their data set with the data collected for this study (compare Table 1 here and Table 1 in Mathiasen and Daugherty 2009). Furthermore, the range of the sizes of the morphological characters measured was similar, which is additional evidence that the two special forms of fir dwarf mistletoe are morphologically nearly identical (Table 1).

Although Hawksworth and Wiens (1996) reported that the two special forms of fir dwarf mistletoe also had similar flowering and seed dispersal periods, their phenograms, illustrating flowering and seed dispersal, indicated that white fir dwarf mistletoe reached its flowering peak about two weeks earlier, around the first of August versus mid August for red fir dwarf mistletoe. Seed dispersal reached its peak at about the same time for both special forms, about the end of September. However, Scharpf and Parmeter (1967) reported that their observations of seed dispersal of both special forms at the same location indicated red fir dwarf mistletoe started seed dispersal one week earlier. My observations of flowering and seed dispersal in the SNM indicated that both flowering and seed dispersal of the special forms overlapped, but white fir dwarf mistletoe did begin flowering and seed dispersal earlier than red fir dwarf mistletoe. This pattern may have been related to white fir dwarf mistletoe typically occurring at lower elevations than red fir dwarf mistletoe as suggested by Scharpf and Parmeter (1967).

While the morphological characteristics of white fir and red fir dwarf mistletoe are similar, their host affinities are clearly defined. All field observations and artificial cross inoculation studies conducted thus far have supported red fir is immune to infection by white fir dwarf mistletoe and California white fir is immune to infection by red fir dwarf mistletoe. However, it is interesting that white fir dwarf mistletoe has a relatively broad host range including not only California white fir, but Rocky Mountain white fir (*Abies concolor* (Gordon & Glend.) Hildebr.), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), Durangan fir (*Abies durangensis* Martínez) and to a lesser extent Pacific silver fir (*Abies amabilis* Douglas ex J. Forbes), Rocky Mountain subalpine fir (*Abies bifolia* A. Murray bis), sugar pine (*Pinus lambertiana* Douglas), Mexican white pine (*Pinus ayacahuite* Ehrenb. ex Schltdl.), western white pine (*Pinus monticola* Douglas ex D. Don), and lodgepole pine (*Pinus contorta* Douglas ex Loudon) (Hawksworth and Wiens 1996). In contrast, red fir dwarf mistletoe has only been reported to parasitize red fir, even though it is commonly found in mixed conifer stands in the SNM (Hawksworth and Wiens 1996). The reasons for its extreme host specificity are still unclear. The wider host range of Wiens' dwarf mistletoe (*A. abietinum* subsp. *wiensii*) which not only severely parasitizes red fir and Brewer spruce, but is also found on California white fir and western white pine, is further evidence that this dwarf mistletoe is genetically distinct from red fir dwarf mistletoe. Wiens' dwarf mistletoe occurs in the Klamath-Siskiyou Mountains of northwestern California and southwestern Oregon, whereas red fir dwarf mistletoe is confined to the SNM and extreme southern Cascade Mountains (Mt. Lassen area) (Mathiasen and Daugherty 2009). The extreme host specialization exhibited by red fir dwarf mistletoe offers a fascinating area for future research which should include molecular analysis of both special forms as well as Wiens' dwarf mistletoe.

Even though the special forms of fir dwarf mistletoe have distinct host affinities that do not overlap, my data and that of Hawksworth and Wiens (1972, 1996) and Mathiasen and Daugherty (2009) have clearly demonstrated that the two special forms are morphologically indistinguishable. While there are some phenological differences between the special forms, their flowering and seed dispersal periods overlap and the phenological differences they demonstrate are not large enough to warrant giving them separate taxonomic status, other than the special form designation already assigned to them based on their host specificity.

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Appendix 1

Location and Collection Data for Specimens of *Arceuthobium abietinum*

Specimens are deposited at the Deaver Herbarium, Northern Arizona University (ASC) or the University of Arizona Herbarium (ARIZ). Population numbers correspond to Fig. 1.

Arceuthobium abietinum f. sp. *concoloris*. All specimens collected from *Abies lowiana*.

CALIFORNIA. **Shasta Co.**: 11 km W of N entrance to Lassen Natl. Park on Rte 44, elev. 1320 m, 40°31′29″N, 121°40′48″W, 26 September 2008, *Mathiasen 0867* (ASC) (Pop. 1); 17 km SE of N entrance to Lassen Natl. Park on Rte 44, elev. 1730 m, 40°34′15″N, 121°34′19″W, 27 September 2008, *Mathiasen 0870* (ASC) (Pop. 2). **Tehama Co.**: 1 km NW of Mineral Summit on Rte 172, elev. 1520 m, 40°19′49″N, 121°35′02″W, 20 August 2010, *Mathiasen 1035* (ARIZ) (Pop. 5). **Lassen Co.**: 13 km S of junction of Rd A 21 and Route 44 on Rte 44, elev. 1720 m, 40°27′19″N, 120°54′57″W, 15 September 2008, *Mathiasen 0862* (ASC) (Pop. 7); 1 km W of Fredonyer Pass on Rte 36, elev. 1660 m, 40°21′08″N, 120°52′39″W, 20 August 2010, *Mathiasen 1033* (ARIZ) (Pop. 11). **Plumas Co.**: 1.6 km E of Humboldt Summit on forest rd 302, elev. 1850 m, 40°09′42″N, 121°26′13″W, 22 August 2010, *Mathiasen 1039* (ARIZ) (Pop. 9); 1 km S of Rte 36 on Rte 89, elev. 1390 m, 40°15′47″N, 121°14′29″W, 22 August 2010, *Mathiasen 1040* (ARIZ) (Pop. 10); 6 km W of Meadow Valley on forest rd 414, elev. 1470 m, 39°54′49″N, 121°06′43″W, 08 August 2007, *Mathiasen 0732* (ASC) (Pop. 12). **El Dorado Co.**: 7 km E of Sly Park rd on forest rd 5, elev. 1270 m, 38°43′51″N, 120°30′12″W, 13 August 2009, *Mathiasen 0944* (ARIZ) (Pop. 14). **Alpine Co.**: Silver Creek Camp Ground on Rte 4, elev. 2070 m, 38°34′43″N, 119°46′38″W, 22 August 2010, *Mathiasen 1042* (ARIZ) (Pop. 17). **Calaveras Co.**: 11 km E of Dorrington on Rte 4 and 1 km N on Black Springs Rd, elev. 1970 m, 38°22′35″N, 120°11′41″W, 24 August 2010, *Mathiasen 1045* (ARIZ) (Pop. 20). **Tuolumne Co.**: NW end of Dodge Ridge Ski Area parking lot, elev. 1875 m, 38°11′23″N, 119°57′55″W, 09 August 2009, *Mathiasen 0941* (ARIZ) (Pop. 22); 9 km E of Crane Flat on Rte 120, elev. 2030 m, 37°46′40″N, 119°44′56″W, 10 August 2008, *Mathiasen 0819* (ARIZ) (Pop. 23). **Madera Co.**:11 km E of Fish Camp on forest rd 6S07, elev. 2100 m, 37°27′20″N, 119°33′56″W, 11 August 2008, *Mathiasen 0820* (ASC) (Pop. 27). **Fresno Co.**: 2 km W of Huntington Lake on rd to Big Creek, elev. 1910 m, 37°13′10″N, 119°14′52″W, 08 August 2009, *Mathiasen 0936* (ARIZ) (Pop. 28). **Tulare Co.**: Parker Pass on Western Divide Hwy, elev. 2060 m, 35°57′08″N, 118°37′20″W, 06 August 2009, *Mathiasen 0931* (ARIZ) (Pop. 32). **Kern Co.**: 1 km S of Tiger Flat on forest rd 25S16, elev. 1870 m, 35°45′48″N, 118°33′33″W, 22 September 2009, *Mathiasen 0975* (ARIZ) (Pop. 34).

Arceuthobium abietinum f. sp. *magnificae*. All specimens collected from *Abies magnifica*.

CALIFORNIA. **Shasta Co.**: 16 km S of N entrance to Lassen Natl. Park on Rte 89, elev. 1940 m, 40°30′23″N, 121°27′13″W, 26 September 2008, *Mathiasen 0868* (ASC) (Pop. 3). **Tehama Co.**: 1 km S of Colby Mountain Lookout Tower on forest rd 27N36, elev. 1750 m, 40°08′21″N, 121°31′03″W, 21 August 2010, *Mathiasen 1036* (ARIZ) (Pop. 4); 2.5 km S of S entrance to Lassen Natl. Park on Rte 89, elev. 1900 m, 40°24′04″N, 121°31′36″W, 20 August 2010, *Mathiasen 1034* (ARIZ) (Pop. 6). **Butte Co.**: Humboldt Summit on forest rd 308, elev. 2020 m, 40°09′07″N, 121°26′10″W, 21 August 2010, *Mathiasen 1038* (ARIZ) (Pop. 8). **Plumas Co.**: 1 km E of Grizzly Summit on forest rd 414, elev. 1700 m, 39°51′06″N, 121°15′16″W, 07 August 2007, *Mathiasen 0731* (ASC) (Pop. 13). **El Dorado Co.**: 1 km E of Lyons Creek trail head on forest rd 4, elev. 1980 m, 38°49′21″N, 121°11′31″W, 16 August 2007, *Mathiasen 0737* (ASC) (Pop. 15); Echo Summit on U.S. Rte 50, elev. 2275 m, 38°48′44″N, 120°01′40″W, 16 August 2007, *Mathiasen 0738* (ASC) (Pop. 16). **Calaveras Co.**: W shore of Lake Alpine on Rte 4, elev. 2250 m, 38°28′43″N, 120°00′32″W, 23 August 2010, *Mathiasen 1043* (ARIZ) (Pop. 18); 12.5 km E of Dorrington on Rte 4, elev. 1980 m, 38°23′08″N, 120°11′10″W, 24 August 2010, *Mathiasen 1044* (ARIZ) (Pop. 19). **Tuolumne Co.**: 1 km W of Dodge Ridge Ski Area parking lot on rd to Aspen Meadows, elev. 1855 m, 38°11′10″N, 119°58′08″W, 09 August 2009, *Mathiasen 0942* (ARIZ) (Pop. 21); 16 km E of Crane Flat on Rte 120, elev. 2260 m, 37°49′43″N, 119°42′07″W, 10 August 2008, *Mathiasen 0818* (ASC) (Pop. 24); 1 km W of Porcupine Creek on Rte 120, elev. 2360 m, 37°48′36″N, 119°32′24″W, 25 August 2010, *Mathiasen 1048* (ARIZ) (Pop 25). **Madera Co.**: 10 km E of Fish Camp on forest rd 6S07, elev. 1840 m, 37°27′31″N, 119°33′57″W, 11 August 2008, *Mathiasen 0821* (ASC) (Pop. 26). **Fresno Co.**: 2 km E of the dam on Huntington Lake on N shore rd, elev. 2050 m, 37°13′51″N, 119°14′02″ W, 09 August 2009, *Mathiasen 0937* (ARIZ) (Pop. 29). **Tulare Co.**: Summit Trail Head at end of forest rd 21S50, elev. 2510 m, 36°12′39″N, 118°34′42″W, 06 August 2009, *Mathiasen 0934* (ARIZ) (Pop. 30); Peppermint Camp Ground along Western Divide Hwy, elev. 2175 m, 36°04′58″N, 118°32′06″W, 06 August 2009, *Mathiasen 0933* (ARIZ) (Pop. 31); Sunday Peak Trail Head along forest rd 28S16, elev. 2230 m, 35°47′40″N, 118°34′43″W, 06 August 2009, *Mathiasen 0929* (ARIZ) (Pop. 33).

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IS *CYLINDROPUNTIA ×FOSBERGII* (CACTACEAE) A HYBRID?

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Abstract

The Mason Valley cholla, *Cylindropuntia ×fosbergii* (C. B. Wolf) Rebman, M.A. Baker & Pinkava, is the putative hybrid of *C. bigelovii* (Engelm.) F. M. Knuth and some other species of *Cylindropuntia*. We used AFLPs to screen chollas of the Anza-Borrego Desert in southern California to test this hypothesis of hybrid origin and identify the parental species involved. Other species scrutinized as potential parents include *C. echinocarpa* (Engelm. & J. M. Bigelow) F. M. Knuth, *C. ganderi* (C. B. Wolf) Rebman & Pinkava, *C. californica* var. *parkeri* (J. M. Coulter) Pinkava, and *C. wolfii* (L. D. Benson) M.A. Baker. Patterns of band sharing clearly testify to the close relationship between *C. ×fosbergii* and *C. bigelovii*. None of the other species screened came close to that level of similarity. Moreover, the numbers of total loci and unique loci in *C. ×fosbergii* do not meet the expectations of a hybrid taxon. We propose the alternative hypothesis that *C. ×fosbergii* is the sister species of *C. bigelovii*.

Key Words: AFLP, Anza-Borrego Desert, cholla, *Cylindropuntia ×fosbergii*, hybridization, speciation.

Long assumed to be a hybrid, *Cylindropuntia ×fosbergii* (C. B. Wolf) Rebman, M.A. Baker & Pinkava, the Mason Valley Cholla (also called the Pink Teddy-bear Cholla), is endemic to the Anza-Borrego Desert region of eastern San Diego County, California. It is triploid, bears fruit with aborted seeds, and exhibits substantial morphological similarities to *C. bigelovii* (Engelm.) F. M. Knuth. Although the total number of plants may only number from the hundreds to the low thousands, *C. ×fosbergii* can be readily spotted along California Highway S2 between Mountain Palm Springs and the ascent to Box Canyon to the west, a stretch of approximately 30 km. This cholla stands out as the tallest and pinkest cactus in the desert vegetation of Vallecito and Mason Valleys' alluvial fans.

If *C. ×fosbergii* is indeed a hybrid, one likely parent is *C. bigelovii* (Parfitt and Baker 1993; Rebman 1995). The two taxa are sympatric and share an erect habit featuring a single trunk with few to several main branches, and terminal segments <10 cm, 4–6 cm in diameter, and easily detached. Flower and fruit features are the same with the exception of a slight difference in inner tepal color. Both taxa are triploid, although diploid individuals of *C. bigelovii* have been found in Gila, Maricopa, and Pinal counties of south-central Arizona, and one diploid plant has been found in southeastern Baja California (Rebman 1995; Pinkava 2002). Additionally, *C. bigelovii* and *C. ×fosbergii* reportedly share identical sequences for *psb*A-*trn*H, a spacer region of the chloroplast genome (A. Salywon, unpublished data).

Other cholla species proposed as possible parents of *C. ×fosbergii* are *C. echinocarpa* (Engelm. & J. M. Bigelow) F. M. Knuth (Parfitt and Baker 1993) and *C. ganderi* (C. B. Wolf) Rebman & Pinkava (Rebman 1995; Pinkava 2002). Of these two, *C. ganderi* is the most common in the habitat where *C. ×fosbergii* occurs, and in fact can be found growing along with *C. bigelovii* at every location where *C. ×fosbergii* grows. *Cylindropuntia ganderi* is shorter than either *C. bigelovii* or *C. ×fosbergii*, but in rare specimens it exhibits a rusty pink spine color, similar to the color of *C. ×fosbergii*.

Hybridization and polyploidization have been key processes in the evolution of *Cylindropuntia*, which numbers approximately 32 species (Pinkava 1999). Hybridization can result in polyploidy or serve as a step toward it (reviewed in Grant 1981). Among the North American chollas, each species is known to hybridize with at least one other species (Pinkava 2002). Further, more than 64% of the species of subfamily Opuntioideae exhibit polyploidy (Pinkava 2002). Both *C. ×fosbergii* and *C. bigelovii* are triploid, which could have resulted from interspecific hybridization or autopolypoidy. However, *C. bigelovii* has also been implicated as a parent, along with *C.*

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acanthocarpa (Engelm. & J. M. Bigelow) F. M. Knuth var. *major* (Engelm.) Pinkava, of the tetraploid *C. ×campii* M.A. Baker & Pinkava (Baker and Pinkava 1999). In this pairing *C. bigelovii* is proposed to have supplied an unreduced ($3n = 33$) gamete and *C. acanthocarpa* var. *major* a reduced ($n = 11$) gamete.

We undertook an investigation to determine if *Cylindropuntia ×fosbergii* originated through hybridization between chollas of the Anza-Borrego desert. If *C ×fosbergii* is truly of hybrid origin, then the finding of identical cpDNA sequences shared between *C. ×fosbergii* and *C. bigelovii* points to a matrilineal connection between the taxa. This assumes maternal plastid transmission in chollas, which has been found in the closely related genus *Opuntia* Mill. (Corriveau and Coleman 1988). The present work extracted data from the nuclear genome so that, if indeed *C. ×fosbergii* has a hybrid ancestry, genetic markers of both parents could be revealed. Amplified Fragment Length Polymorphisms (AFLPs; Vos et al. 1995) are ideal markers for this application, as they are biparentally inherited and rapidly evolving, and therefore can detect differentiation among even recently diverged lineages. AFLP markers contain substantial phylogenetic signal, require no knowledge about the genome under study, and, in contrast to other "fingerprinting" approaches, display high reproducibility (Koopman 2005). The use of these markers in systematic studies has been increasing, and is showing particular value in investigations of putative hybridization (Gobert et al. 2002; Segarra-Moragues et al. 2007; Errazu et al. 2009; Fjellheim et al. 2009; Yang et al. 2009). Patterns and quantities of unique and shared AFLP loci will enable assessment of the degree and nature of the relationship of *C. ×fosbergii* and other *Cylindropuntia* species of the Anza-Borrego Desert.

Materials and Methods

Specimens

We collected multiple exemplars of *Cylindropuntia ×fosbergii*, *C. bigelovii*, and the other candidate parental taxa, *C. echinocarpa* and *C. ganderi* (Table 1) from the Anza-Borrego Desert region. To ensure that we had considered all local candidates, however unlikely, we also included *C. californica* var. *parkeri* (J. M. Coulter) Pinkava and *C. wolfii* (L. D. Benson) M.A. Baker, species found within several miles of *C. ×fosbergii* populations. Multiple stem segments were taken from each specimen for use as voucher material (deposited at SD) and source of DNA. We extracted DNA from fresh, dried, or frozen stem material employing the protocol of Martin et al. (2006).

AFLP Analysis

We followed a modification (noted below) of the AFLP protocol of Vos et al. (1995). Each DNA sample was digested by *Mse*I and *Eco*RI, then ligated with adaptors corresponding to the cuts generated by these enzymes. A first round (pre-selective) of PCR amplification used primers complementary to the adaptors but which included an additional nucleotide (*Eco*RI + A, *Mse*I + C) to generate a subset of fragments. Our thermal cycler profile deviated from Vos et al. (1995) in decreasing the annealing time to 30 sec, increasing the extension time to 2 min, adding 10 more cycles, and including a final 10 min at 60°C. The second round (selective) of PCR employed primers identical to the pre-selective round but which added two more nucleotides to the adaptor sequence. A total of 18 fluorescent dye-labeled primer pair combinations generated the AFLP profiles for each sample: the *Eco*RI adaptor sequence plus AAG, ACC, and AGC; these were paired with primers with the *Mse*I adaptor sequence plus CAA, CAC, CAG, CAT, CTA, and CTC. Second round thermal cycling followed Vos et al. (1995) except that we added 1 min to the extension steps. A total of 29 DNA samples were subjected to AFLP analysis: 27 exemplars and two replicates (Fos617.2 and Wolf594.2). The samples were put through the procedures in three cohorts (Cohort 1–3), partly for convenience but also as a test of the stability of experimental conditions; the replicates were assigned to different cohorts. The AFLP fragments were separated using either the ABI 310 or ABI 3100 Genetic Analyzer and a ROX fragment size standard (CSUPERB Microchemical Core Facility, San Diego State University). Chromatograms were inspected visually and peaks (loci) appearing at 30 RFU's (relative fluorescence units) or higher were scored as present or absent. All loci unique to one taxon or shared exclusively between two taxa were recorded also. To examine the patterns of AFLP variation in relation to taxonomy, morphology, and geography, the data were also subjected to principal components analysis (SPSS Statistics 17.0) and cluster analysis using neighbor-joining approach (PAUP*4.0b, Swofford 1998).

In order to deal with potential error arising from failed or spurious amplification, we created two data sets for analysis. The Total data set included all loci that were polymorphic, even if a locus was resolved in just one exemplar in one cohort. The 2/3 data set comprised loci that were resolved in at least two of the three cohorts, by at least one sample in each of the cohorts. This measure was taken because some primer combinations failed to yield any reaction in some instances.

TABLE 1. SAMPLING OF TAXA IN THE CURRENT STUDY. Exemplars are identified by abbreviated specific or varietal epithets and collection numbers; the number after the decimal point indicates the set of samples (cohort) with which it was processed. Collection site number refers to the closest mile marker along California State Route S2 to the collection location.

Taxon	Exemplar	Collection information
C. ×fosbergii	Fos595.3	Site 46A: Imperial Co., California Rte S-2, 0.25 mi S of intersection with Great Overland Stage Rte, 32°52′25″N 116°12′34″W, 220 m (*Mayer 595*)
	Fos599.3	Site 44: Imperial Co., California Rte S-2, intersection with Canebrake Rd, 32°54′13″N 116°13′69″W, 298 m (*Mayer 599*)
	Fos603.3	Site 46A (*Mayer 603*)
	Fos606.2	Site 42: Imperial Co., California Rte S-2, 0.45 mi N of mile marker 42, 32°56′54″N 116°17′03″W, 353 m (*Mayer 606*)
	Fos612.3	Site 28: San Diego Co., California Rte S-2, Mason Valley, 0.35 mi N of mile marker 28, 32°59′52″N 116°26′50″W, 664 m (*Mayer 612*)
	Fos617.1/Fos617.2	Site 46A (*Mayer 617*)
C. bigelovii	Big597.1	Site 46A (*Mayer 597*)
	Big600.2	Site 44 (*Mayer 600*)
	Big602.3	Site 46A (*Mayer 602*)
	Big605.3	Site 42 (*Mayer 605*)
	Big616.2	Site 46A (*Mayer 616*)
	Big620.3	Site 42 (*Mayer 620*)
C. ganderi	GandL607.3 (long spines)	Site 42 (*Mayer 607*)
	GandS610.3 (long spines)	Site 35: San Diego Co., California Rte S-2, across road from Vallecito Stage Station County Park, 32°58′35″N 116°21′01″, 472 m (*Mayer 610*)
	GandS614.3 (short spines)	Site 46A (*Mayer 614*)
	GandL615.1 (long spines)	Site 46A (*Mayer 615*)
	GandS631.3 (short spines)	Site 27: San Diego Co., California Rte S-2 at crossing with Oriflamme Cyn route of the San Antonio-San Diego Mail, 33°00′27″N 116°27′23″W, 693 m (*Mayer 631*)
	GandS633.2 (short spines)	Site 46B: Imperial Co., California State Rt S2 at junction with dirt road to Indian Canyon, 32°52′46″N 116°12′40″W, 217 m (*Mayer 633*)
	GandL634.2 (long spines)	Site 46B (*Mayer 634*)
	GandR637.3 (red spines)	San Diego Co., Carrizo Gorge Rd, 200 m N of intersection with State Hwy 94 at crossing with Carrizo Creek Rd, 32°37′24″N 116°09′31″W, 873 m (*Mayer 637*)
C. echinocarpa	Ech626.2	Imperial Co., California Rte S2, 2.2 km S of Anza-Borrego State Park boundary, 3246′35″N 11605′09″W, 262 m (*Mayer 626*)
	Ech627.1	Ibid (*Mayer 627*)
C. californica var. *parkeri*	Park624.1	San Diego Co., Old Hwy 80, W of Manzanita, 800 m W of intersection with Tierra Heights Rd, 32°40′29″N 116°19′34″W, 1170 m (*Mayer 624*)
	Park628.2	San Diego Co., Hwy 78, Banner Grade (*Mayer 628*)
	Park629.2	San Diego Co., California State Rte S2, in parking lot 300 m NE of intersection with Hwy 78, 33°06′06″N 116°28′28″W, 704 m (*Mayer 629*)
C. wolfii	Wolf594.1/Wolf594.2	San Diego Co., Mountain Springs Rd near intersection with Interstate 8, 200 m S of old highway, 32°40′26″N 116°05′56″W, 664 m (*Mayer 594*)
	Wolf635.3	San Diego Co., California State Rte S2 (*Mayer 635*)

RESULTS

The Total data set includes 692 polymorphic loci; 430 of these are present in the 2/3 data set. Loci that amplified for every specimen were not included in the data sets. The exemplars of *Cylindropuntia ganderi* exhibited the most loci in the Total data set (405); *C. ×fosbergii* displayed the fewest, but close to *C. bigelovii* (305 vs. 342, respectively; Table 2). Perhaps due to inconsistent amplification among exemplars and cohorts, fixation within a taxon for a given locus was unusual, except for the taxa represented by just two exemplars (*C. echinocarpa* and *C. wolfii*; Table 2). Accordingly, the total number of loci amplified for a given taxon was close to the number of those loci polymorphic within a taxon (Table 2).

TABLE 2. CHROMOSOME NUMBERS OF THE SPECIES REPRESENTED IN THE PRESENT STUDY AND THE NUMBERS OF AFLP LOCI RESOLVED IN THE TOTAL DATA SET. Parenthetical numbers under Exemplars indicate a replicate. [1] Compiled by Pinkava (2002).

	Exemplars	Chromosome number[1]	Total loci	Polymorphic loci
C. ×*fosbergii*	6 (+1)	33	305	300
C. bigelovii	6	33 (22 uncommon)	342	341
C. ganderi	8	22	404	385
C. echinocarpa	2	22	397	249
C. californica var. *parkeri*	3	22	381	366
C. wolfii	2 (+1)	66	356	269

Exclusive sharing of loci between pairs of taxa showed virtually identical patterns between the Total data and the 2/3 data sets (Table 3); e.g., the ordering of the other taxa by degree of band sharing with *C. wolfii* was identical between the two data sets. The pairwise data underscored the close relationship of *C.* ×*fosbergii* to *C. bigelovii*, with which it shared more than ten times the number of exclusive loci than it shared with any other taxon (Total data, Table 3). Consequently, the analysis failed to single out any of the other species as a likely parent. Loci unique to *C.* ×*fosbergii* were nearly lacking in the 2/3 data set, but numbered 18 in the Total data set, a tally only surpassed by *C. bigelovii* and *C. echinocarpa* (Table 3).

The neighbor-joining tree generated with the Total data set using standard distances shows two main clusters, one consisting of *C.* ×*fosbergii* and *C. bigelovii*, and the other primarily bearing the remaining taxa (Fig. 1). The 2/3 data set results in a tree that is nearly identical with the Total data tree; the differences are explained in the caption of Fig. 1. Poor amplification was a problem for several specimens, primarily of Cohort 2. This lack of data depressed the similarity of these specimens to others, particularly of Cohorts 1 and 3. Consequently, the neighbor-joining tree placed several of the Cohort 2 specimens in a cluster (594W2.2, 606F.2, 616B.2, 617F2.2, 600B.2), distant from conspecific relatives (Fig. 1). This cluster included two specimens (594W2.2, 617F2.2) whose replicates were processed in different cohorts and are found in other clusters. Despite these anomalies, the tree shows groupings of conspecific specimens from across the three cohorts of specimens, demonstrating that amplification of these markers was not typically dependent on the cohort to which a specimen belonged (Fig. 1).

The first three principal components resulting from analysis of the Total data set accounted for 25.4%, 11.9%, and 8.7% (cumulatively 46%) of the variance. Graphing the 29 samples by the first two principal components should depict intermediacy of *C.* ×*fosbergii* between two species that are the likely parents. The diagram (Fig. 2) depicts a close association of *C.* ×*fosbergii* and *C. bigelovii,* but a wide separation of these two from the other taxa. The exceptions to this pattern include two samples of *C. californica* var. *parkeri*, one *C. echinocarpa*, and one *C. wolfii* that are distributed closely around the *x*-axis, but distant from their conspecific relatives. These are the same samples of Cohort 2 with the anomalous placement in the cluster analysis. Again, *C.* ×*fosbergii* does not appear to meet the expectations of a hybrid taxon.

The collection sites for *C.* ×*fosbergii*, *C. bigelovii*, and *C. ganderi* along California Route S2 are noted (Fig. 1) so that the relationship between geography and genetics could be assessed. If these places are sites of current or past hybridization, we might expect clusters of exemplars of different species but from the same location. The neighbor-joining tree shows some same-species clustering by site, but no strong mixed-species clustering. One exception is the clustering of Big616.2 with Fos617.2, both of site 46A; but Fos606.2 of site 42 is very similar to

TABLE 3. TALLY OF UNIQUE AND SHARED LOCI ACROSS TAXA OF *CYLINDROPUNTIA* SAMPLES ANALYZED. The cells along the diagonal show unique loci for each taxon in the Total data set and the 2/3 data set, respectively; numbers of exclusive pairwise band sharing are shown for the 2/3 data set and the Total data set, above and below the diagonal, respectively.

	C. ×*fos.*	*C. big.*	*C. gan.*	*C. echino.*	*C. cal.* var. *park.*	*C. wolfii*
C. ×*fosbergii*	18/1	33	4	2	0	0
C. bigelovii	51	33/9	9	5	9	1
C. ganderi	5	10	17/7	3	10	10
C. echinocarpa	3	6	5	42/10	5	4
C. californica var. *parkeri*	0	9	24	8	18/3	5
C. wolfii	1	2	14	8	13	14/3

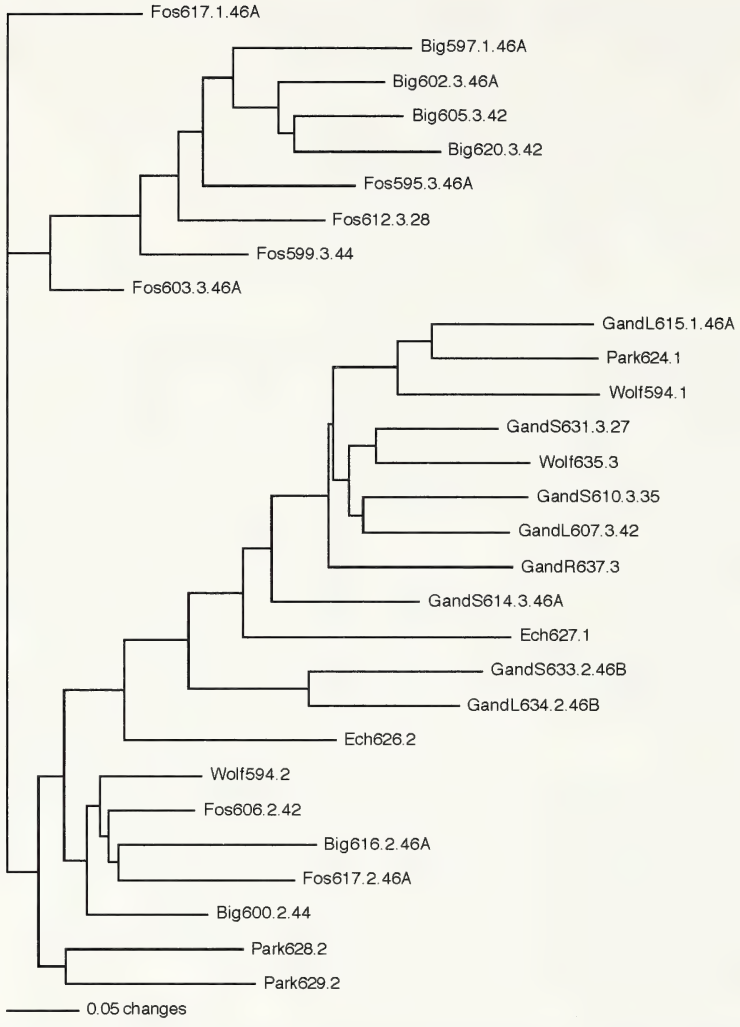

FIG. 1. Neighbor-joining tree of AFLP profiles among the *Cylindropuntia* exemplars employing the Total data set. Exemplars are identified by abbreviated epithet (Big = *C. bigelovii*, Fos = *C.* ×*fosbergii*, Ech = *C. echinocarpa*, Gand = *C. ganderi*, Park = *C. californica* var. *parkeri*, Wolf = *C. wolfii*), collection number, and, after the first decimal point, the group of samples (cohort) with which they were processed; the number after the second decimal point denotes the collection site (Table 1). Exemplars Fos617.2.46A and Wolf594.2 are replicates of Fos617.1.46A and Wolf594.1, respectively. The only topological differences between this tree and the tree resulting from the 2/3 data analysis are (1) the branch bearing GandS633.2 and GandL634.2 is found in the same phyletic grade but between the branches bearing GandR637.3 and GandS614.3, and (2) the positions of Fos606.2 and Fos617.2 are switched.

these two and switches positions with Fos617.2 in the topology of the 2/3 data tree (Fig. 1).

DISCUSSION

The results clearly depict *Cylindropuntia* ×*fosbergii* and *C. bigelovii* as each other's closest relative. The current prevailing view is that *C.* ×*fosbergii* is the hybrid derivative of *C. bigelovii* and some other species. If this hypothesis is to be supported on the molecular level, one should expect a substantial amount of genetic material shared exclusively between parent and hybrid. The high numbers of loci limited to specimens of *C.* ×*fosbergii* and *C. bigelovii* indeed meet this expectation (Table 3). However, no other species has emerged as a likely second parent; patterns of band sharing suggest a relatively distant relationship of *C.* ×*fosbergii* with either *C. ganderi, C. echinocarpa, C. californica* var. *parkeri,* or *C. wolfii*. A stronger similarity of *C.* ×*fosbergii* to *C. bigelovii* might be expected if, as has been suggested (Parfitt and Baker 1993), the triploid *C.* ×*fosbergii* received two sets of chromosomes from *C. bigelovii*. But even if a highly heterozygous *C. bigelovii* was a parent of *C.* ×*fosbergii*, that still could not account for the 10-fold difference in band sharing observed between *C.*

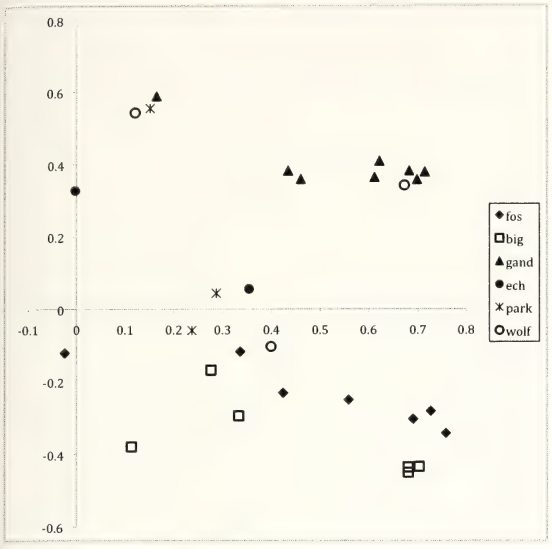

FIG. 2. Scatter diagram of the exemplars by principal components 1 (x-axis) and 2 (y-axis). Taxon abbreviations follow Fig. 1.

×*fosbergii* and *C. bigelovii* versus any other pairing with *C.* ×*fosbergii* (Table 3).

Hybrids, relative to their parents, are expected to possess few or no loci not found in one of their parents, unless the hybridization event was ancient enough for unique mutations to accumulate in the hybrid taxon. Moreover, a sterile triploid status, as in *C.* ×*fosbergii,* virtually rules out gaining genetic variation via gene flow or recombination. *Cylindropuntia* ×*fosbergii* possesses unique alleles, albeit fewer than *C. bigelovii* but comparable in number to *C. californica* var. *parkeri, C. wolfii*, and *C. ganderi* (Total data, Table 3). The discrepancy between the Total data and the 2/3 data sets regarding the numbers of unique loci in *C.* ×*fosbergii* most likely reflects a highly restricted distribution of unique loci in *C.* ×*fosbergii*; i.e., because most of its unique alleles are limited to a single specimen, most of these loci were not included in the 2/3 data set. If *C.* ×*fosbergii* is indeed a hybrid, it is possible we have overlooked another, possibly extinct, taxon that transmitted its unique loci to *C.* ×*fosbergii.*

Another hallmark of hybrids, especially F_1, is a high level of heterozygosity or numbers of loci, or both. Because AFLPs are dominant markers, a hybrid would be expected to exhibit more total bands (alleles/loci) compared to representatives of the parent species. Of all the taxa surveyed in this study, *C.* ×*fosbergii* exhibits the fewest number of loci, counter to the expectation of hybrid status (Table 2).

The sterile, triploid status of both *C.* ×*fosbergii* and the Anza-Borrego populations of *C. bigelovii* makes contemporary formation of hybrids or hybrid swarms involving these taxa unlikely. Moreover, the unique loci and genetic divergence of *C.* ×*fosbergii* specimens from a single location seem to rule out anything but an ancient hybrid origin of the taxon. If a unique hybridization event produced the triploid *C.* ×*fosbergii*, most subsequent reproduction of *C.* ×*fosbergii* would be expected to be vegetative (by detached stem segments). In this case, genetic variation among individuals is expected to be low or nil. If, however, hybridization leading to a triploid *C.* ×*fosbergii* was recurrent and contemporary, then variation among the hybrids could be higher, but patterns of similarity would be expected to show congruency between the distribution of the parents and the hybrids. Patterns of relationship within and between *C.* ×*fosbergii* and *C. bigelovii* or *C. ganderi* do not show strong geographic structuring along the stretch of California Route S2 where the three co-occur (Fig. 1), which is expected if the collection sites are present or past hybrid zones. Moreover, there are no known diploid *C. bigelovii* in California, and the triploid forms have not been shown to produce sexual offspring, with the exception of the formation of C. ×*campii*, which arose from the union of an unreduced triploid gamete of *C. bigelovii* and a reduced haploid gamete of *C. acanthocarpa* var. *major* (Baker and Pinkava 1999).

Alternatively, the findings of the present study can be construed to support the hypothesis of a sister-species relationship between *C.* ×*fosbergii* and *C. bigelovii*. Both species are triploid ($3n = 33$) and propagate vegetatively, except that *C. bigelovii* fruit has been observed to occasionally produce a seed (Rebman 1995), but it is unclear if these are produced sexually or asexually. The numbers of polymorphic loci and unique loci in *C.* ×*fosbergii* and the other taxa in the study are comparable. A peripatric process may have led to the origin of *C.* ×*fosbergii* from ancestral *C. bigelovii*. *Cylindropuntia bigelovii* is a common cholla of the Sonoran Desert of Arizona, California, Sonora, Baja California, and Baja California Sur, whereas *C.* ×*fosbergii* is a narrow endemic, existing in a few small groups in one valley system on the western edge of *C. bigelovii's* range. The widespread *C. bigelovii* exhibits more unique loci, greater polymorphism, and at least a two-fold greater similarity to the other taxa in the study. *Cylindropuntia* ×*fosbergii* may have evolved from isolated populations of *C. bigelovii* and eventually suffered range contraction, bottlenecking, and the resulting decline in genetic variability. The Anza-Borrego region has been a desert for only about 15,000 years (reviewed in Lindsay and Lindsay 1991), and whether or not this provides the time for these processes to occur is unclear.

The data presented do not support the notion that the AFLP patterns are simply a function of sample size or ploidy of the taxa. For example,

diploid *C. ganderi* exhibited the largest number of polymorphic loci but was represented by the largest number of exemplars. The larger sampling (n = 8) resulted from our desire to assess the significance of spine length and color variation in *C. ganderi*. Despite this larger sampling, *C. ganderi* displayed one of the lowest numbers of unique alleles and did not cluster near *C. ×fosbergii*. Plants from the same location collected with short or long spines clustered together (Fig. 1: Gand633.2 + Gand634.2), suggesting only a minor genetic or developmental component underlying this difference. Further, *C. ganderi* plants with the rare red spine color (e.g., GandR637.3) do not seem to be the direct source for the similar spine color in *C. ×fosbergii*, and also does not appear to represent a lineage independent of *C. ganderi* (Fig. 1). *Cylindropuntia wolfii* exhibited the lowest number of polymorphic loci but is a hexaploid, whereas *C. echinocarpa* is a diploid, represented by just two individuals, and displayed the most unique loci (Tables 2, 3). However, *C. wolfii* has a relatively small distribution on the western edge of the Sonoran Desert and produces generally sterile seeds whereas *C. echinocarpa* is sexual species with a range that extends from California and Baja California to Nevada, southwestern Utah, Arizona, and Sonora.

It is clear that AFLP data has great potential for phylogenetic questions in groups with low levels of divergence (Koopman 2005). Moreover, it has been used convincingly to support (Segarra-Moragues et al. 2007) or refute (Yang et al. 2009) hypotheses of hybridization. In the present study, we find that the large reservoir of potential AFLP data can help compensate for the problem of missing data, as evidenced by the similar results from analyses of the 2/3 vs. the Total data sets. These data have successfully excluded all but *C. bigelovii* as a possible parent of *C. ×fosbergii*, but provide no additional support for the hybrid origin hypothesis; instead, the patterns are more suggestive of a sister status of these two taxa.

Cylindropuntia ×fosbergii should be recognized as a species rather than a hybrid. Its unique stature and spine color in the Anza-Borrego Desert do not appear to be the genetic legacy of any extant species. Thus, even if *C. ×fosbergii* is the product of an ancient hybridization event, it harbors a unique combination of genetic information, leaving it distinct among cholla species.

Acknowledgments

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GABBRO SOILS AND PLANT DISTRIBUTIONS ON THEM

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Abstract

Gabbro is a mafic rock with many species that do not occur on soils of granitic or ultramafic rocks. Although some gabbro soils harbor many unique or endemic species, others do not, as botanists have noted from the Appalachian Piedmont to the mountains of California and Oregon. Gabbro soils were sampled in the Peninsular Ranges and in the foothills of the Sierra Nevada to identify special features of the gabbro soils with unique plant species distributions. No soil morphological or chemical differences were found between gabbro soils with and without unique plant species that might explain the differences in plant distributions. Although many unique species may occur only on gabbro soils, apparently their distributions cannot be explained primarily by soil differences among gabbro soils.

Key Words: Gabbro, rare plant species, rocks, soils.

Some soils with gabbro parent materials have unique plant associations (Hunter and Horenstein 1992; Oberbauer 1993), or have plant communities that are intermediate between those of soils on granitic and on ultramafic rocks (Whittaker 1960). Gabbro is a mafic plutonic rock with mineralogy and chemistry that spans the range between granitic rocks, which are silicic rather than mafic, and ultramafic rocks. Therefore, it is reasonable to expect plant communities of gabbro soils to have some aspects of those on granitic soils and some aspects of those on ultramafic rocks, as described by Whitaker (1960). However, no reasons have been found for some endemic species occurring on some gabbro soils and not on others.

Botanists in eastern North America have recognized that some soils with mafic soil parent materials have unique plant associations, especially on the Idedell soils (Dayton 1966). The Iredell series are common soils with mafic parent material on the Piedmont of eastern North America. Several pedons in soils mapped as Iredell were sampled in NRCS (Natural Resources Conservation Service) soil surveys and analyzed in an NRCS laboratory. Exchangeable Ca/Mg ratios <1 were found in most of those pedons, but the soil parent material was not identified specifically for any of the pedons. Ogg and Smith (1993) identified the parent material of a soil mapped as Iredell to be pyroxenite, and exchangeable Ca/Mg ratios <1 prevailed in it, but the ratios were not as low as in ultramafic soils sampled for the same investigation.

Although botanists have recognized unique vegetation on some gabbro soils and not on others, no soil differences have been discovered that might explain vegetation differences. A gabbro soils investigation was conducted to discovery soil differences related to vegetation differences in the Sierra Nevada and in the Peninsular Ranges and to evaluate soil properties that might explain why some gabbro soils have unique vegetation and others do not (Fig. 1).

The Nature of Gabbro

Gabbro is a petrologic term for plutonic rocks that consist of olivine or hornblende, pyroxene, and calcium-feldspar. Its composition spans the range between diorite and peridotite. Among the plutonic rocks, from granite to peridotite, diorite yields the most fertile soils because it has the most favorable balance of magnesium, potassium, and calcium. Soils with peridotite parent materials have very high magnesium and low calcium concentrations, making them much less favorable for most plants. Gabbro has higher concentrations of all ten of the first transition elements than more silicic rocks (Table 1), and some of those elements can be toxic to plants. Peridotite, however, has much greater concentrations of those elements that are most likely to be toxic (Cr, Co, and Ni). Because the composition of gabbro spans the range between diorite and peridotite, gabbro soils might be expected to range from quite fertile to unfavorable for many plants.

Gabbro has 10 to 90% feldspar, 5 to 90% pyroxene, and 5 to 90% olivine or hornblende (Le Maitre 2002). The feldspar is a calcic plagioclase and the pyroxene is mostly augite (monoclinic pyroxene). If the pyroxene is mostly enstatite or hypersthene (orthorhombic pyroxenes) the rock is called norite. Gabbro, with monoclinic pyroxenes, is much more common than norite in western North America. Rock compositions are commonly shown on triangular diagrams (Le Maitre 2002). Only three minerals can be shown on a triangular diagram; therefore separate

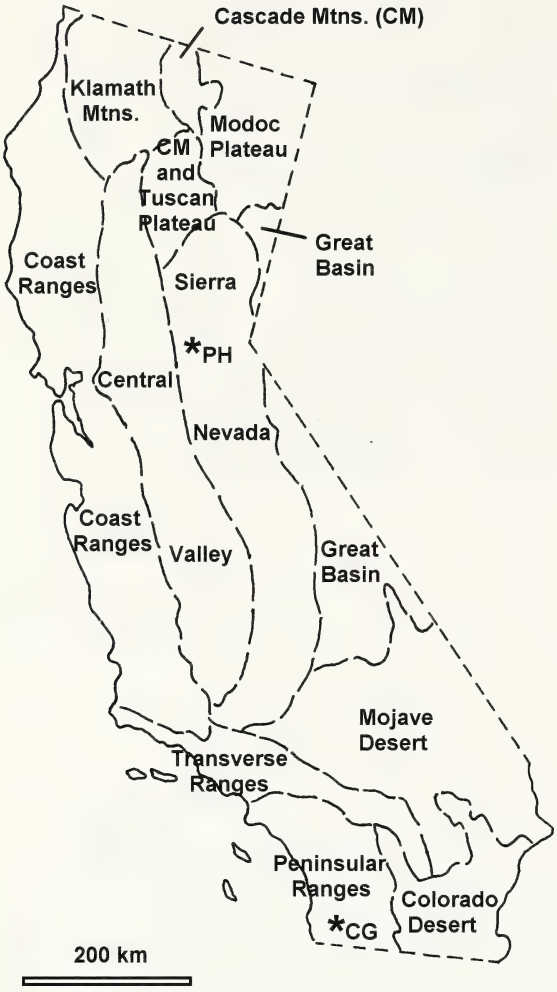

FIG. 1. Locations of the Pine Hill Preserve (PH) in the foothills of the Sierra Nevada and The Cuyamaca-Guatay area (CG) in the Peninsular Ranges Province, CA.

TABLE 1. ELEMENTAL COMPOSITION OF GABBRO AND ITS NEIGHBORS—MORE SILICIC DIORITE AND LESS SILICIC PERIDOTITE. Mean composition of major elements from Le Maitre (1976) and first transition elements from Vinogradov (1962), who included andesite with diorite, basalt with gabbro, and dunite with peridotite. The first transition elements have outer electrons that are in d-orbitals. They are transitional from group 1 and 2 elements with outer electrons in s-orbitals (columns on left side of periodic table) and group 3 to 8 elements with outer electrons in p-orbitals (right side of periodic table of elements).

Major element	Diorite	Gabbro	Peridotite
	g/kg (ppt)		
Si	269	234	198
Al	88	82	22
Ti	6	7	5
Fe	55	80	76
Mn	1	1	3
Mg	22	46	188
Ca	47	67	36
Na	21	14	3
K	12	7	2
P	1.2	1.0	0.4
First trans. element		mg/kg (ppm)	
Sc	2	24	5
Ti	8000	9000	300
V	100	200	40
Cr	50	200	2000
Mn	1200	2000	1500
Fe	58,500	85,600	98,500
Co	10	45	200
Ni	55	160	2000
Cu	35	100	20
Zn	72	130	30

triangles are displayed for olivine gabbro (Fig. 2) and gabbro with hornblende (Fig. 3). Molar Ca/Mg ratios are plotted on Figs. 2 and 3. This requires assumptions about the compositions of the minerals. The compositions were assumed to be $Ca_{0.6}Na_{0.4}Al_{1.6}Si_{2.4}O_8$ for calcium plagioclase (which is designated An_{60} by petrologists), $Ca_{0.4}Mg_{0.4}Fe_{0.2}SiO_3$ for clinopyroxene (augite), $Mg_{1.8}Fe_{0.2}SiO_4$ for olivine, and $Ca_2Mg_3(Al, Fe)Al_2Si_6O_{22}(OH)_2$ for hornblende. The molar Ca/Mg ratios, based on these formulas are infinite for plagioclase, 1.0 for clinopyroxene, 0 for olivine, and 0.67 for hornblende. The molar Ca/Mg ratios of seven gabbro samples from the Pine Hill complex reported by Springer (1980) ranged from 0.58 to 0.76 and averaged 0.69 mol/mol. Olivine has more affect than plagioclase on the Ca/Mg ratios in Fig. 2, because Ca in the plagioclase is only 4.4 moles/kg while Mg in the olivine is 27.7 mol/kg.

Gabbro Compositions in California

Gabbro occurs as components in ophiolites of accreted terranes, in stocks and Alaska-type intrusions, and in laterally extensive layered bodies. Botanists have described plant communities on gabbro in the intrusive bodies of the Peninsular Ranges (Beauchamp 1986; Oberbauer 1993; Cheng 2004) and the Pine Hill complex of the Sierra Nevada foothills (Hunter and Horenstein 1992). Gabbro of these intrusive bodies has been studied comprehensively by Miller (1937), Larsen (1948), and Wallawender (1976) in the Peninsular Ranges and by Springer (1980) in the Pine Hill complex.

Larsen (1948) gave the mineral compositions of 20 rock samples that are representative of gabbro and norite in the Santa Ana Mountains. All contained hornblende and most of them contained at least 10% hornblende, but only 5 samples contained olivine. A hornblende-free

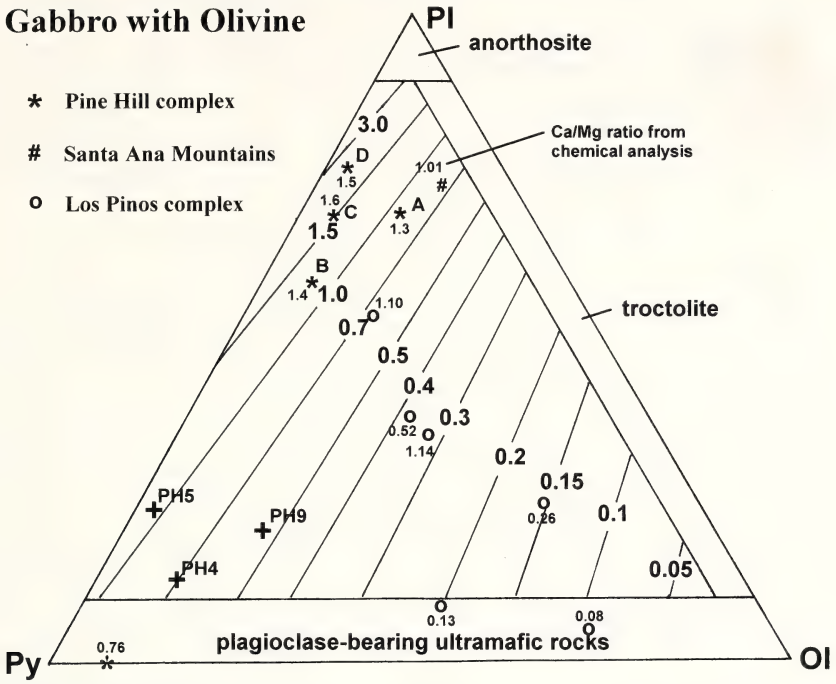

FIG. 2. Olivine-bearing gabbro. Molar Ca/Mg ratios (0.05–3.0) of gabbro composed of plagioclase (Pl), olivine (Ol), and pyroxene (Py). Plagioclase is represented by labradorite ($Ca_{0.6}Na_{0.4}Al_{1.6}Si_{2.4}O_8$), olivine by forsterite or chrysolite ($Mg_{1.8}Fe_{0.2}SiO_4$), and pyroxene by augite ($Ca_{0.4}Mg_{0.4}Fe_{0.2}SiO_3$). Amphiboles are added to pyroxene (2/3 of amphibole) and olivine (1/3 of amphibole). Specific Ca/Mg ratios from chemical analyses are those reported by Springer (1980) for the Pine Hill complex, by Miller (1937) and Larsen (1948) for the Santa Ana Mountains, and by Wallawender (1976) for the Los Pinos complex. Values for the Pine Hill complex are means for four groups of rocks that Spinger (1980) designated A, B, C, and D. Rock samples from the three Pine Hill soils were plotted by the percentages of plagioclase, clinopyroxenes, and olivine (symbols PH4, PH5, and PH9).

gabbro with more than about 15 to 20% olivine will have a molar Ca/Mg < 0.7 (Fig. 3), but none of 8 rocks with chemical analyses had Ca/Mg < 1.0 (Larsen 1948).

Wallawender (1976) gave mineralogical and chemical analyses for 18 rock samples from the Los Pinos pluton. Ten are hornblende bearing gabbro, one with a high Ca/Mg ratio (2.98) and a mean ratio of 1.35 for the nine others, plotted in Fig. 3. One of the 18 samples is an anorthosite. Six of the others have olivine >10% and four of them have molar Ca/Mg ratios <0.7 (Fig. 2). One sample with Ca/Mg = 1.14 seems out of place plotted between 0.3 and 0.4 (Fig. 2), and maybe it is, but it has nearly as much hornblende as olivine.

Springer (1980) showed analyses of 29 samples of gabbro. Only two of them had molar Ca/Mg < 1.0 and one had Ca/Mg < 0.7. He arranged the gabbro into four groups, based on the calcium concentration in the plagioclase: group A, $An_{>85}$; B, An_{70-85}; C, An_{55-69}; and D, $An_{<55}$. The means of the four groups are shown in Fig. 2.

There might have been appreciable additions of aeolian dust, or loess, to the soils developed on gabbro in the Pine Hill area and the Peninsular Ranges. Very fine sand and coarse silt are the major components of aeolian dust (Pye 1995). The main sources of aeolian dust have been the Sacramento Valley, about 40 km from the Pine Hill soil sampling sites, and the coast of the Pacific Ocean, about 60 km from the Peninsular Ranges soil sampling sites. No appreciable amounts of coarse sand are likely to have been carried these distances, but appreciable accumulations of very fine sand are possible in the soils.

Soil Parent Material Influences on Plant Species Distributions

The chemical composition of gabbro is intermediate between ultramafic and granitic rocks. Ultramafic rocks are represented by the base of the triangle in Fig. 2 and granitic rocks (quartz diorite to granite) are more silicic than rocks represented by the left edge of the triangle. Anothosite, represented by the apex of the triangle, is an ancient rock found in California only in the San Gabriel and Orocopia Mountains; it is generally much less calcic than anorthite, which is the plagioclase feldspar with more than 90% Ca and less than 10% Na.

Ultramafic rocks and soils are well known for having unique plant communities and many

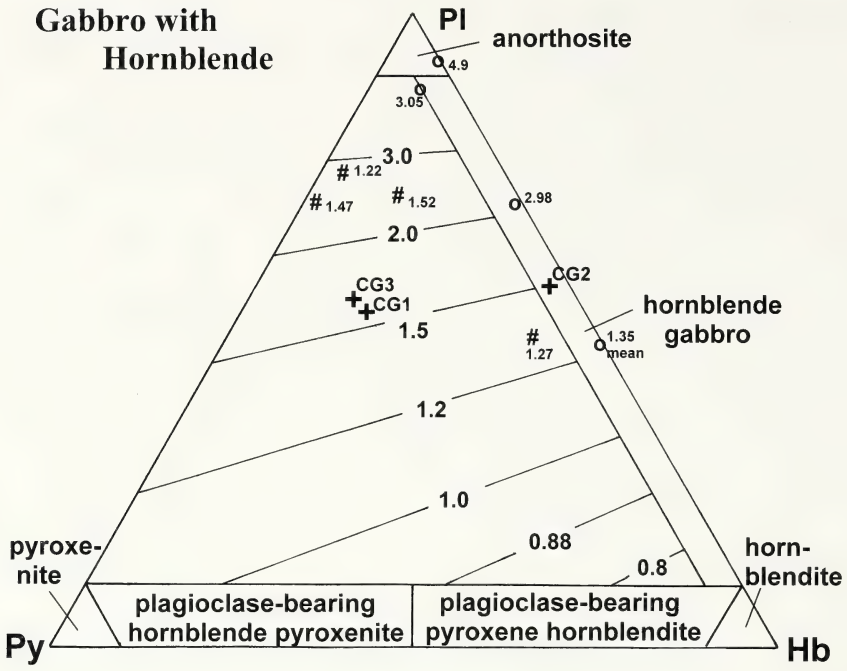

FIG. 3. Hornblende-bearing gabbro. Molar Ca/Mg ratios (0.8–3.0) of gabbro composed of plagioclase (Pl), hornblende (Hb), and pyroxene (Py). Plagioclase is represented by labradorite ($Ca_{0.6}Na_{0.4}Al_{1.6}Si_{2.4}O_8$), hornblende by $Ca_2Mg_3AlFeAl_2Si_6O_{22}(OH)_2$, and pyroxene by augite ($Ca_{0.4}Mg_{0.4}Fe_{0.2}SiO_3$). Symbols as in Fig. 2: o, Los Pinos complex; # Santa Ana Mountains. Rock samples from the three Guatay-Cuyamaca soils were plotted by the percentages of plagioclase, clinopyroxenes, and hornblende (symbols CG1, CG2, and CG3).

endemic species. The absence of many species that are common on soils of more silicic rocks has been attributed to low exchangeable Ca/Mg ratios (Alexander et al. 2007). Some gabbro has low Ca/Mg ratios, but the ratios were not particularly low in the gabbro soils sampled in the Pine Hill area and Peninsular Ranges.

Vegetation differences from gabbro to quartz diorite soils are evident, but not as dramatic as the differences from gabbro to ultramafic soils (Whittaker 1960). More perfuse vegetation on quartz diorite than on gabbro soils (Whittaker 1960) might be explained by greater fertility of quartz diorite soils related to greater amounts of K and P in diorite than in gabbro (Table 1). On a mafic to silicic scale, fertility may be greatest on diorite soils, which generally have a more favorable balance of plant nutrients than either mafic or granitic soils.

An anorthosite soil in the San Gabriel Mountains was sampled and characterized by Graham et al. (1988). Although the parent rock had more than 90% plagioclase, the feldspar was andesine that has slightly more Na than Ca. Nevertheless the soil had much more exchangeable Ca than Na. It had low exhangeable K and presumably low P, although the analyses did not include P.

Vlamis et al. (1954) grew lettuce in 13 soils sampled on gabbro, anorthosite, diorite, and granodiorite. The lettuce responded to N additions on all of the soils and to P on most of them, except on an infertile anorthosite soil where there was no response to a complete N + P + K fertilizer either. Only on an anorthosite soil did the lettuce respond to K addition. Although plant cover appeared to be related to soil productivity, there were no distinct differences in plant species distributions among the soils. Other than sparse trees (*Pinus coulteri* D. Don and *Quercus chrysolepis* Leibm.), only shrubs and *Yucca* sp. were reported from the soil sampling sites; the shrubs were *Adenostoma fasciculatum* Hook. & Arn., *Arctostaphylos* spp., *Ceanothus* spp., *Cercocarpus* sp., *Eriodictyon* sp., *Lotus scoparius* (Nutt.) Ottley, *Quercus* spp., *Malosma laurina* (Nutt.) Abrams, and *Salvia* spp.

METHODS

Gabbro soils and their parent rocks were sampled at two sites with unique vegetation and one without unique vegetation in both Research Natural Areas (RNAs) in the Peninsular Ranges and the Pine Hill Preserve in the foothills of the Sierra Nevada. Altitudes are 460 to 590 m at the Pine Hill sites and 1270 to 1385 m at the Guatay and King Creek RNA sites in the Peninsular Ranges. The mean annual precipitation at these sites is in the 750 to 800 mm range. At a site on the upper one-half of a moderately steep (21–36%

gradient) convex slightly slope in each plant community, three sets of soil and rock samples were taken from subsites three to nine meters apart. The soils were sampled at the 0–15 cm and 30–45 cm depths. Each subsite soil sample was a composite of three subsamples taken from points one to three meters apart. Plants were identified by reference to The Jepson Manual (Hickman 1993) and cover areas were estimated visually. Plant species in a list for the Pine Hill sites were verified by Graciela Hinshaw (Bureau of Land Management, Eldorado Hills, CA) and those in a list for the Peninsular Ranges sites were verified by Todd Keeler-Wolf (California Department of Fish and Game, Sacramento).

Soil samples were dried and sieved to separate the fine-earth (particles <2 mm) for sand and chemical analyses. Texture and consistence of wetted samples were estimated by feel and identified by USDA nomenclature (Soil Survey Staff 1993). Soil family classification follows Soil Taxonomy of the USDA (Soil Survey Staff 1999). Minerals were estimated in 36 fields of view in thin-sections of rocks–one rock from each sample site. Sand was separated from fine-earth samples following treatments overnight in household bleach, decantation of clay, and overnight with Na dithionite in Na citrate solution. Coarse silt (30–62 μm) was obtained from the Pine Hill samples by decantation. Sand separates were dry sieved to obtain five size fractions, and the fine sand (0.125–0.25 mm) fraction was separated into light and heavy grains with bromoform (SG = 2.85). Magnetic grains were separated from the fine sand, very fine sand, and coarse silt fractions with a hand magnet. Percentages of very fine sand and coarse silt with low refractive indices (RI < 1.56) were ascertained by observing 300 grains from each Pine Hill soil.

Soil pH was ascertained with a glass electrode in 1:1 water:soil suspensions. Calcium and magnesium were extracted with molar KCl and measured by atomic absorption (AA) spectrometry. Exchangeable acidity was extracted with 0.5 molar KCl-triethanolamine pH 8.2 buffer and back-titrated with 0.08 molar HCl to a methyl red endpoint (Peech 1965). Soil organic matter was approximated by loss-on-ignition (LOI) at 360°C.

Results of chemical analyses are displayed as means of three samples from each site with standard deviations in parenthesis. One-way ANOVA was run for the three Pine Hill sites and the three Peninsular Ranges sites; that is three sites with three replications at each site in each run of ANOVA. Differences between means in each set of three sites were evaluated by the least significant differences (Snedecor and Cochrane 1967). Where the differences are significant at the 95% level of confidence ($\alpha < 0.05$), the values are designated a and b if the means are on two levels, or a, b, and c if they were on three

TABLE 2. SITE CHARACTERISTICS, SOILS, AND PLANT COMMUNITIES. Sites PH are from Pine Hill, El Dorado Co., sites CG are from Cuyamaca-Guatay, San Diego Co.

Site	Lat. (deg. N)	Long. (deg. W)	Alt. (m)	Slope		Precipitation (cm/yr)	Soil	Soil class	Surface stoniness	Plant community
				Aspect	% gradient					
PH4	38.722	120.989	589	NW	26	80	Boomer variant	Clayey-skeletal, smectitic, mesic Ultic Haploxeralf	Slight	Black oak/toyon–Lemmon ceanothus
PH5	38.719	120.988	577	SE	28	80	Rescue, stony	Clayey-skeletal, smectitic, thermic Mollic Haploxeralf	Very stony	Mixed chamise chaparral
PH9	38.719	120.964	458	SE	23	80	Rescue, clayey	Fine, smectitic, thermic Mollic Haploxeralf	Sparse	Chamise-manzanita chaparral
CG1	32.932	116.614	1385	S	21	90	Las Posas, stony	Clayey-skeletal, smectitic, thermic Typic Rhodoxeralf	Extremely cobbly	Cuyamaca cypress/chamise–golden-yarrow
CG2	32.933	116.632	1275	S	36	80	Las Posas var.	Fine, smectitic, thermic Ultic Haploxeralf	Very cobbly	Eastwood manzanita chaparral
CG3	32.849	116.574	1270	N	34	70	Mollisol	Loamy-skeletal, mixed, superactive, thermic Ultic Argixeroll	Extremely stony	Tecate cypress/scrub oak–cupleaf-lilac

TABLE 3. MINERALS (PERCENT BY VOLUME) IN THE ROCKS. Sites PH are from Pine Hill, El Dorado Co., sites CG are from Cuyamaca-Guataty, San Diego Co. [a]Black, opaque minerals, mostly magnetite. [b]Some alteration of feldspars, apparently to clinozoisite.

Site	Pyroxene	Hornblende	Olivine	Feldspar	Opaque[a]	Other
PH4	64	2	10	11	13	Biotite, clinozoisite[b]
PH5	58	trace	3	24	15	Green spinel
PH9	56	1	15	18	10	Biotite, green spinel
CG1	29	17	1	52	1	
CG2	3	34	4	55	4	
CG3	30	12	3	54	1	

levels of magnitude. Where the differences are significant at the 99% level of confidence ($\alpha < 0.01$), A, B, and C are the level designations.

RESULTS

Pine Hill Preserve Sites

Soils at the three sites in the Pine Hill Preserve, two in the Pine Hill unit and one in the Penny Lane unit, are all Alfisols. One site in the Pine Hill unit has a very stony variant of Rescue soil (site PH5) with a mixed chamise chaparral plant community and the other has a clayey variant of Boomer soil (site PH4) with a black oak/toyon–Lemon ceanothus plant community (Table 2). The site in the Penny Lane unit has a clayey variant of Rescue soil (site PH9) with a chamise–manzanita chaparral plant community. Rock samples representing the soil parent materials of these sites are composed of predominantly clinopyroxene, with lesser amounts of plagioclase feldspar and olivine (Table 3). The compositions of these rocks plotted on Fig. 2 indicate that they are expected to have Ca/Mg ratios about 0.5 to 1.0 mol/mol. Sand separates from the soils showed medium (0.25–0.5 mm) and coarse (0.5–1.0 mm) sand modes. Light separates were about 0.2 (20%) of fine sand fractions, comparable to the feldspar estimates in thin-sections (Table 3). About 1/3, or more, of the heavy fine sand separates from sites PH4 and PH5 and about 1/5 to 1/4 from site PH9 were black opaque grains attracted to a hand magnet, suggesting that the black opaque minerals were mostly magnetite. The means of fine sand, very fine sand, and coarse silt from the 0–15 cm depth in soils at the Pine Hill sites were 93, 71, and 33 g/kg and the masses of magnetic grains were 34, 12, and 2 g/kg. Grains with low refractive indices (RI < 1.56) averaged 5, 8, and 11% in these size fractions and about 1% of the grains in the coarse silt fraction were isotropic (presumably volcanic glass) and the isotropic grains were subrounded to rounded, in contrast to other grains which were mostly angular to subangular. Most, or practically all, of the grains with low refractive indices could be feldspars and vein quartz from the gabbro parent rock. Although the glass is presumed to be from an aeolian source, its mass is <0.1% of the mass of the surface (0–15 cm) soil.

The clayey Rescue variant at site PH9 had vegetation that is common on Rescue soils and the soils at sites PH4 and PH5 had unique vegetation (Table 4). Mature Jeffrey pine trees on the north side of Pine Hill are about 38 m tall, indicating moderate site productivity even with the relatively low precipitation on Pine Hill. There are no Jeffrey pine trees on the Rescue soils.

The plants that are local endemics are Pine Hill ceanothus (*Ceanothus roderickii* W. Knight), Pine

TABLE 4. VASCULAR PLANTS ON THE GABBRO SOILS. Botanical authorities are those given in Hickman (1993). PH9 site: *Pinus sabiniana* and *Quercus wizlizenii* occur on adjacent slopes. Abundance symbols: ++++, 30–100%; +++, 10–30%, ++, 3–10%, +, 1–3%; –, trace; 0, none.

	PH4	PH5	PH9
A. Pine hill			
Trees			
Pinus sabiniana	0	–	0
Quercus kelloggii	+++	0	0
Quercus wislizenii	0	+	0
Cercis occidentalis	+	–	++
Shrubs			
Adenostoma fasciculatum	0	+++	++++
Arctostaphylos viscida	+	++	+++
Ceanothus lemmonii	++	+	++

TABLE 4. CONTINUED

	PH4	PH5	PH9
Ceanothus roderickii	0	+	0
Heteromeles arbutifolia	++	++	0
Quercus durata	−	0	0
Rhamnus ilicifolia	+	−	+
Rhamnus tomentella	0	++	+
Salvia sonomensis	0	++	++++
Toxicodendron diversilobum	−	0	0
Eriodictyon californicum	0	−	−
Forbs			
Calochortus albus	0	0	+
Chlorogalum grandiflorum	0	−	−
Chlorogalum pomeridianum	0	−	−
Dichelostemma multiflorum	0	0	+
Dichelostemma volubile	−	0	0
Fritilaria micrantha	−	0	0
Galium californicum ssp. *sierrae*	−	0	0
Galium spp.	+	+	+
Geranium molle	−	0	0
Sanicula bipinnatifida	0	−	−
Senecio (Packera) layneae	0	0	−
Triteleia bridgesii	−	0	0
Wyethia angustifolia	−	0	0
Wyethia reticulata	−	−	0
Grasses			
Avena fatua	−	0	0
Bromus diandrus	−	0	−
Bromus laevipes	+	0	0
Bromus madritensis ssp. *rubens*	−	0	0
Cynosurus echinatus	−	0	0
Elymus glaucus	+	0	0
Elymus multisetus	−	0	0
Fritilaria micrantha	−	0	0
Gastridium ventricosum	0	0	−
Melica sp.	+	0	−
Nassella lepida	−	0	++
B. Cuyamaca-Guatay	CG1	CG2	CG3
Trees			
Callitropis stephensonii	+++	0	0
Callitropis forbesii	0	0	+++
Shrubs			
Adenostoma fasciculatum	+++	++	++
Arctostaphylos glandulosa	+	+++	−
Ceanothus foliosus	0	+	0
Ceanothus greggii var. *perplexens*	−	0	++++
Cercocarpus betuloides	0	0	−
Ericameria parishii	+++	++	0
Heteromeles arbutifolia	+	0	0
Rhamnus crocea	−	+	0
Quercus berberidifolia	++	0	++++
Salvia sonomensis	+	0	0
Subshrubs and succulents			
Eriophyllum confertifolium	++	0	0
Trichostema parishii	+	−	0
Hesperoyucca whipplei	−	0	0
Forbs			
Calystegia collina	−	+	0
Dichelostemma capitatum	+	0	0
Grasses			
Calamagrostis koeleroides	0	+	0

Hill flannelbush (*Fremontodendron californicum* (Torr.) Coville ssp. *decumbens* (R. M. Lloyd) Munz), El Dorado bedstraw (*Galium californicum* Hook. & Arn. ssp. *sierrae* Dempster & Stebbins), and El Dorado mule-ears (*Wyethia reticulata* Greene). All four of these species are present in the vicinity of sites PH4 or PH5 in the Pine Hill unit, but only El Dorado bedstraw and El Dorado mule-ears are present in the Penny Lane unit (G. Hinshaw, U.S. Bureau of Land Management personal communication).

Surface soil Ca concentrations are relatively high on the very stony Rescue variant (PH5) and the Mg relatively high on the clayey Rescue variant (PH9). The Ca/Mg ratios are significantly higher in the very stony Rescue variant than in the other soils, and the organic matter (LOI, Table 5) and exchangeable acidity are higher, also. The relatively high soil organic matter and high CEC (mostly exchangeable Ca and acidity) at site PH5 may be related to a thick O-horizon of predominantly live oak, toyon, and coffeeberry leaves. The O-horizon was not analyzed chemically. Aqua regia digestion recovered relatively low amounts of Ca for the soil at site PH5, raising doubts about the usefulness of results from the digestion. Aqua regia is an aggressive solvent, but it does not recovery the total amounts of all elements in soils.

Peninsular Ranges, Cuyamaca-Guatay Sites

Soils at two sites sampled in the Cuyamaca area (CG1 and CG2) are Alfisols and the one on Guatay Mountain (CG3) is a Mollisol. Site CG1 site is on an extremely stony variant of Las Posas soil with a Cuyamaca cypress/chamise–golden-yarrow plant community; site CG2 is on a yellowish red variant of the dark reddish brown Las Posas soil with an Eastwood manzanita plant community; and site CG3 on a soft, or friable, black soil (a Mollisol) with a Tecate cypress/scrub oak–cupleaf lilac plant community (Table 2). Rock samples representing the soil parent materials of these sites are predominantly plagioclase feldspar, with substantial amounts of clinopyroxene and hornblende, and only minor olivine (Table 3). The compositions of these rocks plotted on Fig. 3 indicate that they are expected to have Ca/Mg ratios about 1.5 mol/mol. Sand separates from the soils showed fine sand (0.125–0.25 mm) modes. Light separates are about 0.6 (60%) of fine sand fractions, comparable to the feldspar estimates in thin-sections (Table 3). About 0.3 (30%) of the heavy fine sand separates were black opaque grains attracted to a hand magnet, suggesting that the black opaque minerals are mostly magnetite.

The yellowish red Las Posas variant at site CG2 has vegetation that is common on Las Posas soils and the soils at sites CG1 and CG3 have unique vegetation (Table 4).

Exchangeable Ca and Mg in the surface and K in the subsoil are relatively high in the Mollisol (site CG3, Table 5). As at site PH5 on Pine Hill, the Mollisol at site CG3 has a relatively thick O-horizon, but the surface soil organic matter content (LOI, Table 5) is higher in the extremely stony Las Posas variant at site CG1 that had been burned a year or two prior to sampling. Differences in element recovery by aqua regia digestion, such as relatively low P content in the yellowish Las Posas variant, may not be related to vegetation distributions.

Potentially toxic elements (Cr, Co, and Ni) are as high in the soil at site CG2 lacking cypress as they are in the soil at site CG3 with Tecate cypress (Table 6). Although P is lower in the soil at site CG2, that might be a result of the denser vegetation and cypress trees at sites CG1 and CG3 recycling more P rather than an indication of lower inherent soil fertility at site CG2.

Discussion and Conclusions

The chemistry of gabbro soils is sufficiently different from others that some plants that grow on them do not grow on soils of either granitic or ultramafic rocks. In both the Pine Hill area and the Peninsular Ranges, chemical differences between the gabbro soils with common vegetation and those with unique vegetation do not appear to explain the differences in vegetation. The soil differences, other than stoniness, appear to be related to differences in the plant communities on them, rather than the reverse. The hypothesis that the exchangeable CaMg ratios of gabbro soils are important in the distributions of unique species is not verified from the chosen sites.

Perhaps the unique plants would grow on all of the gabbro soils sampled, but they have not all been colonized by those plants. The sites lacking unique species are the hottest and driest sites, which may have limited colonization of them. Site PH9 is lower in elevation than sites PH4 and PH5 that have more unique plants, and site GC2 lacking cypress is on a steep south-facing slope at a lower elevation than site GC1 which is also on a south-facing slope.

Some aeolian dust, or loess, may have been added to the coarse silt fractions of the gabbro soils, but these fractions are small. Only 3.3% of the Pine Hill surface soils were coarse silt, not much more than the 1.0% coarse silt at the 15–30 cm depth. The small amounts of alkali (K and Na > Ca) feldspars and sparse quartz in the coarse silt and other particle-size fractions suggests that the contributions of loess have been minor. Any possible aeolian inputs do not alter the fact that four plants are endemic on the Pine Hill gabbro (Wilson et al. 2010) and that in San Diego Co. *Cupressus arizonica* Greene ssp. *stephensonii* (C.B. Wolf) R. M. Beauch (Cuya-

TABLE 5. SOIL PROPERTIES. The laboratory analyses are means of samples from three subsites, with the standard deviations for each site in parentheses. Samples PH are from Pine Hill, El Dorado Co., samples CG are from Cuyamaca-Guataty, San Diego Co. Text. = texture: C, clay; Cb, cobbly; CL, clay loam; L, loam; St, stony; v, very. Cons. = consistence: ss, s, vs for slightly sticky, sticky, and very sticky; sp, p, and vp for slightly plastic, plastic, and very plastic. BS = base saturation, sum of basic cations divided by the cation-exchange capacity as estimated by basic cations plus acidity extracted with a pH 8.2 buffer. LOI = loss-on-ignition at 360°C. Comparisons among sites in each of the two sample areas: subscripts after sample means indicate levels that are significantly different (lower case letters) or highly significant (upper case letters), with subscript o indicating no significant differences (α 0.05).

Sample	Munsell color		Text.	Cons. wet	pH	Exchangeable cations, pH 8.2 (mmol/kg)				Ca/Mg mol/mol	BS %	LOI g/kg
	Dry	Moist				Ca	Mg	K	Acidity			
PH4-A	7.5YR 4/4	5YR 3/4	StL	ss, sp	6.0	$106_a(20)$	$31_a(5)$	$3.1_o(0.8)$	$51_A(10)$	$3.6_a(1.2)$	$73_A(1)$	$4.1_a(0.9)$
PH4-B	5YR 4/5	5YR 3/4	vStCL	vs, p	5.9	$81_o(16)$	$47_o(16)$	$0.5_o(0.1)$	$45_o(9)$	$1.8_a(0.4)$	$74_o(7)$	—
PH5-A	5YR 4/4	5YR 3/4	vStL	ss, sp	5.8	$153_b(17)$	$26_a(3)$	$4.6_o(2.2)$	$116_B(17)$	$6.0_b(1.2)$	$61_B(2)$	$9.9_b(3.0)$
PH5-B	5YR 4/6	5YR 3/4	vStCL	vs, p	5.8	$136_o(30)$	$53_o(18)$	$0.5_o(0.1)$	$55_o(3)$	$2.7_b(0.5)$	$77_o(6)$	—
PH9-A	5YR 4/4	5YR 3/4	L	ss, sp	6.1	$104_a(7)$	$38_b(6)$	$1.7_o(0.7)$	$67_A(6)$	$2.8_a(0.3)$	$68_C(1)$	$5.6_a(0.8)$
PH9-B	2.5-5YR 4/6	5YR 4/6	CL	vs, p	6.2	$116_o(14)$	$79_o(13)$	$0.4_o(0.1)$	$67_o(2)$	$1.5_a(0.1)$	$82_o(2)$	—
CG1-A	7.5YR 4/4	5YR 3/3	vCbL	ss, sp	5.9	$124_A(4)$	$43_a(6)$	$7.2_A(0.3)$	$104_A(4)$	$2.9_a(0.4)$	$62_A(1)$	$7.1_A(0.9)$
CG1-B	5YR 4/5-5/6	2.5YR 3/5	vCbC	vs, vp	5.8	$90_a(17)$	$81_o(18)$	$1.0_A(0.2)$	$85_A(7)$	$1.1_A(0.1)$	$67_o(6)$	—
CG2-A	7.5YR 4/4	5YR 3/4	CbL	ss, sp	5.7	$76_B(18)$	$37_a(6)$	$7.0_A(0.5)$	$56_B(8)$	$2.0_b(0.2)$	$68_B(2)$	$3.9_B(1.2)$
CG2-B	5YR 5/6	5YR 4/6	clay	vs, vp	6.2	$64_b(3)$	$73_o(6)$	$0.9_A(0.3)$	$59_B(3)$	$0.9_A(0.1)$	$70_o(2)$	—
CG3-A	7.5YR 3/3	7.5YR 2/2	vStL	ss, sp	6.1	$171_C(7)$	$62_b(0)$	$5.4_B(0.2)$	$101_A(5)$	$2.8_a(0.1)$	$71_B(2)$	$6.7_C(0.6)$
CG3-B	7.5YR 4/5	7.5YR 3/4	vStCL	vs, p	5.9	$104_a(9)$	$64_o(4)$	$3.1_B(0.4)$	$76_A(2)$	$1.6_B(0.1)$	$69_o(1)$	—

TABLE 6. SELECTED ELEMENTS FROM AQUA REGIA DIGESTION. PH samples are from Pine Hill, El Dorado Co., CG samples are from Cuyamaca-Guataty, San Diego Co. Mg and Fe are measured in g/kg; all others are mg/kg.

Sample	Al	Mg	Ca	V	Cr	Mn	Co	Ni	Cu	Zn	P	Fe
PH4-A	28.2	18.7	8.3	755	212	1089	87	223	212	53	95	—
PH4-B	39.9	8.0	9.1	722	180	1021	81	87	180	35	91	—
PH5-A	37.0	4.7	6.4	1410	116	1404	92	68	116	46	169	—
PH5-B	35.9	6.5	5.4	991	65	867	73	48	65	28	98	—
PH9-A	32.8	7.2	8.0	830	287	1050	85	109	287	31	112	—
PH9-B	33.5	10.8	7.2	607	182	765	68	82	182	18	54	—
CG1-A	35.3	4.5	5.3	101	239	909	35	41	29	39	426	40.4
CG1-B	60.2	4.6	2.6	157	347	1023	58	54	56	31	465	57.2
CG2-A	37.7	4.8	5.1	322	191	922	37	37	27	42	286	73.4
CG2-B	54.3	3.0	2.0	306	125	835	44	25	58	20	233	83.6
CG3-A	19.2	3.2	6.9	230	59	581	19	15	16	33	329	43.8
CG3-B	39.6	4.9	4.1	370	112	1323	48	28	30	51	399	74.8

maca cypress) and *Cupressus forbesii* Jeps. (Tecate cypress) are only on gabbro soils.

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FURTHER FLORISTICS ON LATE TERTIARY LACUSTRINE DEPOSITS IN THE SOUTHERN ARIZONA DESERTS

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Abstract

The unusual edaphic habitats of late Tertiary lacustrine deposits in Sonoran Desert basins of central Arizona have previously been shown to harbor endemic taxa and disjunct taxa from other floristic regions, which inhabited the Sonoran Desert during previous climatic regimes. The infertile limestone soils contrast sharply with the surrounding volcanic soils, excluding the dominant Sonoran Desert vegetation and thereby providing an ecological opening for the disjuncts. The disjunctions provide clues for interpreting the biogeographical history of Arizona. Here, thirteen additional examples are documented. Taxonomic changes to two of the earlier examples, *Eriogonum apachense* and *Hymenoxys acaulis* var. *arizonica*, are discussed. *Erigonum apachense* from the San Carlos Basin is revealed to be a disjunct population of the northern *E. heermannii* var. *argense*, not a separate endemic species; and, a recently named taxon, *Tetraneuris verdiensis*, from the Verde Valley, is shown to be a rayless form of *T. acaulis* var. *arizonica*, not a separate endemic species. The biogeography of *Ericameria nauseosa* var. *juncea* and *Quercus havardii* are considered in more detail. The type locality of *Ericameria nauseosa* var. *juncea* is one of the disjunct localities, not from the main range of the variety. An unusual thicket-forming oak in the Verde Valley is determined to be a disjunct population of *Quercus havardii* from Staked Plains of New Mexico and Texas and the Four Corners of the Colorado Plateau.

Key Words: Arizona deserts, disjuncts, edaphic habitats, endemics, *Ericameria nauseosa* var *juncea*, *Eriogonum apachense*, *Hymenoxys acaulis* var *arizonica*, *Quercus havardii*.

Plant distributions, their geographic ranges, are effected both by current environmental conditions, their ecology, and past environmental conditions, their biogeographical history. In the cases of disjuncts and endemics, biogeographical history can be the most important factor effecting their present day distribution. These species are remnants of previous floras and environmental conditions whose continued existence provides evidence of the regional biogeographical history (Gankin and Major 1964). However, unlike the dominant vegetation adapted to the present environmental conditions, they can only survive in specialized edaphic and climatic microhabitats. These microhabitats allow the relict species to survive in areas of "compensation" that are more favorable to them within an otherwise hostile environment (Cain 1944).

Late Tertiary lacustrine deposits of limy tuffs in basins in the geological Transition Zone across central Arizona (Titley 1984) along the northern edge of the Sonoran Desert within its *Larrea tridentata-Canotia holocantha* Series of the Arizona Upland Subdivision (Brown 1982) provide edaphic refugia for many disjunct and endemic species of various other floristic affinities (Anderson 1996). The infertile limestone soils of the lacustrine deposits present a sharp edaphic contrast with the predominately volcanic derived soils of the Sonoran Desert mountain ranges. The dominant species of the surrounding Sonoran Desert, *Larrea tridentata* (DC.) Coville and *Parkinsonia microphylla* Torr., which are adapted to the zonal volcanic soils are not able to grow on the azonal limestone soils affording an ecological opening for the relict disjunct species to survive. Another factor aiding an ecological opening for relicts is their occurrence at the northern edge of the Sonoran Desert that places the Transition Zone basins both in an ecotonal area where the surrounding vegetation type is not as dominant, and in an area with a comparably more equable climate that is similar to the more mesic paleoclimate in the region (Axelrod 1979; Anderson 1996).

Thus, the microhabitat refugia contain plant communities of biogeographically unusual species combinations not found anywhere else. These refugia consist of disjunct taxa of different floristic origins from north, south and east that normally are far removed in range from each other. In a sense they represent azonal plant communities that occur as an archipelago of atypical vegetative islands within the dominant Sonoran Desert "sea." The documentation of the presence of these relicts as indicators of the past climatic and topographic variability of Arizona and of past floras occupying the current Sonoran Desert provides clues to past floristic patterns and migrations and enhances the knowledge of the biogeographical history of Arizona.

Anderson (1996) documented the only Sonoran Desert occurrences of thirty of these relict taxa in the Transition Zone lacustrine basins

TABLE 1. SPECIES DISTRIBUTIONS AMONG LATE TERTIARY LACUSTRINE DEPOSITS ACROSS CENTRAL ARIZONA. Basins listed left to right from west to east. Species listed alphabetically by genus.

Species	Anderson mine	Burro creek	Verde valley	San carlos basin	Duncan basin
Allium bigelovii S. Watson	X	X	X		
Astragalus amphioxys A. Gray var. *modestus* Barneby	X	X			
Cryptantha humilis (Greene) Payson		X			
Ericameria nauseosus (Pall. ex Pursh) G. L. Nesom & G. I. Baird var. *junceus* (Greene) H. M. Hall		X			X
Eriogonum heermannii Durand & Hilg. var. *argense* (M. E. Jones) Munz			X	X	
Eriogonum microthecum Nutt. var. *simpsonii* (Benth) Reveal		X	X		
Frasera albomarginata S. Watson			X		
Houstonia rubra Cav.			X		
Pediomelum verdiense S. L. Welsh & M. Licher			X		
Quercus havardii Rydb.			X		
Stanleya pinnata (Pursh) Britton			X		
Tetraneuris acaulis (Pursh) Greene var. *arizonica* K. F. Parker			X		
Townsendia incana Nutt.			X		

whose main ranges were from the Chihuahuan, Mohave, and Navajoan (Colorado Plateau) deserts. Following fieldwork in these basins and in two additional lacustrine deposits, the Anderson Mine and the Duncan Basin, thirteen more such examples have been delineated including the newly described Verde Valley endemic, *Pediomelum verdiense* S. L. Welsh & M. Licher, (Welsh and Licher 2010). The taxonomic status of two of the examples considered by Anderson (1996) have been reassessed (Table 1). The lacustrine deposit at the Anderson Mine area (an old 1950's uranium mine site recently test drilled for resumed mining) above the Santa Maria River in Yavapai County at 590 m is part of the mid-Miocene Chapin Wash Formation (Otton 1981). It is approximately 35 km southwest of the Burro Creek deposit at 770 m, and is the furthest west and lowest elevation lacustrine deposit in the Sonoran Desert (Fig. 1). The Duncan Basin containing the Gila Group lacustrine deposit (Nations et al. 1982; Reid and Buffler 2004) is in the Chihuahuan Desert at 1100 m and is the farthest east in Arizona, approximately 5 km from the Arizona/New Mexico stateline.

With two exceptions, *Allium bigelovii* S. Watson and *Houstonia rubra* Cav., all of the additional taxa listed in Table 1 have floristic affinities to the north, primarily to the Colorado Plateau Subprovincial Element (McLaughlin 2007) with extensions into the Great Basin or Mohave Desert. *Astragalus lentiginosus* Douglas var. *wilsonii* (Greene) Barneby (*Anderson 2009-13* ASU) is another northern taxa disjunct in the Verde Valley but not on the lacustrine deposits. Similarly, in Anderson (1996), more of the disjuncts listed (eighteen of thirty) had northern floristic affinities. These southward disjunctions are the result of the more recent southward movement of northern biotic communities, Great Basin Conifer Woodlands and Great Basin Desertscrub (Brown 1982) from the Colorado Plateau into areas of present day Sonoran Desert in Arizona during Pleistocene glacial cycles as documented by pack rat midden studies (Betancourt et al. 1990). The presence of these northern floristic remnants in the Sonoran Desert Provincial Element (McLaughlin 2007) presents another line of evidence, in addition to the pack rat midden studies, for interpreting the biogeographical history of Arizona.

Allium bigelovii is now determined to be a northwestward disjunct from the Chihuahuan Desert whose main range is in southwestern New Mexico and southeastern Arizona (Sivinski 2003). The occurrences in the Arizona Sonoran

FIG. 1. Anderson Mine with late Tertiary lacustrine deposit (Chapin Wash Formation), Yavapai County. Note surrounding volcanic mountains.

Desert at the Verde Valley, Burro Creek and the Anderson Mine are disjunct from this main range by as much as 400 km. Previously, the correct floristic status of *Allium bigelovii* in Arizona had been masked by the misidentification of many *Allium* herbarium specimens examined by the author at ARIZ, ASC, and ASU which greatly expanded its apparent geographic range to northern Arizona. *Houstonia rubra* is an eastward disjunct taxon in the Verde Valley from its main range to the southeast in the semi-desert grasslands of southeastern Arizona, eastward to New Mexico, Texas, and Mexico and northeastward in the Colorado Plateau where it extends into pinyon-juniper woodland.

Subsequent systematic research has led to the taxonomic reevaluation of two of the taxa included in Anderson (1996). *Eriogonum apachense* Reveal was listed by Anderson (1996) as an endemic at the San Carlos Basin. At the time of its publication (Reveal 1969), *E. apachense* was described as being closely related to *E. heermannii* Durand & Hilg.; and, its distinction was partially based on its geographic isolation. More recent field work by M. Baker (Southwestern Botanical Research) and R. Denham (private botanist) led to the discovery of *Eriogonum heermannii* var. *argense* (M. E. Jones) Munz on the lacustrine deposits in the Verde Valley; and, the reevaluation of the taxonomic status of *E. apachense* as a possible disjunct population of *E. heermannii* var. *argense*. Later, based on joint field visits to the Verde Valley and San Carlos populations and close examination of their respective *Eriogonum* populations, J. Reveal (Cornell University) and the present author came to the conclusion that the San Carlos *Eriogonum* populations represent disjunct populations of *E. heermannii* var. *argense* and not a different endemic species (Reveal 2005). The biogeographical pattern of these *E. heermannii* var. *argense* populations in the San Carlos Basin follows and further confirms that of the other disjuncts on lacustrine deposits described in Anderson (1996) and helps explain a seeming distributional anomaly.

The locality data of another seemingly out of range collection in southern Arizona of *Eriogonum heermannii* var *argense* (M. E. Jones *s.n.* 1903 RSA!) near Vail, Arizona, had been doubted (Kearney and Peebles [1960] state, "The locality as stated is almost certainly erroneous.") However, another lacustrine deposit, the Oligocene Pantano Formation, outcrops in the Vail area (Brennan 1962; Nations et al. 1982). Its presence could provide potential edaphic habitat for a disjunct population of *E. heermannii* var. *argense* similar to the biogeographical pattern described above and shows that the label locality is not "certainly erroneous." Although it has not been rediscovered during subsequent searches there, a new *Eriogonum* species, *Eriogonum terrenatum* Reveal, was discovered on the Pantano Formation by the present author (Reveal 2004). Its only other occurrences are on another lacustrine deposit, the Pleistocene St. David Formation along the San Pedro River approximately 50 km southeast of Vail (Anderson 2007). Its nearest relatives are *Eriogonum ericifolium* Torr. & A. Gray var. *ericifolium* on lacustrine soils in the Verde Valley and *E. pulchrum* Eastw. farther north on the Colorado Plateau. These related *Eriogonum* species provide another example of the lacustrine biographical disjunct pattern (Anderson 2007).

Anderson (1996) listed *Hymenoxys acaulis* (Pursh) K. F. Parker var. *arizonica* (Greene) K. F. Parker, now treated as *Tetraneuris acaulis* (Pursh) Greene var. *arizonica* (Greene) K. F. Parker (Bierner and Turner 2003, 2006) as a disjunct in the Verde Valley. Later, an endemic to the Verde Valley lacustrine deposits, *Tetraneuris verdiensis* R. A. Denham & B. L. Turner, has been described based on "discoid heads...dwarf habitat, relatively short broad leaves, and long pilose vestiture" (Denham and Turner 1996). The subpopulations described as *T. verdiensis* occur on four small gypsum hills only 10 km to the east of the nearest known population of *T. acaulis* var. *arizonica* (Anderson 1996; Denham and Turner 1996; Godec 2001). A more detailed morphological comparison of these two *Tetraneuris* populations showed that the discoid head is the only consistent morphological difference between them (Godec 2001). Individual discoid plants of *T. acaulis* are known elsewhere within its range (described as *T. eradiata* A. Nelson) but are considered to be conspecific (Bierner and Turner 2003). Although the populations of *T. verdiensis* are entirely discoid, this is a minor morphological difference. *Tetraneuris verdiensis* and *T. acaulis* var. *arizonica* share similar edaphic habitats (Nations et al. 1981), associated species such as the other disjuncts, *Eriogonum ericifolium* var. *ericifolium* and *Salvia dorrii* (Kellogg) Abrams ssp. *mearnsii* (Britton) E. M. McClintock, and close proximity to one another (Godec 2001). Based on these factors, it seems more accurate to consider *T. verdiensis* as a discoid form of *T. acaulis* var. *arizonica*, not as a distinct species (Bierner and Turner 2006).

The type locality of *Ericameria nauseosa* (Pall. ex Pursh) G. L. Nesom & G. I. Baird var. *juncea* (Greene) G. L. Nesom & G. I. Baird is a disjunct population in the Chihuahuan Desert on "calcareous bluffs of the Gila River in eastern Arizona very near the New Mexican boundary," (Greene 1881). This locality is far to the south from its normal range of the Colorado Plateau in northern Arizona, southern Utah and adjacent Colorado. A late Tertiary Pliocene lacustrine deposit, the Gila Group, outcrops in this area (Nations et al. 1982; Reid and Buffler 2004) and

FIG. 2. Duncan Basin with late Tertiary lacustrine deposit (Gila Group), Greenlee County. Note lacustrine mudstone in the foreground and volcanic mountains on the horizon.

FIG. 3. *Ericameria nauseosa* var. *juncea* on lacustrine mudstone of the Gila Group, Duncan Basin, Greenlee County.

may be the "calcareous bluffs" habitat mentioned on Greene's label (Fig. 2). The author collected *E. nauseosa* var *juncea* (Fig. 3) on lacustrine badlands of the Gila Group (*Anderson 2009-10* ASU) in the same vicinity as L. Anderson whose collection label (*L. Anderson 4757* 4 Oct 1978 RSA!) states "probable type locality." The variety is also present at the Burro Creek lacustrine site. In addition, another Colorado Plateau/Great Basin disjunct, *Atriplex confertifolia* (Torr. & Frem.) S. Watson, occurs with the *Ericameria* in the Duncan Basin (*Anderson 2009-09* ASU). It is also present in the San Carlos Basin (Anderson 1996).

A peculiar thicket-forming, deciduous oak was discovered by the present author and N. D. Atwood (Brigham Young University) on lacustrine soils of the Verde Formation in the Verde Valley (*Anderson and Atwood 93-13* ASU). L. Landrum (Arizona State University) made a population series of collections (*Landrum 8241-8256, 8258, 8261, and 8263a* ASU) in 1994 and determined it to be *Quercus havardii* Rydb (Fig. 4). Typical *Q. havardii* is a species from the Staked Plains of the Texas panhandle and adjacent New Mexico that occurs in areas of shifting sands in which its thickets form small sand dunes. Other populations attributed to *Q. havardii* also occur in the Four Corners region of southeastern Utah and northeastern Arizona (Tucker 1970; Nixon 1997). Tucker (1970) has interpreted them as ancestral *Q. havardii* populations introgressed by *Q. gambelii* Nutt., not pure *Q. havardii* although he states that the populations are "moderately homogeneous" and not a hybrid swarm. The sandy habitat of *Q. havardii* in the Four Corners is similar to that of the Stake Plains. The anomalous occurrence of the typically sandy habitat dwelling *Q. havardii* on lacustrine limestone in the Verde Valley is an example of substrate switching whereby a disjunct population occurs on a different, even opposite, edaphic habitat from that of its normal range that provides an azonal edaphic refugia (Anderson 1996).

FIG. 4. *Quercus havardii* thicket on Verde Formation limestone, Verde Valley, Yavapai County. Note lacustrine edaphic habitat in foreground and *Canotia holacantha* Torr. in background.

Based on his research that "the species is more or less stable and tends to be habitat specific," Welsh (2003) has recognized the Four Corners populations as a separate species, *Quercus welshii* R. A. Denham ex Welsh. The Verde Valley population appears morphologically similar to the Four Corners populations and could thus be treated as a disjunct population of *Q. welshii*.

As a more southwestern population location, the discovery of *Quercus havardii* in the Verde Valley gives credence to Tucker's postulation that the present day disjunct distribution pattern of *Q. havardii* between Texas/New Mexico and Utah/Arizona is due to its migration northward along both sides of the Rocky Mountains in New Mexico with the glacial retreat from a previously

more continuous ancestral distribution to the south and west of its present distribution (Tucker 1970). The documentation of *Q. havardii* in the Verde Valley is another important instance of the use of species distributions to elucidate past biogeographical patterns.

The biogeogaphical documentation of the many disjuncts in the Verde Valley (Table 1) demonstrates its importance for botanical conservation. Based on the large number of special status plant species occurrences and its rapid population growth, the Verde Valley has a high priority need for botanical conservation. A portion of the Verde Valley lacustrine deposits around the occurrences of the federally endangered *Purshia subintegra* (Kearney) Henrickson and other of the rare Verde Valley plants mentioned above has been designated the Verde Valley Botanical Area by the U.S. Forest Service.

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Appendix 1

Specimen Citations for Disjuncts and Endemics

Specimen citations are listed by taxonomic family and basin location within family: Anderson Mine (AM), Burro Creek (BC), Verde Valley (VV), San Carlos Basin (SC), and Duncan Basin (DB). Herbarium labels contain more specific habitat and locality data (see SEINet for electronic database of Arizona herbaria including species descriptions, pictures, label data, and distribution map; data for rare species may be masked and permission from herbaria curators is required for access). All cited specimens are deposited at ASU unless otherwise indicated or duplicates of ASU specimens are present at other Arizona herbaria.

ALLIACEAE

Allium bigelovii S. Watson – AM: 20 Apr 1980, *Butterwick and Hillyard 6165*; 7 Apr 2008, *Anderson 2008-03*. BC: 20 Apr 1938, *Crooks & Darrow s.n.* (ARIZ); 18 Apr 1941, *Darrow & Benson 10906* (ARIZ); 10 Apr 1980, *Butterwick and Hillyard 4504*; 24 Apr 2008, *Anderson 2008-07*. VV: 22 Apr 1978, *Wetherill s.n.* (MNA); 30 Apr 1978 *Haskell & Deaver 2149* (MNA); 22 Apr 1978, *Lambrechtse 30* (ASC); 16 Apr 1988, *Morefield and Windham 1324* (ASC).

ASTERACEAE

Ericameria nauseosa (Pall. ex Pursh) G. L. Nesom & G. I. Baird var. *juncea* (Greene) H. M. Hall – BC: 17 Sept 1935, *Peebles 12587* (ARIZ); 31 Oct 1978, *Butterwick 4137*; 27 Sept 2008, *Anderson 2008-22*. DB: 5 Sept 1880, *E. L. Greene s.n.* (NDG); 4 Oct 1978, *L. C. Anderson 4757* (RSA); 30 Apr 2009, *J. L. Anderson 2009-10*.

Tetraneuris acaulis (Pursh) Greene var. *arizonica* (Greene) K. F. Parker – VV: 22 Apr 1987, *Boucher 770* (ASC); 8 June 1995, *Anderson 95-17*; 2 Feb 1999, *Anderson with Godec 99-1*; 26 May 1999, *Anderson with Godec 99-15*; 17 Nov 1999, *Baker 13675*; 14 May 1995, *Denham, Forbes, and Searle 1835, 1836, 1837, 1838, 1839* (all paratypes of *Tetraneuris verdiensis*) and 1840 (holotype of *Tetraneuris verdiensis*) (TEX).

Townsendia incana Nutt. – VV: 15 Apr 1978, *Lehto 22583*; 24 June 1979; *Ertter and Strachen 2941*; 7 May 1995, *Anderson 89-39*; 28 May 1993, *Rebman 1865*; 1 May 1999, *Anderson 99-10*.

BORGINACEAE

Cryptantha humilis (Greene) Payson – BC: 20 Apr 1938, *Crooks & Darrow s.n.* (ARIZ); 18 Apr 1941, *Darrow & Benson 10905* (ARIZ); 10 Apr 1947, *Gould & Darrow 4248* (ARIZ); 11 Apr 1976, *Fugate & McLaughlin 1090* (ARIZ); 10 Apr 1979, *Butterwick/ Hillyard 4502*; 6 Apr 1987, *Anderson 86-7*; 27 Apr 2000, *Anderson 2000-4*; 8 Apr 2004, *Anderson 2004-5*.

BRASSICACEAE

Stanleya pinnata (Pursh) Britton – VV: 1 June 1970, *Harris s.n.*; 26 May 1999, *Anderson 99-17*.)

FABACEAE

Astragalus amphioxys A. Gray var. *modestus* Barneby – AM: 20 Apr 1980, *Hillyard 6166, 6170*; 10 May 1995, *Anderson 95-12*. BC: 18 Apr 41, *Benson 10904* (ARIZ); 10 Apr 1979, *Hillyard 4491*; 9 May 1995, *Anderson 95-11*.

Pediomelum verdiense S. L. Welsh & M. Licher – VV: 9 Jun 1941, *Chas. F. Harbison 41.312* (ARIZ); 7 May 1961, *D. Demaree 43936* (ARIZ); 7 May 1989, *Anderson 89-43*; 23 Apr 1992, *Wojciechowski & Sanderson 212* (ARIZ); 30 May 1998, *Hodgson 10397*; 25 Apr 2003, *Rink & Murov 1840* (ASC); 18 Apr 2003 *M. Licher 1911* (BRY holotype, ASC isotype).

FAGACEAE

Quercus havardii Rydb. – VV: 10 June 1993, *Anderson and Atwood 93-13*; 22 June 1994, *Landrum et al 8241-8256, 8258, 8261, 8263a*; *Anderson 2009-47, 48, 49*.

GENTIANACEAE

Frasera albomarginata S. Watson – VV: 2 May 1964, *Eaton 47*; 18 May 1984, *Ricketson 1227*; 26 May 1999, *Anderson 99-16*.

POLYGONACEAE

Eriogonum heermannii Durand & Hilg. var. *argense* (M. E. Jones) Munz – VV: 23 Oct 1995, *Baker 12078*; 10 Oct 2003, *Baker 15652*; 17 Oct 2003, *Reveal 8412, 8413*. SC: 7 Sept 1968, *Pinkava, Keil, & Lehto 13400* (isotype of *Erigonum apachense*); 4 Oct 1967, *Keil, Pinkava, & Lehto 10134*, 8 May 1968, *13018* (both paratypes); 21 Oct 2003, *Reveal 8418, 8419*.

Eriogonum microthecum Nutt. var. *simpsonii* (Benth) Reveal – BC: 17 Sept 1935, *Kearney 12588* (ARIZ); 31 Oct 1978, *Butterwick 4135*; 5 Nov 1983, *Parfitt 3160*; 27 Sept 2008, *Anderson 2008-23*. VV: 19 Sept 1976 *Lehto 20696*, 20718; 29 May 1981, *Van Devender s.n.* (ARIZ); 20 Sept 1984, *Schaack 1326* (ASC); 8 Sept 1988, *Ruffner s.n.* (ASC); 20 Sept 1992, *Baker 10245*; 23 June 1993, *Rowlands s.n.* (ASC); 22 Oct 1994, *Fishbein 2004* (ARIZ); 1 July 1995, *Wright 1597*; 20 Aug 1995, *Baker 11919*; 17 Oct 2003, *Reveal 8414*.

RUBIACEAE

Houstonia rubra Cav. – VV: 2 May 1969, *Pinkava 4960*; 12 Feb 1999, *Anderson 99-2*; 1 May 1999, *Anderson 99-11*.

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ERRATUM

In the article by Harrison and Hebda (2011), an error introduced during printing resulted in a misprint of the species name in Fig. 1 under the left-most box plot. The correct spelling is "*E. alaskanus*," as indicated in the figure legend.

Literature Cited

Harrison, K. and R. J. Hebda. 2011. A morphometric analysis of variation between *Elymus alaskanus* and *Elymus violaceus* (Poaceae): implications for recognition of taxa. Madroño 58:32–49.

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