Ecology and Distribution of Braunton's milkvetch (*Astragalus brauntonii*) and Lyon's pentachaeta (*Pentachaeta lyonii*)

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I. EXECUTIVE SUMMARY

The federally-listed endangered *Astragalus brauntonii* and *Pentachaeta lyonii* (which is also state-listed) persist in disjunct populations in coastal southern California mountain ranges. These regions are heavily affected by urban development and thus there is an urgent need for understanding the impact of this potential threat, and how to best manage these species. The purpose of this study was to evaluate the status of recorded populations and investigate aspects of their ecology.

Most *Astragalus brauntonii* populations had either been extirpated or comprised small fragmented populations. The largest population, unknown at the time of federal listing, occupied a ridge top fuel break and the population is probably being maintained by disturbance associated with fuel break construction, mountain bikes, etc. Germination experiments demonstrated a substantial degree of dormancy that may be broken by soil heating during fire or solar heating of bare substrates. Physical scarification also induces germination, suggesting other disturbances may also be effective in stimulating germination. These seed characteristics indicate this species may maintain a dormant soil seed bank that could recruit after fire. Even so, there is little evidence that fire suppression represents a threat to these populations, since, in these low elevation coastal sites, fires are as abundant now as ever.

Comparisons of *Pentachaeta lyonii* populations with documented populations from other years shows that this species typically fluctuates dramatically from year to year, apparently in response to precipitation. Germination experiments indicate this species does not produce deeply dormant seeds stimulated by fire -- suggesting no close relationship with fire. However, seeds of *Pentachaeta lyonii* do apparently remain dormant during years of low rainfall, although the cues that time germination to adequate rainfall are unknown.

For either target species, preliminary studies of their pollination biology do not suggest this is an important limiting factor to reproductive success. Flowers on both species are visited by native bees or flies, which were found to carry significant loads of their pollen. The importance of pollinators, however, may differ between these species, since *A. brauntonii* is apparently self-compatible whereas *P. lyonii* is apparently self-incompatible, and unlike *A. brauntonii,* it is an annual.

The distribution of these species is correlated with soils derived from different substrates, *A. brauntonii* is restricted to limestone and *P. lyonii* is largely found on red clays often of volcanic origin. This substrate preference is at least partially physiologically determined as greenhouse studies showed that both species had substantially reduced establishment, survival and growth off of their normal substrate.

Both species are often found on disturbed sites and this is likely related to their demonstrated inability to tolerate shading. These species will not tolerate most forms of human-caused disturbance, but under the right conditions of shrub removal, minimal soil disturbance and inhibition of invasive weeds, in proximity to soil seed banks, these species may expand their population size. Presently, wildfires are the only widespread natural disturbance affecting the habitats of both species. However, unlike the case with many chaparral herbs, neither *A. brauntonii* nor *P. lyonii* is a strict fire-dependent species. Both target species are opportunistic and are capable of establishing after only a very limited range of disturbances.

Both species appear to be able to maintain populations for sustained periods without disturbance, if they are not crowded out by shrubs or non-native grasses. This is in marked contrast to the pattern with hundreds of fire-type herb species in chaparral, which are largely incapable of establishing anywhere except on recent burn sites. Unlike fire-type species, it is hypothesized that both target species can maintain populations on undisturbed "safe sites," such as on ridgetops or shallow soils, where, due to soil drought, competition for light is reduced. Both species possess the ability to expand from these refuges out into disturbed sites, following removal of the shrub canopy. It is possible that the present rarity of these species is in part a natural effect of major landscape changes that have occurred since the end of the Pleistocene, primarily due to habitat loss that likely followed the elimination of large grazing and browsing mammals.

II. INTRODUCTION

Braunton's milkvetch, *Astragalus brauntonii* Parish, and Lyon's pentachaeta, *Pentachaeta lyonii* Gray, are federally listed endangered species (USFWS 1997) and the latter is also state listed (Skinner and Pavlik 1994). Both are distributed in widely scattered populations in coastal southern California, north of San Diego County and south of Santa Barbara County (Hickman 1993). They are restricted to urban-mountain ranges, e.g., the Santa Monica Mountains, which are under threat from development and of concern to the California Department of Fish and Game Endangered Plant Program (Ikeda et al. 1991).

The purpose of this study was to document the present distribution and status of populations and investigate aspects of their ecology that would contribute to recommendations for improved management of these rare species. A better understanding of the biology of these species may provide clues to the cause(s) of their rarity. Conservation biologists have expressed different views on the causes of rarity in plants (Rabinowitz 1981) and almost certainly it differs between species. Thus, there is no *a priori* reason to believe that the two species under study here are rare for the same reason. Examples of factors that could play a role in the rarity of *Astragalus brauntonii* and *Pentachaeta lyonii* are lack of suitable habitat, reproductive failure due to lack of appropriate pollinator vectors, and disruption of natural ecosystem processes, none of which are entirely independent of one another. Recognition of the important factors is critical to effective management of rare plants because they may have an origin in anthropogenic activities that could be altered to improve conditions. Of course it must be acknowledged that rarity may be due to natural causes beyond the control of management.

III. RESEARCH OBJECTIVES

1) Role of Disturbance

Both *Astragalus brauntonii* and *Pentachaeta lyonii* are recorded from "disturbed" sites and therefore attention was paid to this factor in the preparation of this report. However, it is apparent from our observations that not all forms of disturbance have a similar impact on these plants.

Disturbances relevant to both species can be classified in two distinct groups, natural and human-mediated. The primary source of natural disturbances in California chaparral, coastal sage scrub, and grasslands is fire, although human disruption of natural fire regimes are well documented throughout the world (Whelan 1996). Regardless of the source, fire acts to remove above ground vegetation and does little to disturb the soil beyond adding nutrients and possibly heat-sterilizing the topmost layers. Additionally, many species in chaparral are dependent on fire-related cues for germination such as smoke, charred wood, and heat (Keeley 1991, Keeley and Fotheringham 1997, 1998). It has been suggested

(Skinner 1991; USFWS 1997) that fire suppression represents a threat to these rare species. However, the mountain ranges occupied by *Astragalus brauntonii* and *Pentachaeta lyonii* have no shortage of fires, and there is substantial evidence from fire history studies to suggest that fires are more common now than prior to human occupation of coastal southern California (Keeley et al. 1989, Mensing 1989, Woods 1992, Conard and Weise 1998, Keeley 1998). The greatest threat from human disruption of the fire regime is increased fire frequency, which favors non-native grasses (Zedler et al. 1983, Haidinger and Keeley 1993, Keeley 1995a), an acknowledged threat to these species (USFWS 1997). This threat is particularly high in habitat fragments surrounded by development.

Another threat to both target species is habitat destruction due to urban expansion. On rare occasions, human disturbance, if not resulting in total habitat destruction, may provide a disturbance beneficial to both target species., but detrimental disturbances are manifold. For example, vegetation removal by scraping with heavy equipment may provide the open conditions necessary for establishment of both target species, but such disturbance have the potential for removing seed banks necessary for regeneration of both species, plus seeds of associated native species. If such disturbance occurs adjacent to populations of target species, colonization onto those disturbances is possible. However, such disturbances, encourage establishment of non–native grasses and forbs, potential threats to many native herbaceous species (Keeley and Swift 1995, USFWS 1997). Scraping, like fire, removes the above ground vegetation, but unlike fire does not increase availability of mineral nutrients in the soil and nor does it stimulate germination of dormant seed banks for the majority of postfire native species. Also, scraping removes other native species, both seeds and resprouting parts, which are required to inhibit invasion by aggressive exotic species (Haidinger and Keeley 1993, Keeley 1995a). Excavation is a more extreme form of human disturbance in that it disturbs and displaces entire horizons in the soil. Even when soil is replaced following excavation, it is altered in texture, being loosened and less compacted (Winegardner 1995), conditions that favor invasive grasses.

Thus, particular note was made of prior disturbances evident during visits to all populations and extent of non-native invasive plant establishment. Intensive field studies focused on factors responsible for maintenance, including characteristics of surrounding vegetation as well as demographic patterns within the populations. However, it is recognized that in annual species, such as *Pentachaeta lyonii*, demographic data at a single point in time is of limited value due to extreme inter-annual variation (Keeley and Keeley 1992).

2) Habitat Factors

It is unknown what factors limit populations of either target species in mature vegetation. Sorting this out may advise on the appropriate disturbance for these species. Shading by the overstory canopy and reduced soil moisture are two factors commonly evoked to explain the lack of herbaceous species in chaparral (Keeley and Keeley 1989) and can be tested by growing plants in different light and soil moisture conditions. In the Santa Monica Mountains dark red-brown clay soils derived from volcanic substrates are common a substrate for *Pentachaeta lyonii*. *Astragalus brauntonii* is excluded from these soils and is restricted to carbonate limestone substrates that occur as rare outcroppings in disjunct parts of the Los Angeles Basin. Reasons for substrate preference are unknown for both species but such information may be of value in evaluating sites for establishing new populations. In some species restricted to particular edaphic conditions distribution is due to physiological preference for particular substrate conditions while in other species it is tied more to the elimination of competitors that are unable to grow on that substrate. It is unknown whether or not either species can grow successfully off its normal substrate and examination of this will give some insight into the extent to which distribution is controlled by physiological specialization versus other factors such as asymmetric patterns of competition.

3) Reproductive Biology

Species establishing on disturbed sites may do so from a dormant soil-seed bank. Evaluating the extent of persistent seed banks that carry-over from year to year is made difficult by the limitation imposed by state-regulations that prohibit destructive sampling methods. Extent of persistent seed banks, however, can be inferred from germination experiments that examine the levels of dormancy and factors triggering germination. Previous studies on *Pentachaeta lyonii* (Keeley 1995b) suggest a rather short-lived, non-fire-stimulated seed pool. Dormancy and germination studies had not previously been conducted on *Astragalus brauntonii*. The seeds are typical of the Fabaceae and other families that require heat or physical scarification, with a hardened seed coat covered by an exterior cuticle.

In addition to factors directly controlling seedling recruitment, other aspects of the reproductive biology may be critical to persistence of rare species (Fiedler and Jain 1992). Little is known about the pollination biology of either *Astragalus brauntonii* or *Pentachaeta lyonii* and therefore studies were conducted to better understand their pollination biology. One step is some understanding of the insect fauna associated with each target species and the potential role each insect plays in pollination. In addition to knowing which vectors are responsible for pollination, an understanding of compatibility barriers is necessary. There are trade-offs inherent both in self-pollinating (inbreeding) and self-incompatible (outcrossing) strategies. Inbreeding species are better colonizers for a specialized environment, but may lack the genetic variability necessary to respond to environmental change.

Outcrossing promotes genetic variation with the ability to adapt to changing environment, but includes a genetic load that can be maladaptive by disrupting well-adapted gene complexes.

IV. *ASTRAGALUS BRAUNTONII*

1) Background

A) Species Description

Astragalus brauntonii is a short-lived tomentose herbaceous perennial in the legume family (Fabaceae). Dependent upon growing conditions, plants vary from 0.7 - 1.5 m, and it is one of the more robust species in the genus (Hickman 1993). Flowering begins in early spring and within the same population extends to June (Munz 1968). Inflorescences are spike-like and produce 35 to 60 flowers each. Fruits are not inflated (bladdery) as in some *Astragalus* species and are 7 - 9 cm long, 3-angled and double chambered in the lower one half, producing three to six seeds.

B) Geographical Range

Astragalus brauntonii is restricted to limestone outcroppings in a disjunct distribution in the western and central Transverse Ranges (Santa Monica and San Gabriel ranges) and the northern Peninsular Ranges (Santa Ana Range). The restriction to unusual substrates is not uncommon in the genus and other closely related species in section Micranthi are also soil endemics (Barneby 1964). Its distribution includes Orange, Los Angeles and Ventura counties. Populations are restricted to low elevations below 550 m (Appendix I, the upper range is 100 m higher than indicated in Hickman 1993). Skinner (1991) has suggested that this species is "headed for extinction" due to fire suppression and because of its apparent fire-dependence, "accurate surveys for this plant are nearly impossible unless one carries a flamethrower." Status of extant populations, made without a flamethrower, are summarized in Appendix I

C) Ecological Requirements

Astragalus brauntonii is commonly described as a transient in chaparral following disturbances such as fires (Skinner 1991), "above firebreaks" (Raven et al. 1966) or, as observed in this study, on recently graded sites. Post-disturbance colonization is likely from a dormant soil stored seed bank, as there is little morphological evidence that fruits and seeds are widely dispersed and thus the plant is not likely to be a good colonizer. Seeds are similar to other species of Fabaceae in being hard seeded, which means they do not imbibe water until some environmental factor breaks the impermeability of outer seed coat layers (Keeley 1991). Factors that could produce such scarification include expansion effects of wetting and drying, microbial degradation, heat from fire or physical abrasion by soil disturbance. Germination follows winter rains. The apparent dependence upon disturbed sites suggests *Astragalus brauntonii* is a weak competitor and is crowded out by larger-stature vegetation. Prior to this study, little was known about the pollination and breeding biology of this species.

2) Research Objectives and Methods

Studies were conducted in the field, greenhouse and laboratory. Field studies were directed at reconnaissance and observation of habitat characteristics of all extant populations and intensive study of a single population. Greenhouse studies were designed to test growth and survivorship of plants in different soils and under different conditions of soil moisture and irradiance levels. Laboratory studies were directed at seed germination characteristics.

A) Field Reconnaissance of Sites

One purpose was to visit as many populations as feasible in order to evaluate their status and record associated vegetation and other habitat characteristics. Notes were made of any evidence of recent disturbance and extent of non-native plant invasion. At each site a GPS location was obtained and a Natural Diversity Data Base inventory form was submitted to CDFG.

B) Community Characterization (Intensive Study Site)

Intensive field studies were done the Temescal Ridge (EO15) population, selected because of the large number of plants and reasonable accessibility (there were no other reasonable sized accessible populations). Studies focused on documenting the density and of cover of the target species and associated species and soil depth. Three line transects with 1-m^2 plots every 5 m (n=18 subplots) were established at the site and subplots were sampled through the growing season for density, height and diameter of the target species. Areal cover of *Astragalus brauntonii* was calculated using areal diameter and assuming the canopy approximated a circle. Additionally, a census was made of other species in the plot coupled with a visual estimate of percentage cover, bare ground, and rock cover. Soil depths were estimated adjacent to each plot by hammering a reebar into the ground up to 21 cm.

C) Pollination Studies (Intensive Study Site)

Studies consisted of pollinator identification and observation of behavior, pollinator exclusion for degree of self pollination and quantification of pollen on observed visitors. Visitation rates were determined on six randomly selected plants for 20 minute observation periods at mid-day (± 2 hr) on three occasions during early spring. All insects coming in contact with the plant, in addition to the duration of their contact were recorded.

Insects were collected by sweep net of the inflorescences and carefully transferred to vials in order to minimize loss of pollen from their bodies. In order to identify pollen, flowers were collected from *Astragalus* and other plants in the vicinity and anthers dissected and squashed on a glass slide for examination of pollen under 100 x magnification. This reference collection was used to compare with pollen taken from insects.

To test for self-compatibility, inflorescences were enclosed in bridal veil supported by an aluminum wire frame, erected prior to flower opening. Prior to flower opening, on each of 10 plants, 4 inflorescences were tagged and treated as follows: (1) control with no manipulation, (2) bagged with fine nylon mesh and no further manipulation, (3) bagged with mesh and later 10 flowers manually self-pollinated and marked with a thin colored wire, and (4)) bagged with mesh and later 10 flowers manually cross-pollinated (with pollen grains from a plant > 5 m away) and marked with a thin colored wire. After the end of the flowering season inflorescences were collected and examined for viable seeds. Seeds produced by enclosed inflorescences were tested for germination (see Section C).

D) Other Insect Interactions (Intensive Study Site)

In order to describe the associated aerial invertebrate fauna, all insects and spiders were captured from 62 random *A. brauntonii* plants in the main population and several surrounding smaller populations over a 5 day period in May, 1997. All insects and spiders on a plant were captured by net or aspirator, transferred to vials, killed and stored in the refrigerator until identified to order. Three insects were particularly common: bruchid beetles (Coleoptera: Bruchidae), aphids (Hemiptera: Aphididae) and ants (Hymenoptera: Formicidae). Interactions of these insects with this *Astragalus* were examined in more detail.

The bruchid beetles are known seed predators so we evaluated seed predation. Random samples of seeds were mounted in paraffin wax and examined at low power under a dissecting microscope. Seeds that were parasitized were soft and easily cut with a razor blade and if they contained a larva they were scored as predation. Older seeds were observed for adult insects emerging; these were collected for identification.

Aphids feed on the phloem sap of the plant and are often tended by ants that harvest sugar secretions from the aphid. Aphids have a potentially negative effect on plant vitality but ants may have a positive effect since they reduce harmful insect herbivores on the plant. *Astragalus* were randomly assigned to one of four treatments (n=12): 1) control plants, 2) no ant treatment, ants were barred access to the plants by Tanglefoot ® encircling the base of the plant, 3) "no" aphids, new growth on the tips of branches was washed with Concern insecticidal soap, which greatly reduced aphid populations, and 4) no ants + no aphids. Experiments began in late winter and applications continued weekly for six weeks. At that time aphid and ant abundance and plant vitality was assessed by measuring active meristematic growth and seed set. Treatment effects were tested with the non-parametric Kruskal Wallis test and Tukey pairwise comparison test and relationships were examined with Spearman correlation.

E) Growth Response to Irradiance, Soil, and Moisture (Greenhouse)

The purpose of these studies was to evaluate growth and survival of *Astragalus brauntonii* on different substrates, and under different shading and soil moisture conditions.

The silty-loam limestone soil typical of *Astragalus brauntonii* sites was collected adjacent to the Temescal Ridge (EO15) population and the more common clay soil derived from volcanic substrates was collected from a site adjacent to a *Pentachaeta lyonii* population in Lake Eleanor Hills (EO28). Soils were sifted through 6 mm wire mesh and used to fill 225 mm plastic pots. Seeds of each species were sown separately in 120 pots, 60 of each soil type. Pots were watered as needed until seedlings established and then thinned to one plant per pot. Experimental treatments were all combinations soil moisture (low, moderate and high watering regimes) in combination with different light or irradiance levels. Watering regimes consisting of the extremes of constantly moist soil (high) to allowing soils to dry thoroughly, often cracking before re-watering (dry) and an intermediate watering regime (moderate). Irradiance levels were with full sun (approximately 1000 μmol m^{-2} s^{-1}) or shade generated by shade cloth (60 μmol m^{-2} s^{-1}). For each treatment there were n=6 replicates, although the final growth comparisons were reduced in some treatments due to poor survivorship. The experiment was terminated after 3 months and survivorship recorded, height and areal diameter measured and then plants were harvested, separated into aboveground and belowground parts, oven dried at 50°C for 24 hours and weighed. Treatments were compared with the multi-way ANOVA and regression with the Pearson regression analysis using SYSTAT (Evanston, IL).

F) Germination Response (Laboratory)

Germination experiments were conducted to evaluate the degree of dormancy, the extent of heat shock stimulated germination and contrast germination behavior of inbred and outcrossed seeds.

Seeds were collected under permit, cleaned and stored under room conditions in glass bottles.

Seeds of both species were kept separate by pollination treatment. Also, due to the observation that after dehiscence of the fruit and dispersal of seeds, some seeds remained in the back locule (even remaining in dropped fruits), seeds were separated by location in the front and back locule.

Prior to the initiation of germination some seeds were treated with dry heat of 95 °C or 105 °C for 5 minutes. Controls consisted of unheated seeds. All seeds were placed in 60mm plastic petri dish lined with filter paper. Seeds were wetted with 2ml deionized water (plus additional water added as necessary for the duration of the experiment). Seeds were cold treated for one week at 5 °C and moved to incubators at 12hr day/night at 18 °C/12 °C, respectively. Germination was scored until all seeds were germinated or until no occurred for more than 2 weeks.

3) Results and Discussion

A) Field Reconnaissance of Sites

Natural Diversity Database reports were filed with Ms. Mary Meyer. See Appendix I for list of sites and current status.

Astragalus brauntonii were found at eight of the listed occurrences. Two of these sites, EO20 and EO21, were extirpated this year by development. Three of the remaining sites, EO11, EO16, and EO19, had one or two remnant plants from larger previously recorded populations. The transplant population in Oak Park, at last visit contained 150 plants, but has more recently been reported to have died out (Ms. Mary Meyer, personal communication). The Temescal Ridge population, EO 15, is the largest naturally occurring population. It persists in a fuel break created for installation of power lines.

B) Community Characterization (Intensive Study Site)

At the Temescal Site (EO15) *Astragalus brauntonii* (abbreviated *Astragalus* from here on) had an average density of 1½ mature plants per m^2 and about 1 seedling per

20-m^2 (Table 1). Bareground comprised 20% of the ground surface area and *Astragalus* comprised only about 10% of the relative cover. The majority of species and bulk of the cover consisted of non-native grasses and forbs (Table 1), which reflects the disturbed nature of the site (Appendix I). There was a significant negative correlation between *Astragalus* density with both total cover of other species and exotic grass cover (Fig. 1). Due to the very sparse shrub cover at the site there was no significant relationship between *Astragalus* cover and shrub cover ($P>0.05$, $r^2=0.06$). Seedlings were uncommon and there was a highly significant positive correlation between seedling recruitment and bareground ($P<0.01$, $r^2=0.25$) and between seedling density and adult density ($P<0.05$, $r^2=0.16$), indicating successful establishment near parent plants and in the absence high annual grass and forb cover.

There was also a significant (Fig. 2) positive correlation between soil depth and *Astragalus* density. Soil depths were taken only to 21 cm due to mechanical restrictions so these measurements are capable of distinguishing only very shallow and moderately deep soils. It appears that while *Astragalus* can establish successfully on shallow substrates, higher densities are more likely on deeper soils.

C) Pollination Studies (Intensive Study Site)

Fourteen species of insect visitors exhibited potential pollination behavior. There were many Hymenoptera, including honey bees, a large and small megachilid or leafcutting bee, three species of bumblebees, and five species of wasps. Also, Diptera such as small hover flies and a large fly, plus a Lepidoptera butterfly. The majority of these species were observed only occasionally, whereas five species made up the bulk of the visitations. The most common visitor was a small megachilid bee (~1 cm) (Order Hymenoptera: Family Megachilidae), accounting for 47% of the visitations observed. On average, each plant was visited 9.1 times by these bees in any 20 minute observation period. The four other common species each comprised 9-10% of the total visitations; these included a larger megachilid bee, the honey bee and a bumble bee sp. (Hymenoptera: Apidae), a wasp (Hymenoptera: Vespidae), and a chalcidid wasp (Hymenoptera: Chalcididae). For the latter two species, if pollination was effected, it was likely incidental as the vespid wasp is predatory and the chalcidid wasp is parasitic, often on bruchid beetle larvae (Borror and White 1970). Other insects that may have played a role in pollination include ants, which were abundant (see Section D), and can be effective pollinators (Hickman 1974). Ants, however, were not commonly observed on open flowers of *Astragalus*.

Based on frequency of visitations it would appear that the megachilid bees were important pollinators of *Astragalus*. This was supported by the study of pollen attached to the five most common insects. Of these, 3 were not observed to have any *Astragalus* pollen attached, whereas 6 of 13 megachilid bees that were examined had

Astragalus pollen; two had pollen loads that consisted primarily (>80%) of pollen from *Astragalus*. The one other species observed with *Astragalus* pollen was a bumble bee, *Bombus* sp. Both of these pollinators also carried pollen of the following species: *Lupinus* (*succulentus*), *Erodium* (*cicutarium*), *Anagalus arvensis*, *Adenostema fasciculatum*, *Marubium vulgaris*, *Encelia californica*, *Salvia* (*mellifera*), and *Malacothrix saxatilis*. *Lupinus* was the most common pollen. Thus, the main pollinators for *Astragalus brauntonii* at the Temescal Site are generalists that visit other, mostly native, plant species.

There was no statistically significant difference ($P>0.05$) between bagged and unbagged controls in flower abortion (Fig. 3) or seeds per fruit (Fig. 4), indicating this *Astragalus* is self-compatible. Other studies of geographically restricted *Astragalus* species, which are also self-compatible, are known to exhibit low levels of genetic variation, relative to more widespread *Astragalus* species (Karron et al. 1988). Detailed comparative study of variation in *A. brauntonii* has not been done to determine if the same holds and whether or not it has any role in rarity of that species.

In an experiment designed to test the extent to which pollination was limiting to seed set, in addition to the control and bagged treatments, two other bagged treatments were included: bagged inflorescences with 10 flowers manipulated to effect self pollination and bagged with 10 flowers manipulated to effect cross pollination. In this experiment the flowers that were manipulated (either self or cross-pollinated) had statistically significantly ($P<0.05$) greater number of seeds per pod (1.1 - 1.6 for un-manipulated flowers, bagged or not) and 2.2 - 2.8 for manipulated flowers). This suggests that although these flowers are self-compatible, seed production is limited by pollen transfer.

There was a slight, but statistically insignificant ($P>0.05$) tendency for higher seed production per fruit in bagged ($X \pm$ S.E.= 2.2 ± 0.3) vs unbagged ($X \pm$ S.E. = 1.6 ± 0.3) treatments. If these patterns represent a real difference between treatments it could be attributable to predator exclusion (see next section) or a more favorable microclimate created by the bags. Seeds from both bagged and unbagged treatments germinated, although there was some variability in the degree of seed coat imposed dormancy, such that bagged seeds sometimes exhibited greater dormancy.

D) Other Insect Interactions (Intensive Study Site)

The sedentary insect fauna associated with *Astragalus* included the common orders of insects in the area: Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, and Thysanoptera. A few spiders were also recorded. However, there was a disproportionate number of bruchid beetles (Coleoptera: Bruchidae), which comprised 60% of the sedentary insects, aphids (Hemiptera: Aphididae) 22%, and ants (Hymenoptera: Formicidae) 12%. On average each *Astragalus* plant had 6.5 coleoptera, 2.4 hemiptera, and 1.3 hymenoptera present on it at any given time.

The most abundant of these sedentary insects, bruchid beetles, likely had negative effects on the *Astragalus*. These beetles spent much time in the flowers feeding upon pollen and other flower parts. Since they were not observed to move between plants there seems little likelihood they play a role in pollination, although they potentially destroyed critical flower parts and may have inhibited visitation by pollinators. In addition, they were observed ovipositing on developing fruits, which is consistent with the fact that the vast majority of bruchid species are known seed parasites of the Fabaceae family (Labeyrie 1981). Therefore, studies of seed predation were conducted. Seed parasites accounted for a loss of 21% ± 4% (X ± S.E., n=100) of seeds. While scoring seed predation, chalcid wasps were observed hatching from the *Astragalus* seeds and bruchid beetle larvae were identified in the seeds. It was not determined whether the chalcid wasps were parasitizing the bruchid beetle larvae or the seeds themselves; both instances are known to occur (Labeyrie 1981, Green and Palmbald 1975).

The ant and aphid exclusion experiments illustrated the close interaction between these two insects. Reduced aphid abundance significantly reduced ant abundance ($P<0.05$) and reduced ant abundance significantly reduced aphid abundance. Across all treatments there was a significant positive correlation between ant and aphid abundance. There is no evidence that aphids affect growth of *Astragalus* as there was no significant difference ($P>0.05$) between controls and treatments in number of active meristems or in seed set. However, there was a significant positive correlation between aphid abundance and meristem abundance, suggesting that aphids are attracted to actively growing plants.

E) Growth Response to Irradiance, Soil, and Moisture (Greenhouse)

Survivorship of *Astragalus* was significantly affected by treatments and there were interactions between treatments (Table 2). Survivorship was reduced in the shade and in full sunlight survivorship was greatly reduced when grown on volcanic soils. The best survivorship was observed in full sunlight on limestone soils (Table 3). Under these conditions watering regime played no significant role in survivorship. All other combinations of irradiance and soil produced quite variable response to moisture regime (Table 3), contributing to the highly significant interaction terms between light and soil type (Table 2).

Growth of *Astragalus* was significantly affected by shade, soil type, and watering (Table 4). Shading had no significant affect on size, as measured by height and areal cover (Table 5). However, biomass, both aboveground and belowground was greater in full sun. Also, in full sun a significantly greater allocation of carbon went to roots, than for plants in the shade. All growth characteristics except height were significantly greater in limestone than in volcanic soil. As with survivorship, watering regime played a relatively minor role in size or biomass production (Table 5). Thus, this *Astragalus* is most robust when grown in limestone soil in full sun, suggesting that the restriction of *Astragalus brauntonii* to limestone may derive from a competitive advantage over other species less able to tolerate such conditions. These results suggest that soil moisture differences between limestone and volcanic soils is not a likely explanation for this edaphic endemism.

F) Germination Response (Laboratory)

Germination of *Astragalus brauntonii* seeds is rather typical of "hard seeded" legumes. In two populations studied, the bulk of the seeds were dormant, although there was a statistically significant difference ($P < 0.01$) in control germination between the Temescal Ridge and Clamshell Canyon populations (Fig. 5). Both populations exhibited nearly complete germination with scarification of the seed coat. Heat, which is a natural means of scarifying seed coats --- e.g., soil heating during fires --- was also shown to significantly ($P<0.01$) increase germination over controls (Fig. 5).

This indicates that some populations are represented by a polymorphic seed pool in which a portion of the seed bank may germinate following dispersal and others persist in a dormant soil seed bank. Germination of the dormant seeds may be triggered by fire, solar heating of bare soil, or physical disturbance of the soil profile (Keeley 1991).

Comparison of front and back locule seed germination showed no significant differences (data not shown) beyond the ones mentioned above.

The seeds do not have an apparent dispersal agent and probably rely on water and gravity as primary methods of dispersal. The Temescal Ridge site may be experiencing some seed dispersal/displacement by recreational users such as hikers and mountain bikers.

4) Conclusions and Management Implications

Astragalus brauntonii is restricted to limestone outcrops, in part because of inferior growth and survivorship off of this substrate (Table 3). Therefore, one component of its restricted distribution is tied to the limited distribution of limestone outcroppings in coastal southern California. Presence of such substrate, however, is no guarantee of a viable population of this rare limestone endemic. It grows poorly when shaded (Table 3) and since most sites are capable of sustaining larger stature shrub associations, disturbance may contribute to population expansion. Under natural conditions, wildfires could generate such safe sites for establishment and at least one stand of several hundred *A. brauntonii* has been reported from a (recent?) burned site (USFWS 1997). Although we know nothing of the metapopulation characteristics for this (or most) species, it seems unlikely that A.

brauntonii colonizes burns from distant populations (fruits and seeds lack obvious structures for long-distance dispersal). Recruitment after fire would require either a dormant soil seed bank or a nearby population, perhaps persisting in some refuge such as a shrub canopy gap. Postfire recruitment from dormant soil seed banks is a common pattern in many native annual species, some of which are strictly fire-dependent (Keeley 1991). However, *Astragalus brauntonii* clearly is not fire-dependent, rather it is opportunistic and is capable of establishing on a variety of disturbances, which distinguishes it from most "fire-dependent" species. This is consistent with the germination experiments that show germination in response to various types of seed coat scarification.

It is of interest that few herbaceous perennial species in chaparral maintain dormant soil seed banks --- most herbaceous perennials are represented after fire by resprouts from underground vegetative parts (Keeley and Bond 1997). One other exception to this rule is the rare legume *Thermopsis macrophylla*, which establishes after fire as well as in fire breaks (Borchert 1989). Both of these rare herbaceous perennials have in common the fact that they produce polymorphic seed banks capable of establishing after fire-scarification of seeds or in other disturbances where seeds are not fire-scarified.

As discussed above (Section II) wildfire frequency is presently as high or higher than under conditions without human influence. However, in light of the very localized distribution of *A. brauntonii*, and the fact that localized patches of chaparral may escape fire for unusually long periods, prescribed burning may be a useful management tool for known sites that currently lack *Astragalus brauntonii*. Sites with known records of *A. brauntonii* should be examined for age of canopy species to gauge how long it has been since the last fire. Sites unburned for more than several decades may warrant intervention in the form of prescribed burning, although the seed banks on sites of this age may not be in any immediate danger of deterioration. Concerns over prescribed burning at the urban/wildland interface (USFWS 1997) are probably of less importance than concern over accelerated accidental fires near developed areas (Keeley and Scott 1994). It is clear that other forms of disturbance will also suffice to establish this species, but not all types of disturbance are good for this species. Active management of sites to create appropriate disturbances might be considered

V. *PENTACHAETA LYONII*

1) Background

A) Species Description

Pentachaeta lyonii Gray [*Chaetopappa lyonii* (Gray) Keck, in Munz, 1968) is a small annual in the sunflower family (Asteraceae). As with other annuals, size is plastic, and dependent upon moisture and other soil conditions, it may range from 5 - 50 cm and be single-stemmed or multi-branched (Hickman 1993). Germination occurs during the early spring rainy season and flowering extends from March to August (Munz 1968). Plants may have from 1 - 30 or more flower head (capitula) and each head produces 20 to 40 1 mm seeds (achenes) with microscopic bristles and a crown of 8 to 12 pappus bristles, which are readily deciduous when touched, suggesting limited spatial dispersal (Keeley and Keeley 1992).

B) Geographical Range

Today *Pentachaeta lyonii* is restricted to the mainland of coastal northern Los Angeles Co. and southern Ventura Co. (York 1989), although the original distribution included Santa Catalina Island (the latter is thought to be based on an accidental introduction, Carl Wishner, personal communication). Extant populations occur on clay soil of volcanic origin in the western end of the Transverse Ranges, specifically, the Santa Monica Mountains, San Fernando Valley, and Simi Valley (Keeley 199?). Status of extant populations are summarized in Appendix II.

C) Ecological Requirements

Pentachaeta lyonii habitat is an open herbaceous vegetation or smaller localized, seemingly permanent gaps within chaparral and coastal sage scrub. Throughout its range it is reported from clay soils on relatively level to gently sloping terrain, often in saddles between hills or benches (Baier and Sproul 1991). *Pentachaeta* apparently competes poorly with annual grasses such as species of *Avena* and *Bromus*, as dense growth by these non-natives appears to preclude it from a site (Keeley and Keeley 1992). Disturbances, such as soil scraping by construction equipment, may favor the species, particularly if soil depth reduces annual grass growth and a seed source is available from adjacent fruiting plants. Disturbance by wildfire may promote *Pentachaeta lyonii* by removing shrub cover, but the relationship between fire and this plant is not clear. One site (EO 33) has persisted with good size populations in the presence of horse grazing, although the duration and intensity of grazing is unknown (Mary Meyer, personal communication).

The relationship between *Pentachaeta* and cattle grazing and burrowing by small rodents is also unknown. Prior to this study, little was known about the pollination and breeding biology of this species.

2) Research Objectives and Methods

Studies were conducted in the field, greenhouse and laboratory. Field studies were directed at reconnaissance and observation of habitat characteristics of all extant populations and intensive study of a single population. Greenhouse studies were designed to test growth and survivorship of plants in different soils and under different conditions of soil moisture and irradiance levels.

A) Field Reconnaissance of Sites

One purpose was to visit as many extant populations as possible in order to evaluate their status and record associated vegetation and other habitat characteristics. Notes were also made of any evidence of recent disturbance and extent of non-native plant invasion. For each accessible site a GPS location was obtained and a Natural Diversity Data Base inventory form was submitted to CDFG.

B) Community Characterization (Intensive Study Site)

Intensive field studies at two of the larger populations (Cal. Lutheran, EO21, and Triunfo Canyon Road, EO27) were focused on documenting the density and of cover of the target species and associated species and soil depth. One line transect with 0.25-m^2 subplots every 5 m ($n=20$ subplots) were sampled through the growing season for density, height and diameter of target species. Cover of *Pentachaeta lyonii* was calculated using diameter and approximating a circle. Additionally, a census was made of other species in the plot coupled with a visual estimate of percentage cover, bare ground, and rock cover. A crude estimate of soil depth was made adjacent to each plot by hammering a reebar into the ground up to 21 cm.

C) Pollination Studies (Intensive Study Site)

Pollination studies were done at two *Pentachaeta* sites (Wood Ranch EO14 and Lindero and Triunfo Canyon roads, EO27). Studies consisted of pollinator identification and observation of behavior, quantification of pollen on observed visitors and effect of pollinator exclusion on flower abortion.

Visitation rates were determined on six randomly selected plants for 20 minute observation periods at mid-day ($\pm$ 2 hr) on three occasions during late spring. All insects coming in contact with the plant, in addition to the duration of their contact were recorded.

Insects were collected by sweep net of the inflorescences and carefully transferred to vials in order to minimize loss of pollen from their bodies. In order to identify pollen, flowers were collected from *Pentachaeta* and other plants in the vicinity and anthers dissected and squashed on a glass slide for examination of pollen under 100 x magnification. This reference collection was used to compare with pollen taken from insects.

To test for self-compatibility, 10 plants with several flower heads were enclosed in bridal veil supported by an aluminum wire frame, erected prior to flower opening. Adjacent unbagged plants were controls. After the end of the flowering season flower heads were collected and examined for flower abortion, evident by the grossly shriveled nature of aborted achenes.

D) Growth Response to Irradiance, Soil, and Moisture (Greenhouse)

The purpose of these studies was to evaluate growth and survival of *Pentachaeta lyonii* on different substrates, and under different shading and soil moisture conditions.

The silty-loam limestone soil typical of *Astragalus brauntonii* sites was collected adjacent to the Temescal Ridge (EO15) population and the more common clay soil derived from volcanic substrates was collected from a site adjacent to a *Pentachaeta lyonii* population in Lake Eleanor Hills (EO26). Soils were sifted through 6 mm wire mesh and used to fill 225 mm plastic pots. Seeds of each species were sown separately in 120 pots, 60 of each soil type. Pots were watered as needed until seedlings established and then thinned to one plant per pot. Experimental treatments were all combinations soil moisture (low, moderate and high watering regimes) in combination with different light or irradiance levels. Watering regimes consisting of the extremes of constantly moist soil (high) to allowing soils to dry thoroughly, often cracking before re-watering (dry) and an intermediate watering regime (moderate). Irradiance levels were with full sun or shade generated by 1-layer of shade cloth. For each treatment there were n=6 replicates, although the final growth comparisons were reduced in some treatments due to poor survivorship. The experiment was terminated after 3 months and survivorship recorded, height and areal diameter measured and then plants were harvested, separated into aboveground and belowground parts, oven dried at 50°C for 24 hours and weighed. Treatments were compared with the multi-way ANOVA and regression with the Pearson regression analysis using SYSTAT (Evanston, IL).

3) Results and Discussion

A) Field Reconnaissance of Sites

Natural Diversity Database reports were filed with Ms. Mary Meyer. See Appendix II for list of sites and current status.

Pentachaeta lyonii occurs in two somewhat different habitats, interior and coastal sides of the inland valleys. Interior sites are generally disturbed grassland, or ecotones between grassland and cactus scrub or patches within shrublands. At sites where significant shrub cover was present, *P. lyonii* was seldom found beneath the shrubs, rather it occupied large canopy gaps. These sites had dense localized populations (often 100 m^{-2}) with rather distinct population boundaries. *Pentachaeta lyonii*, and other species that co-occurred with it in these gaps (e.g., *Bromus hordaceus, Plantago erecta*, and *Stylocline gnaphaloides*) were generally quite stunted in height. The sites were almost exclusively located in saddles between hills or on the tops of small knolls. Most of these sites had inclines between 0-9°. In grasslands, *Avena barbata* and *Centaurea melitensis* are important competitors that are apparently capable of excluding *P. lyonii* (e.g., EO14, EO23, EO15). *Avena barbata* does particularly well in deep soil while the *P. lyonii* occurs in shallower soils. Gophers (*Thomomys bottae*) may tend to favor non-native species by churning the soil over and eliminating the cryptogamic soil seemingly preferred by *P. lyonii*.

On the coastal sides of the interior valleys in the Santa Monica Mountains are sites often dominated by *Adenostema fasciculatum* chaparral, with *P. lyonii* growing in canopy gaps of several meters diameter or in open disturbed sites. These sites tended to occur on slopes steeper than those in the interior and many of these sites extended into flat areas at the base of slopes. These sites also had extensive non-native grasses, including *A. barbata* and *B. hordeaceus*. However, other grasses that were a significant component of the community include the non-native *Gastridium ventricosum* and *Bromus madritensis* and the native *Vulpia octoflora*. Plants were more sparsely distributed than at inland sites, with a typical density of <25 m^{-2}. Two exceptions were highly disturbed sites (EO 27 and EO 11) where *P. lyonii* was growing along a trail or in a road-cut, and density was typically about 50 m^{-2}. The *P. lyonii* at these sites also were generally larger, up to 20 cm in height.

B) Community Characterization (Intensive Study Sites)

At the two intensive study sites *Pentachaeta lyonii* (just *Pentachaeta* from here on) had an average density of 30-38 plants m^{-2} (Tables 6 & 7). At both sites bareground comprised >60% of the ground surface area and *Pentachaeta* comprised only about 2-3% of the relative cover. The majority of species and bulk of the cover consisted of native subshrubs and annuals.

There was also a significant positive correlation ($P<0.05$) between soil depth and *Pentachaeta* density at both sites, one of which is illustrated in Figure 6. Soil depths were taken only to 21 cm due to mechanical restrictions so these measurements are capable of distinguishing only very shallow and moderately deep soils. It appears that while *Pentachaeta* can establish successfully on shallow substrates, higher densities are more likely on deeper soils. Soil depth also acted to increase the length of the growing season. This is reflected in the fact that the decline in population size between March and June was lower on microsites with deeper soil (Fig. 7).

In summary, large populations of *Pentachaeta* are characterized by substantial bareground and limited presence of non-native invasive species.

C) Pollination Studies (Intensive Study Sites)

Nine species of insect visitors exhibited potential pollination behavior. These were mostly Hymenoptera and Diptera, including four bee species, three wasp species and two fly species. The most common visitors by far were digger bees (Order Hymenoptera: Family Apidae, Subfamily Anthophorinae) followed by bee flies (Diptera: Bombyliidae).

The fact that digger bees were the most common visitors to *Pentachaeta lyonii* suggests they were important pollinators. This is further supported by the fact that *Pentachaeta lyonii* pollen was recovered from pollen leg baskets on 6 of 7 digger bees and in one case it comprised 90% of the total pollen load. Other pollen collected from digger bee leg baskets include *Hemizonia fasciculata, Eriogonum fasciculatum, Erodium cicutarium, Brassica nigra,* and *Encelia californica*, the most abundant of which was *H. fasciculata*. Thus, while these bees are likely to be important pollinators, it is clear they visit other associated species. It is of interest that the other species most commonly visited is *H. fasciculata*, a common annual with a superficial resemblance to *Pentachaeta lyonii*.

There was a statistically significant difference ($P<0.01$) between bagged and unbagged controls in flower abortion, evident by the very shriveled achenes in bagged flower heads (Fig. 6). Thus, it would appear that *Pentachaeta lyonii* is self-incompatible. Many California native annuals are self-incompatible, a factor that is thought to have given rise to the rapid speciation evident in many annual genera (Raven 1973).

There is reason to believe that self-incompatibility is not conducive to long distance invasive ability (Zedler 1990).

D) Growth Response to Irradiance, Soil, and Moisture (Greenhouse)

Survivorship of *Pentachaeta* was significantly affected by shade and most particularly by soil, but soil moisture had minimal impact (Table 8). Regardless of irradiance level, *Pentachaeta* survived poorly on limestone (Table 9). Not only was survivorship on limestone low, but as evident by the greatly reduced sample size on limestone, there was substantially reduced germination and establishment on limestone. On the natural volcanic substrates moisture had no significant effect on survivorship.

Growth of *Pentachaeta* followed a very similar pattern as survivorship; significant effects due to irradiance and soil but no significant effect due to soil moisture (Table 10). All traits were significantly greater in full sunlight with the exception of root/shoot ratios (Table 11). In fact biomass was 2½ times greater in full sun than in the shade. Both seedling recruitment and survivorship were so low on limestone that comparison of growth on different substrates is not shown in Table 11. Watering regime had no significant effect on most growth parameters.

In general, *Pentachaeta lyonii* is incapable of establishing on limestone soils and likely grows poorly if shaded by overstory plants.

4) Conclusions and Management Implications

Pentachaeta lyonii showed a highly restricted ability to establish on limestone substrate (Tables 9 & 11), suggesting that further studies should be done to evaluate the extent to which it is restricted from other substrates. However, considering the extent of seemingly suitable substrate, other factors are further restricting its distribution. Since it grows poorly when shaded (Table 11), and since most sites are capable of sustaining larger stature shrub associations, disturbance may contribute to population expansion. However, unlike species that recruit after fire (Keeley 1991) *P. lyonii* apparently does not produce refractory seeds capable of sustained dormancy in the soil (Keeley 1995b). Thus, recruitment may depend upon other types of disturbance for population expansion.

It is of interest that its "typical" habitat is variously described as grassland "dominated by introduced [O]ld [W]orld grass and herb genera" and also as a habitat with "a low percentage of total plant cover and exposed soils with a microbiotic crust" (USFWS 1997). These descriptions do not describe the same type of site. Our observations suggest that the former grassland habitat represents a highly disturbed condition and the latter habitat a relatively stable undisturbed condition. We hypothesize that *Pentachaeta lyonii* has the capacity to persist in stable populations without disturbance where site conditions inhibit invasion by shrubs and non-native grasses (see next section). The primary management required for these latter sites is protection from disturbance.

From these relatively stable refuges, *P. lyonii* has the capacity to colonize disturbances, however, the deciduous pappus typical of this species (Keeley and Keeley 1992) suggests it is not a good colonizer. Thus, colonization events are likely to be relatively localized and thus dependent upon the close proximity of a source population.

VI. CONCLUSIONS

Both *Astragalus brauntonii* and *Pentachaeta lyonii* are dependent upon sites where the dominant shrub vegetation has been excluded, either through disturbance or microhabitat conditions that inhibit shrub growth. The physiological basis for this niche preference is very limited tolerance to shading, although the tolerance to shading interacts in less predictable ways with soil type and moisture conditions.

Our model of the life history strategy for these species is that within the chaparral community there are particular microsites, that preclude shrub growth. These two target species, and other herbaceous plants, may persist indefinitely on such sites --- these microhabitats are a refuge for the target species in the absence of disturbance. Precise microhabitat characteristics of refuges are unknown, but we presume shallow soils are likely to be important, but also well-drained ridgetops as well. Such conditions would not only exclude shrubs but invasive annuals would also not fare well on such sites. Whether or not these target species would persist in these refuges under long term equilibrium or steady state conditions requires careful analysis. Field observations of potential refuges in chaparral and coastal sage scrub vegetation (i.e., seemingly undisturbed sites not dominated by shrubs) are often relatively small in areal extent. This is an important feature of the refuges, because habitat area will affect population size and population size will determine the long term probability of localized extinction. We at this point in time do not know what the minimum viable population (MVP) size is for either of these species. We predict that some natural refuges are not large enough to sustain populations indefinitely without recolonization from other populations, and the meta-population dynamics (specifically the proximity of other populations) may be critical under steadystate conditions. Determining the probability of successful recolonization requires greater knowledge of dispersal shadows and spatial relationships of extant populations. It remains to be determined to what extent these target species could persist in the absence of disturbance conditions that upset the long term equilibrial dominance by shrubland.

A further refuge is the soil seed bank *Astragalus brauntonii* has the ability to accumulate a dormant seed bank, from which it can recruit after fire, although it is clearly not fire-dependent. *Pentachaeta lyonii* appears to have the capacity for soil storage of seeds during extended dry spells. In the case of both species, the seed bank also acts as a "refuge," from which they can colonize local disturbances. In the case of this latter species, most populations are not associated with fires and those populations on disturbed sites are generally associated with anthropogenic disturbances. Prior to human occupation of this landscape it is likely that the massive mammalian fauna, which persisted until the end of the Pleistocene (Keeley and Swift 1995), may have played an important role in the ecology of this species.

IX. ACKNOWLEDGMENTS

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Appendix I.

Site Summary and Recommendations for *Astragalus brauntonii*

Site	Comments (Spring 1997)
EO1	Insufficient information, population presumably extirpated.
EO2	Insufficient information, population presumably extirpated.
EO3	Not found, presumably a displaced individual.
EO4	Coal Canyon. No *Astragalus* were found but habitat is undisturbed and possibly seed bank is present. Assumed location supports *Adenostema fasciculatum* dominated chaparral.
EO5	Insufficient information, population presumably extirpated.
EO6	Monrovia. Two populations occur here, in or adjacent to a proposed housing project (Mary Meyer, personal communication).
EO7	Insufficient information, population presumably extirpated.
EO8	No reproducing A. *brauntonii* were found and canyon is very disturbed by non-native grass and forb invasion
EO9	Insufficient information, population presumably extirpated.
EO10	Coal Canyon. No individuals were found but habitat is undisturbed and presumably seed bank is present. Assumed location supports *Adenostema fasciculatum* dominated chaparral.
EO11	(34 11' 19" N, 118 46' 20"W) The large population (at 350 m) was recorded in 1993 by R. Burgess (284+ individuals) has been reduced to 2 plants growing in the roadway margins at the Oak Park Community Park. The plants that were surrounding the Oak Park Community Park were "weed whacked" by park maintenance personal with subsequent addition of redwood mulch. A. *brauntonii* did not recolonize the area. This population is at risk due to: 1) Extermination of adults, 2) depletion of seed bank, 3) radical land use modification. This occurrence will most likely be extirpated in the immediate future without intervention. As of January 1998 there were 7 plants persisting here (Mary Meyer, personal communication).

EO12 Insufficient information, population presumably extirpated.

EO13 Insufficient information, population presumably extirpated.

EO14 Trailer Canyon. Reports (Mike Merril) indicate that there is a reproducing population in Trailer Canyon, however we were unable to locate it (but see note in EO15).

EO15 Temescal Ridge. (34 04' 51" N, 118 32' 42"W)
This is the largest reproducing population of *A. brauntonii* with >1000 individuals. The bulk of the population is located on an unnamed 550 m peak. In addition to the ridgeline population, there are occurrences on the south facing slope of a 520 m ridge south of the 550 m peak and along the Temescal Ridge Fire Road. Collectively, these two populations plus comprise about 2000 plants. *Astragalus brauntonii* at this location presents a self-sustaining population with vigorous recruitment, despite the apparent absence of fire for many decades (based on size of shrubs). The larger of the two populations is on a hill that was cleared more than 17 years ago (Mr. Greg Nelson, Topanga State Park Ranger, personal communication) for installing of power lines and there appears to have been fuel-break clearing at some point but not in the past 7 years (Mr. Mike Merril, personal communication). Since then few woody plants have reestablished on site, a likely factor in the persistence of the *Astragalus*. Additionally, the few woody species that have established in this area appear stunted, possibly due to hardships imposed by the rocky, limestone soil.

Astragalus brauntonii have also been identified adjacent to a water tower above Pacific Palisades, in an active home construction area, and in drainage basins off Michael Lane, these latter may be a part of the Trailer Canyon occurrence (EO14). Recruitment is occurring to varying degrees in all these places. Heavy foot and mountain-bike traffic was evident and contributed to damaged plants. This site should be monitored closely for effects of increasing mountain bike and foot traffic use. This area should be considered for intervention, such as placement of blockades to dissuade the above uses by the public.

EO16 Clamshell Canyon. (34 10' 15"N, 118 00' 54"W)
Two plants, one adult in fruit and one seedling, were identified along Clamshell Canyon Road (290 m). This population has presumably been crowded out due to an extensive fire-free period. The area should be monitored following fire to gauge the extent of recovery from the seed pool that is presumably present.

EO17 Temescal Canyon. This occurrence is the same, or should be considered a meta-population of EO15

EO18 Will Rogers State Park. No plants were found at this site but a seed pool presumably exists. This area should be monitored following fire for degree of recovery from seed.

EO19 Palo Commado Canyon. (34 11' 21"N, 118 44' 43"W)
Five plants were located growing along an eroded stream bed (370 m). This area, and areas down stream should be monitored following fire.

EO20 Part of EO21.

EO21 N. Deerhill. (34 11' 17" N, 118 45' 28"W 34 11' 08" N, 118 45' 21"W)
This population was originally identified by Rachel Tierney -- 15 plants in 1990 by the water tank. Five young plants now occur at the water tank (Mary Meyer, personal communication). This population is quite spread out and was once very extensive with >1000 plants reported at the Deerhill Park Site in 1995 and in the nearby Oak Park III development 450 plants were located in September 1995. As part of a mitigation, these plants were moved and most of the site was graded. Only 150 plants survived the initial move and none of the plants survived beyond the second year. At the Oak Park III development site plants still persist, with approximately 150 young plants on the western portion of the site.

EO22 Terminus of Falling Star. (34 12' 03" N, 118 47' 56"W)
No plants were found at this location, but habitat is fairly undisturbed, with the exception of a jeep trail and a couple small foot paths. Presumably a soil seed bank exists, however this is in jeopardy due to nearby development and resulting fire suppression regimes.

EO23 Site was inaccessible and status of population is unknown.

EO24 This is probably the same population as EO16.

Appendix II.

Site Summary and Recommendations for *Pentachaeta lyonii*

Site	Comments (Spring 1997)
EO1	Presumed extirpated, was unable to locate.
EO2	Insufficient information, population presumably extirpated.
EO3	Stunt Ranch. No P. lyonii found, presumed extirpated.
EO4	Presumed extirpated, was unable to locate.
EO5	Westlake Boulevard. Extirpated, presumably during road widening activities. Site was described as adjacent to the road, an area currently occupied by *Avena fatua* and other non-native invasives. Area further off the road (>10m) could possibly be recolonized, preferably with seed from the nearest extant populations.
EO6	Rocky Oaks. (34 05' 57"N, 118 48' 43"W) Population (525 m) is small. Extensive invasion by *Centaurea melitensis* and *Avena barbata* puts this population at risk. National Park Service (land owner) is developing a recovery plan in conjunction with mitigation (John Tiszler-NPS botanist, personal communications.)
EO7	Insufficient information, population presumably extirpated.
EO8	Insufficient information, population presumably extirpated.
EO9	Reagan Ranch (Called Malibu Ck State Park, Ms. Mary Meyer, personal communication). (34 06' 20"N, 118 44' 20") This population has been extirpated but habitat remains. Should be re-established using seed from Malibu Lake population.
EO10	Carlisle Canyon. (34 07' 51"N, 118 51' 16"W & 34 07' 36"N, 118 51' 21") Population is ongoing though sparse, typical of the Santa Monica Mountain sites. *P. lyonii* begin approximately 20 m from the road and extend to about 80 m up the hill (320 m). The hill has an incline of 23° and south-southeast aspect. *P. lyonii* occurs in breaks of *Adenostema fasciculatum, Ceanothus crassifolius, Salvia mellifera, S. leucophylla* and *Quercus berberidifolia* chaparral along with occurrence of *Yucca whipplei*. Native herbaceous plants associated closely with *P. lyonii* are *Plantago*

erecta, Silene antirrhina, Navarretia atractyloides, Sisyrinchium bellum, Carex sp., and *Vulpia octoflora.* Moderately dense non-native invasive grasses and herbaceous plants (*Centaurea melitensis, Vulpia myuros, Gastridium ventricosum, Bromus hordeaceus, B. madritensis, Avena barbata*) may put this population at risk, but current impact doesn't appear critical.

An additional small sighting (± 50 plants / 2-m^2) located on the same slope near the intersections of Decker and Carlisle roads could reasonably be considered an extension of either EO10 or EO28. The habitat is more of an interface between chaparral, coastal sage, and grassland communities. Associated species are *Eriophyllum confertiflorum, Erigeron foliosus, Centaurea melitensis, Vulpia myuros, Avena barbata*, and *Bromus hordeaceus.*

EO11 Lk. Eleanor Ridge. (34 07' 48"N, 118 51' 03"W)
Approximately 200 *P. lyonii* are located along foot path on ridge at end of Denver Springs Road (360 m). Closely associated plants are *Stylocline gnaphaloides, Bromus hordaceus, B. madritensis, Centaurea melitensis, Erodium cicutarium*, and *Brassica nigra.* Habitat is an interface between *Adenostema fasciculatum* chaparral, *Malosma laurina, Lotus scoparius*, and *Eriogonum fasciculatum* coastal sage, and disturbed grassland (primarily *Avena barbata.*). Increase in foot traffic and presence of non-native invasive grasses put this population at risk. A recent burn on the west end of the ridge occurred in the spring of 1996, was checked in spring 1997 for *P. lyonii* but with the exception of 10 plants growing on the most easterly edge of the burn, the end nearest the other *P. lyonii*, none were found within the burned area itself.

EO12 Wildwood Park. (34 13' 01"N, 118 54' 39"W)
Population is dense and very localized (approx. 1200 plants / <100-m^2). Closely associated species are entirely non-native invasives, specifically *Bromus hordeaceus, B. madritensis, Centaurea melitensis*, and *Brassica nigra.* Habitat is an interface between disturbed grassland (*Avena barbata*) and cactus sage scrub (*Rhus integrifolia, Opuntia* sp.., *Yucca whipplei*). Suitable habitat is abundant along the ridge to the east and elsewhere in the park (190 m). This population is a good candidate for intervention and population expansion.

EO13 Insufficient information, population presumably extirpated.

EO14 woodranch. (34 14' 50"N, 118 49' 44"W)
This site has a 9° incline and a slight north-northwest aspect (300 m). The habitat is disturbed inland scrub/grassland interface and has extensive trash dumping. The *P. lyonii* is doing fairly well but non-native invasives, such as *Centaurea melitensis, Vulpia myuros, and Avena barbata*, and dumping activity puts this population at risk. Native species closely associated with *P. lyonii* are *Hemizonia fasciculata, Stylocline*

gnaphaloides, Lessingia filaginifolia, Artemisia californica, and *Encelia californica. Isomeris arboreus.* The population could be expanded, contingent on cooperation of land owner.

EO15 Status of population unknown.

EO16 Status of population unknown.

EO17 Status of population unknown.

EO18 Site was inaccessible, but observations from Mulholland Highway indicate that this population may have been disked. Status of population is unknown.

EO19 Site was inaccessible and status of population is unknown.

EO20 Mont Cleff Ridge. (34 13' 59"N, 118 53' 12"W)
This is a small, localized population (± 50 m^2) located along a jeep trail on Mont Cleff Ridge, approximately 70 m from the eastern terminus of the ridge (300 m). Site is flat and habitat is composed of disturbed inland scrub with *Eriogonum fasciculatum, Artemisia californica, Lessingia filaginifolia, and Lotus scoparius.* Species closely associated with *P. lyonii* are *Erodium cicutarium, Centaurea melitensis, Bromus madritensis, B. hordaceus, Brassica nigra, Stylocline gnaphaloides, and Chorizanthe* sp. This population is at risk from ORV use and non-native invasion. There is extensive habitat available in adjacent areas to which population should be expanded to minimize this risk.

EO21 Cal Lutheran. (34 13' 17"N, 118 53' 02"W)
The site, as is typical with the more inland sites, is basically flat and located in the saddle between two knolls (270 m). Habitat is composed of disturbed cactus scrub (*Opuntia littoralis, Eriogonum fasciculatum, Lotus scoparius, Nicotiana attenuata, Encelia californica, Mirabilis californica,* and *Marrubium vulgare*) with dense patches of *Avena barbata* and an extensive area of predominantly bare ground composed of hard-packed canejo volcanic clay soils in which the *P. lyonii* occur. Species closely associated with *P. lyonii are Vulpia myuros, Lamarckia aurea, Brassica nigra, Thysanocarpus* sp., *Crassula connata, Dichelostema capitata, Lotus salsuginosus, Linanthus* sp., *Eremocarpus setigerus, Schismus barbatus, Plagiobothrys* spp., *Cryptantha* spp. *Pectocarya linearis, Erodium cicutarium, and E. botrys.* Site is disturbed by extensive foot traffic and littering from neighboring urban community. The site does, however, maintain a fairly large population and there is adjacent habitat that is not occupied by *P. lyonii*, making it an ideal candidate for intervention in the form of population expansion.

EO22 Newberry Park Academy. (34 11' 49"N, 118 56' 28"W)

The site at 200 m is predominantly flat and the habitat is very disturbed grassland (*Avena barbata*). Species closely associated with *P. lyonii* are *Bromus madritensis*, *B. hordeaceus*, and *Plantago erecta*. This population is on the verge of extinction due to abundant ORV (four-wheel drive) use, possible prior scraping, and extensive invasion by *Avena barbata*. This site typifies the early statement that this is not a species compatible with extensive mechanical disruption of the habitat. Unless immediate action is taken to eliminate ORV use and re-establish *P. lyonii* (possibly with seed from EO23) the site will most likely be extirpated in the immediate future.

EO23. (34 11' 49"N, 118 56' 07"W)
This site is located on the west side of the water tower north of Newberry Park Academy (270 m) and doing reasonably well. Habitat is disturbed grassland (*Avena barbata*). Species closely associated with *P. lyonii* are *Plantago erecta*, *Bromus madritensis*, *B. hordeaceus*, *Centaurea melitensis*, and *Stylocline gnaphaloides*. Gopher activity, which loosens the top soil and increases *Avena barbata* invasion, may pose some threat to this population.

EO24 Lynnmere Open Space. (34 12' 37"N, 118 53'15"W, 34 12' 38"N, 118 53' 26"W)
This population is more extensive than originally recorded, extending in patches along the foot trail to the western side of a small creek crossing (200 m). Microsites are primarily flat. Habitat is disturbed grassland (*Avena barbata*) and *Ceanothus megacarpus*, *Salvia mellifera*, *Eriogonum fasciculatum* chaparral. Species closely associated with *P. lyonii are Centaurea melitensis*, *Lamarckia aurea*, *Bromus hordeaceus*, *B. madritensis* and *Erodium cicutarium*. The plants restricted to within 5m of the path, apparently due to reduced competition with non-native grasses that dominate further off the path. There is suitable habitat in the area and population is a candidate, in conjunction with EO12 and EO37 (presumed number) for expansion.

EO25 Insufficient information.

EO26 West of Las Virgenes Reservoir. (34 07' 42" N, 118 50' 24"W)
This population is dense for a coastal site and occurs in an old road cut (330 m). Site has a 10-15° incline with a north-northeast aspect. Population is doing reasonably well, and will most likely retreat to gaps as shrubs recruit into the roadcut. Dominant shrubs in the area are *Quercus berberidifolia*, *Adenostema fasciculatum*, *Ceanothus spinosus*, *Salvia mellifera*, and *Yucca whipplei*. Species closely associated *with P. lyonii are Bromus hordeaceus*, *B. madritensis*, *Avena barbata*, *Centaurea melitensis*, *Plantago erecta*, *Stylocline gnaphaloides, and Hemizonia fasciculata*. At this time, there are no recommendations for intervention with this population beyond occasional monitoring for increase in foot traffic or new road cutting activity.

EO27 (34 07' 42" N, 118 49' 25"W 34 07' 43" N, 118 49' 18"W,
34 07' 41" N, 118 49' 09"W)
Santa Monica Mountains Conservancy Land at intersection of Triunfo Canyon Road and Lindero Canyon Road (290 - 340 m). There are numerous dense patches in disturbed areas (previously scraped and/or foot paths) and more sparse populations in gaps between shrubs in the chaparral, which is typical of the more coastal sites. This site should be monitored for effects of foot traffic but it does not seem to be in imminent danger.

EO28 (34 07' 35" N, 118 51' 15"W)
This metapopulation comprises several small populations that were still as described in (Keeley and Keeley 1992).

EO29 Reagan Library population was extirpated and mitigation failed. There are still populations south of the library that are in yet-to-be-built lots (Mary Meyer, personal communication).

EO30 Tierra Rejada. (34 15' 55" N, 118 51' 45"W)
Recent trenching and dumping activities has damaged the population (200 m) and promoted non-native invasion (visible from the road). Estimated population still present is 230,000 plants, largest known population (Mary Meyer, personal communication).

EO31 Site was inaccessible and status of population is unknown.

EO32 Bridgegate. (34 09' 26" N, 118 51' 35"W, 34 09' 16" N, 118 51' 28"W
34 09' 10" N, 118 51' 23"W, 34 09' 02" N, 118 51' 17"W)
Population is current and in the coastal-type community, that is sparse and occurring in openings in chaparral (300 - 350 m). Proposed development of adjacent properties puts this population at risk from an increase in recreational use of mitigated areas.

EO33 Fire Station. (34 08' 05"N, 118 45' 08"W)
This population (280 m) is widely dispersed.

EO34 Ladyface. (34 08' 09"N, 118 45' 03"W)
The site (285 m) is threatened by proposed development. The population itself is sparse and growing in gaps in the chaparral, typical of the coastal sites.

EO35 Malibu Lake. (34 06' 20"N, 118 44' 53"W)
The site (270 m) is healthy and does not appear to be threatened. Limited access to this site protects it.

Table 1. Community Characterization for the Temescal Intensive Study Site for *Astragalus brauntonii.* Cover is expressed as percentage ground surface covered based on line intercept method.

Species	Growthform[a]	Cover (%GSC) $\bar{X} \pm$ S.E.	Density (# m^{-2}) $\bar{X} \pm$ S.E.
Astragalus brauntonii	HP		
Seedlings		0.0 ± 0.0	0.06 ± 0.06
Mature plants		11.9 ± 3.3	1.56 ± 0.37
*Bromus hordeaceus***	A	36.7 ± 8.4	
*Avena barbata***	A	16.4 ± 5.6	
*Bromus diandrus***	A	10.7 ± 3.4	
Heterotheca grandiflora	HP	8.6 ± 1.9	
Malosma laurina	ES	7.5 ± 5.5	
*Bromus madritensis***	A	6.4 ± 3.4	
*Medicago polymorpha***	A	3.6 ± 1.6	
*Centaurea melitensis***	A	3.2 ± 1.2	
*Marrumbium vulgare***	HP	2.5 ± 1.5	
Gnaphalium leucocephalum	HP	2.0 ± 1.9	
Eriogonum fasciculatum	ESS	1.1 ± 1.1	
*Hirschfeldia incana***	A/HP	0.4 ± 0.3	
Gnaphalium californicum	HP	0.1 ± 0.1	
Lotus scoparius	DSS	0.1 ± 0.1	
*Erodium cicutarium***	A	0.1 ± 0.1	
Rock cover		2.9 ± 2.2	
Bareground		20.1 ± 6.9	

[a] A = annual, DSS = deciduous subshrub, ES = evergreen shrub, ESS = evergreen subshrub, HP = herbaceous perennial.

** Non-native species.

Table 2. Multi-way Analysis of Variance (MANOVA) for *Astragalus brauntonii* survivorship in greenhouse experiment for shade vs full sun irradiance, limestone vs volcanic soil, and high, medium and low soil moisture, plus interactions.

Treatment	F-ratio	P-value
Irradiance	4.32	0.040
Soil	9.71	0.002
Moisture	18.16	0.000
IxS	44.82	0.000
IxM	1.35	0.265
SxM	3.98	0.022
IxSxM	18.69	0.000

Table 3. *Astragalus brauntonii* survivorship in greenhouse experiment (X + S.E., ANOVA results in Table 2).

Irradiance	Full Sun (n=58) 58 ± 16%						Shade (n=54) 45 ± 18%					
Soil	Limestone (n=28) 90 ± 6%			Volcanic (n=30) 27 ± 18%			Limestone (n=27) 33 ± 33%			Volcanic (n=27) 56 ± 17%		
Moisture	Hi (n=9) 89%	Med (n=9) 100%	Low (n=10) 80%	Hi (n=9) 60%	Med (n=9) 20%	Low (n=10) 0%	Hi (n=9) 100%	Med (n=9) 0%	Low (n=10) 0%	Hi (n=9) 50%	Med (n=9) 89%	Low (n=10) 30%

Table 4. Multi-way Analysis of Variance (MANOVA) for *Astragalus brauntonii* growth in greenhouse experiment for shade vs full sun irradiance, limestone vs volcanic soil, and high, medium and low soil moisture, plus interactions.

Treatment	F-ratio	P-value
Irradiance	45.03	0.000
Soil	20.70	0.000
Moisture	4.12	0.019
IxS	7.98	0.006
IxM	3.62	0.030
SxM	0.04	0.964
IxSxM	1.86	0.162

Table 5. *Astragalus brauntonii* growth after 3 months in greenhouse experiment

Treatment	Height (cm)	Areal Cover (cm2)	Total Biomass (g)	Aboveground Biomass (g)	Belowground Biomass (g)	Root/Shoot
Full Sun	22	239	4.4	3.1	1.2	0.4
Shade	23	241	2.4	1.9	0.4	0.2
P	0.528	0.944	0.000	0.000	0.000	0.000
Limestone Soil	22	283	4.2	2.9	1.2	0.4
Volcanic Soil	23	201	2.7	2.3	0.4	0.2
P	0.607	0.000	0.000	0.024	0.000	0.000
High Moisture	23	260	4.0	2.9	1.0	0.3
Medium Moisture	23	249	3.6	2.7	0.9	0.3
Low Moisture	21	214	2.8	2.1	0.5	0.3
P	0.600	0.133	0.048	0.055	0.212	0.809

Table 6. Community Characterization for the EO21 Intensive Study Site for *Pentachaeta lyonii.* Cover is expressed as percentage ground surface covered based on line intercept method.

Species	Growthform[a]	Cover (%GSC) X ± S.E.	Density (# m^{-2}) X ± S.E.
Pentachaeta lyonii	A	0.7 ± 0.2	37.90 ± 12.08
Eriogonum fasciculatum	ESS	5.0 ± 3.1	
*Schismus barbatus***	A	4.3 ± 1.3	
*Erodium cicutarium***	A	3.8 ± 1.0	
*Brassica nigra***	A	1.7 ± 0.7	
*Bromus madritensis***	A	1.3 ± 0.8	
Mirabilis californica	DSS	1.3 ± 1.3	
Pectocarya linearis	A	1.2 ± 0.6	
*Erodium botrys***	A	1.2 ± 0.9	
Encelia californica	DSS	0.8 ± 0.6	
Linanthus dianthiflorus	A	0.7 ± 0.4	
*Marrumbium vulgare***	HP	0.6 ± 0.5	
Dichelostemma capitatum	HP	0.3 ± 0.1	
Hemizonia fasciculata	A	0.3 ± 0.1	
Thysanocarpus curvipes	A	0.3 ± 0.1	
Cryptantha sp.	A	0.2 ± 0.1	
Lotus salsuginosus	A	0.1 ± 0.1	
*Lamarkia aurea***	A	0.1 ± 0.1	
Plantago erecta	A	0.1 ± 0.1	
Rock cover		18.6 ± 5.1	
Bareground		62.9 ± 7.6	

[a] A = annual, DSS = deciduous subshrub, ESS = evergreen subshrub, HP = herbaceous perennial.

** Non-native species.

Table 7. Community Characterization for the EO27 Intensive Study Site for *Pentachaeta lyonii.* Cover is expressed as percentage ground surface covered based on line intercept method.

Species	Growthform[#]	Cover (%GSC) $X \pm$ S.E.	Density (# m^{-2}) $X \pm$ S.E.
Pentachaeta lyonii	A	0.5 ± 0.2	30.11 ± 6.97
Eriogonum fasciculatum	ESS	11.8 ± 5.7	
*Bromus madritensis***	A	9.3 ± 2.8	
Stylocline gnaphalioides	A	4.8 ± 1.4	
*Bromus hordeaceus***	A	3.7 ± 1.9	
*Vulpia myuros***	A	2.6 ± 1.3	
Plantago erecta	A	2.1 ± 0.8	
*Erodium cicutarium***	A	3.8 ± 1.0	
Eriophyllum confertiflorum	DSS	0.8 ± 0.3	
*Centaurea melitensis***	A	0.6 ± 0.4	
*Avena barbata***	A	0.3 ± 0.3	
Lotus salsuginosus	A	0.3 ± 0.3	
Camissonia sp.	A	0.1 ± 0.1	
Rock cover		41.5 ± 7.0	
Bareground		64.0 ± 7.0	

[#] A = annual, DSS = deciduous subshrub, ESS = evergreen subshrub, HP = herbaceous perennial.

** Non-native species.

Table 8. Multi-way Analysis of Variance (MANOVA) for *Pentachaeta lyonii* survivorship in greenhouse experiment for shade vs full sun irradiance, limestone vs volcanic soil, and high, medium and low soil moisture, plus interactions.

Treatment	F-ratio	P-value
Irradiance	7.79	0.007
Soil	226.13	0.000
Moisture	1.59	0.212
IxS	4.29	0.042
IxM	9.78	0.000
SxM	3.91	0.024
IxSxM	6.28	0.003

Table 9. *Pentachaeta lyonii* survivorship in greenhouse experiment (X + S.E., ANOVA results in Table 2).

Irradiance	Full Sun (n=42) 67 ± 18						Shade (n=40) 52 ± 20%					
Soil	Limestone (n=12) 33 ± 22%			Volcanic (n=30) 100 ± 0%			Limestone (n=12) 8 ± 8%			Volcanic (n=28) 96 ± 4%		
Moisture	**Hi** (n=4) 25%	**Med** (n=5) 75%	**Low** (n=3) 0%	**Hi** (n=10) 100%	**Med** (n=10) 100%	**Low** (n=10) 100%	**Hi** (n=4) 0%	**Med** (n=4) 0%	**Low** (n=4) 25%	**Hi** (n=9) 100%	**Med** (n=9) 89%	**Low** (n=10) 100%

Table 10. Multi-way Analysis of Variance (MANOVA) for *Pentachaeta lyonii* growth in greenhouse experiment for shade vs full sun irradiance, limestone vs volcanic soil, and high, medium and low soil moisture, plus interactions.

Treatment	F-ratio	P-value
Irradiance	19.0	0.000
Soil	67.6	0.000
Moisture	1.8	0.212
IxS	17.2	0.000
IxM	1.0	0.381
SxM	1.7	0.185
IxSxM	0.9	0.428

Table 11. *Pentachaeta lyonii* growth after 3 months in greenhouse experiment (growth comparison in different soils is omitted because *Pentachaeta* failed to establish or survive in > 90% of the limestone soil pots).

Treatment	Height (cm)	Areal Cover (cm2)	Total Biomass (g)	Aboveground Biomass (g)	Belowground Biomass (g)	Root/Shoot
Full Sun	29	1195	2.2	1.8	0.4	0.2
Shade	17	554	0.9	0.7	0.1	0.2
P	0.008	0.072	0.000	0.000	0.000	0.182
High Moisture	23	841	1.6	1.5	0.2	0.1
Medium Moisture	22	841	1.5	1.2	0.3	0.2
Low Moisture	20	380	0.9	0.7	0.2	0.3
P	0.813	0.207	0.307	0.169	0.551	0.034

FIGURE LEGENDS

Figure 1. Relationship between non-native grass cover and density of *Astragalus brauntonii* at the Temescal Intensive Study Site.

Figure 2. Relationship between soil depth and density of *Astragalus brauntonii* at the Temescal Intensive Study Site.

Figure 3. Percentage flower abortion for unbagged control inflorescences and bagged inflorescences in which pollinators were excluded, for *Astragalus brauntonii* at the Temescal Intensive Study Site.

Figure 4. Number of seeds per fruit for unbagged control inflorescences and bagged inflorescences in which pollinators were excluded for *Astragalus brauntonii* at the Temescal Intensive Study Site.

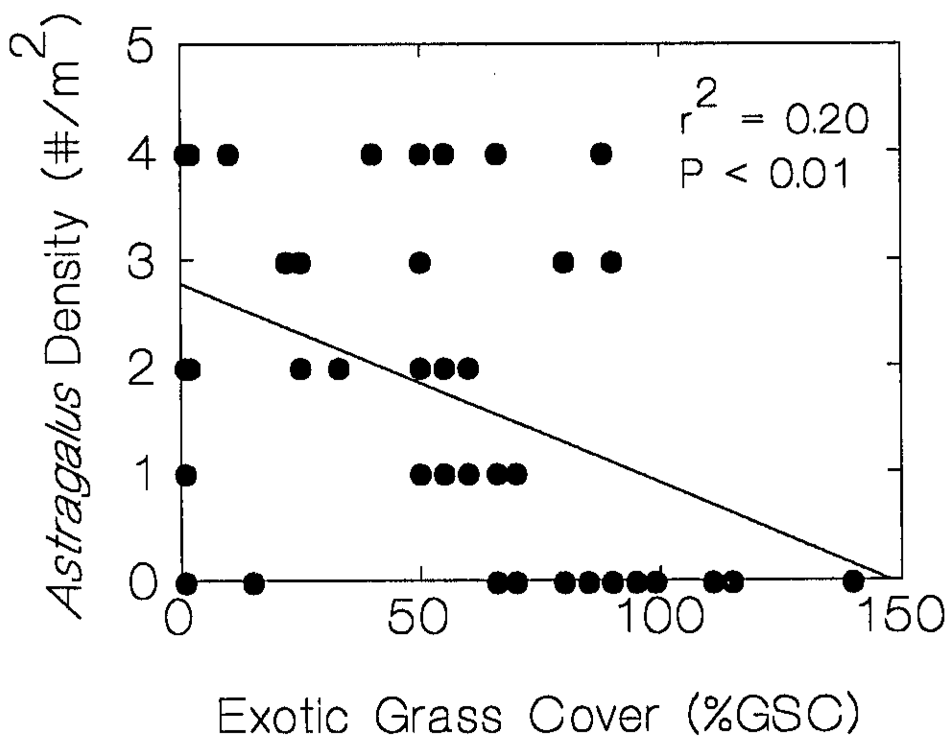
Figure 5. Percentage germination of *Astragalus brauntonii* seeds from the Temescal Ridge Intensive Study Site and from Clamshell Canyon. Heat treatments were for 5 minutes. Scarification treatments were either a shallow cut (Cut) through the seed coat or a needle puncture (Punc) through the seed coat.

Figure 6. Relationship between soil depth and density of *Pentachaeta lyonii* at the Cal Lutheran Intensive Study Site.

Figure 7. Relationship between soil depth and change in density of *Pentachaeta lyonii* Between January and April, 1997, at the Cal Lutheran Intensive Study Site.

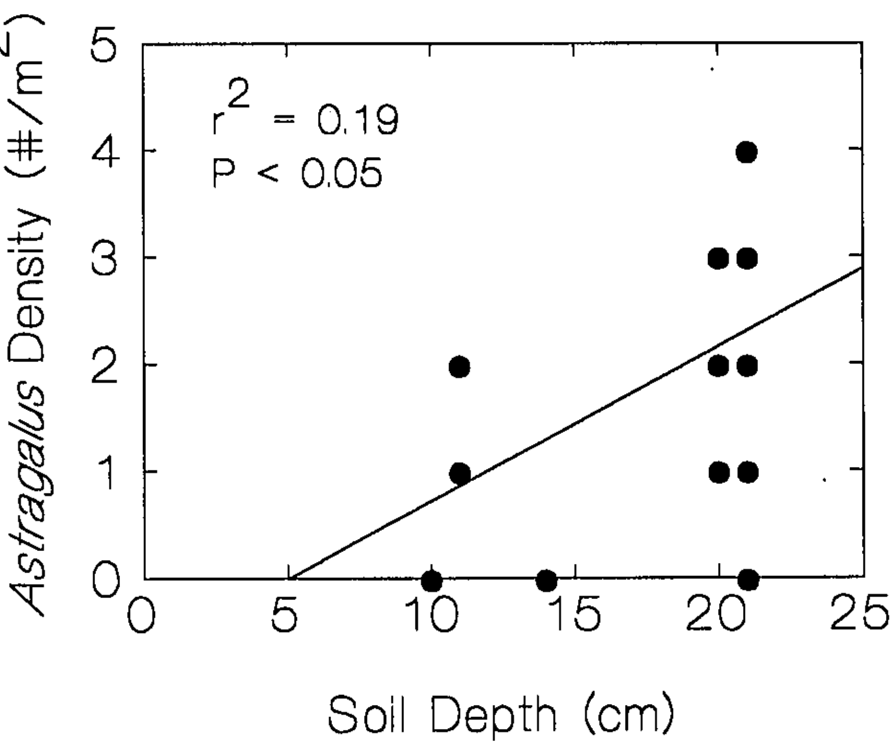
Figure 8. Percentage germination of *Pentachaeta lyonii* achenes for unbagged control plants and bagged plants in which pollinators were excluded at the Wood Ranch Intensive Study Site and the Lindero/Triunfo Canyon Intensive Study Site.

Fig. 1



$r^2 = 0.20$
$P < 0.01$
Astragalus Density (#/m^2)
Exotic Grass Cover (%GSC)
0
1
2
3
4
5
0
50
100
150

Fig 2



Astragalus Density (#/m2)
r2 = 0.19
P < 0.05
0
1
2
3
4
5
0
5
10
15
20
25
Soil Depth (cm)

Fig. 3

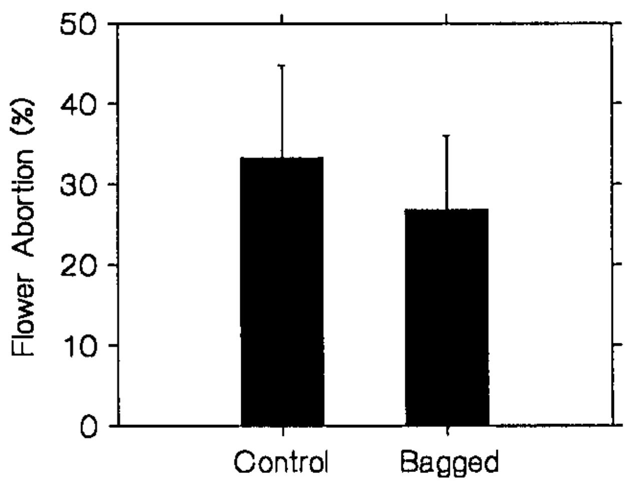


Fig 4

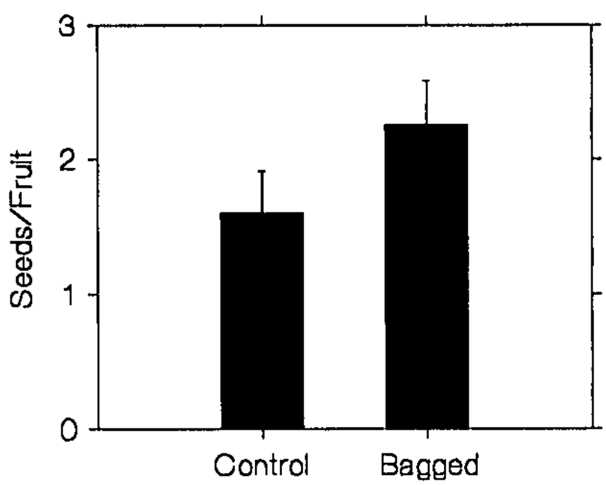
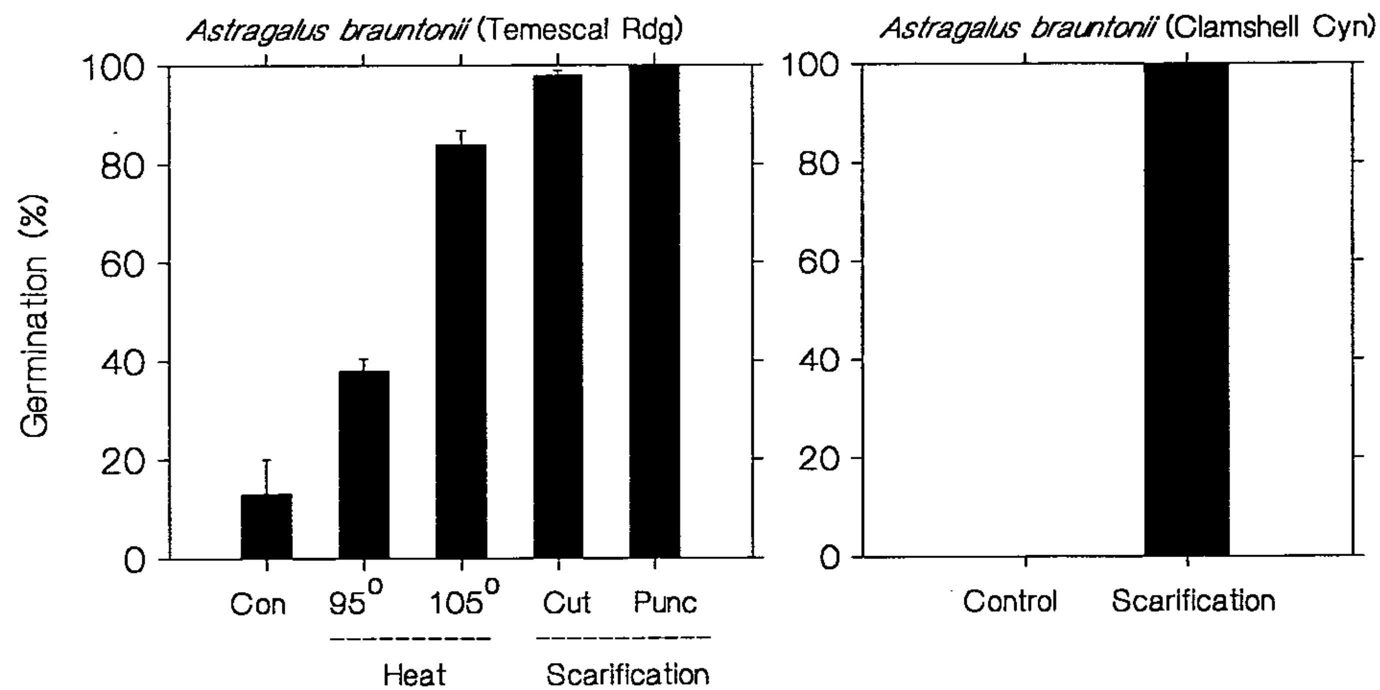
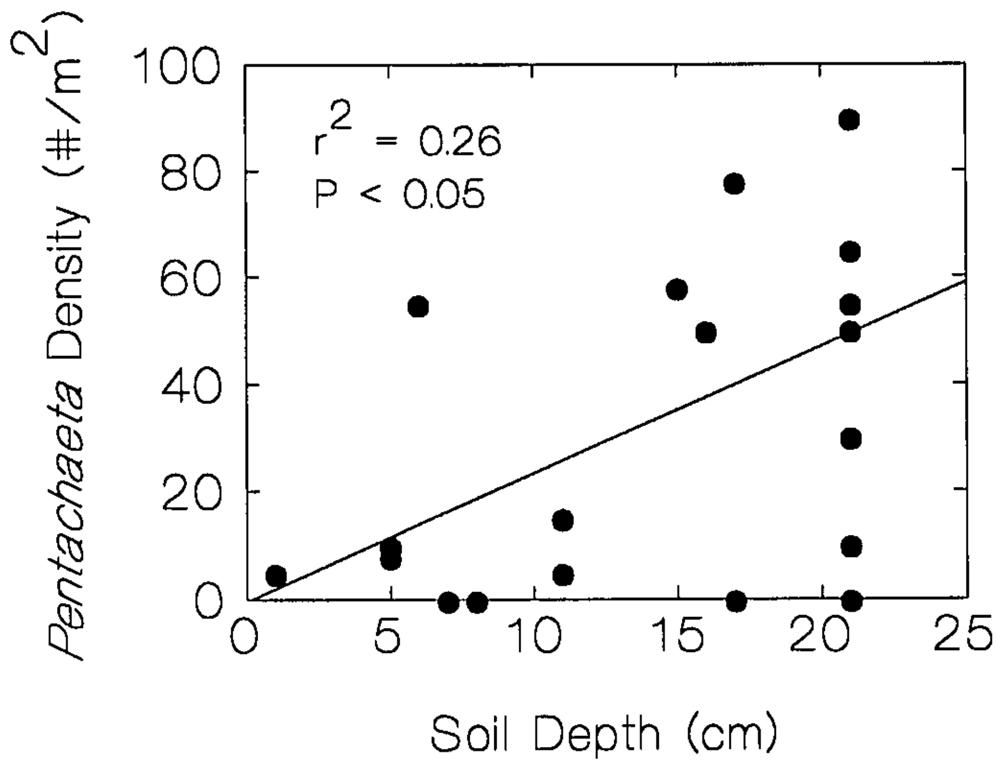


Fig 5



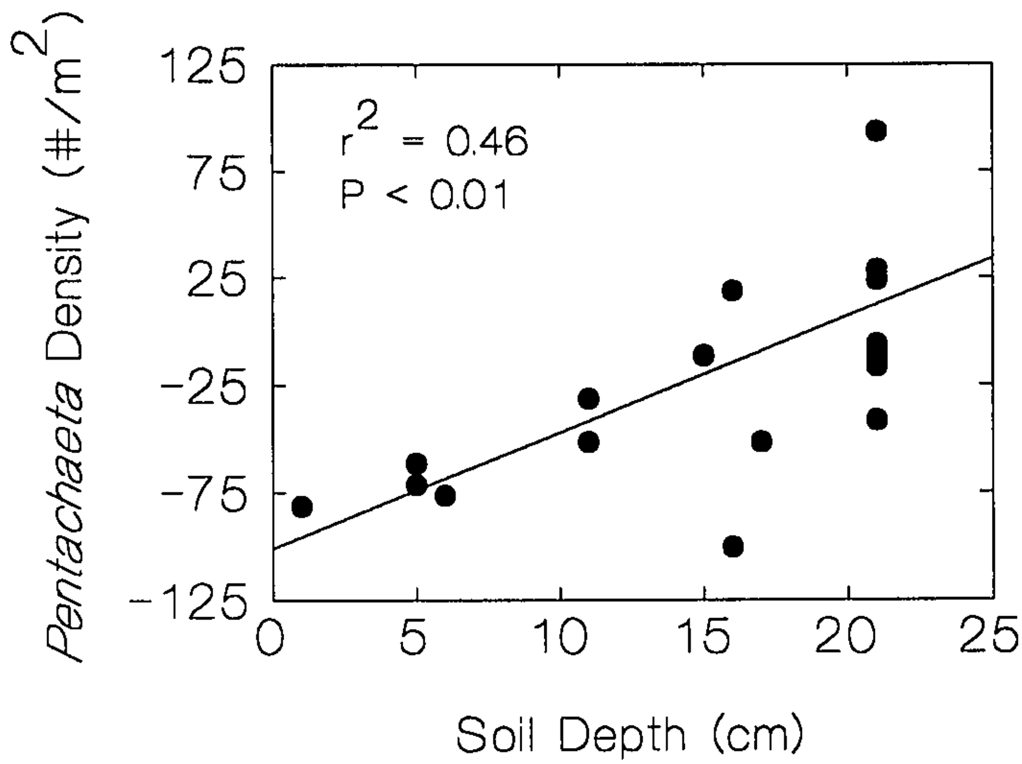
Astragalus brauntonii (Temescal Rdg)
Germination (%)
100
80
60
40
20
0
Con
95°
105°
Cut
Punc
Heat
Scarification
Astragalus brauntonii (Clamshell Cyn)
100
80
60
40
20
0
Control
Scarification

Fig 6



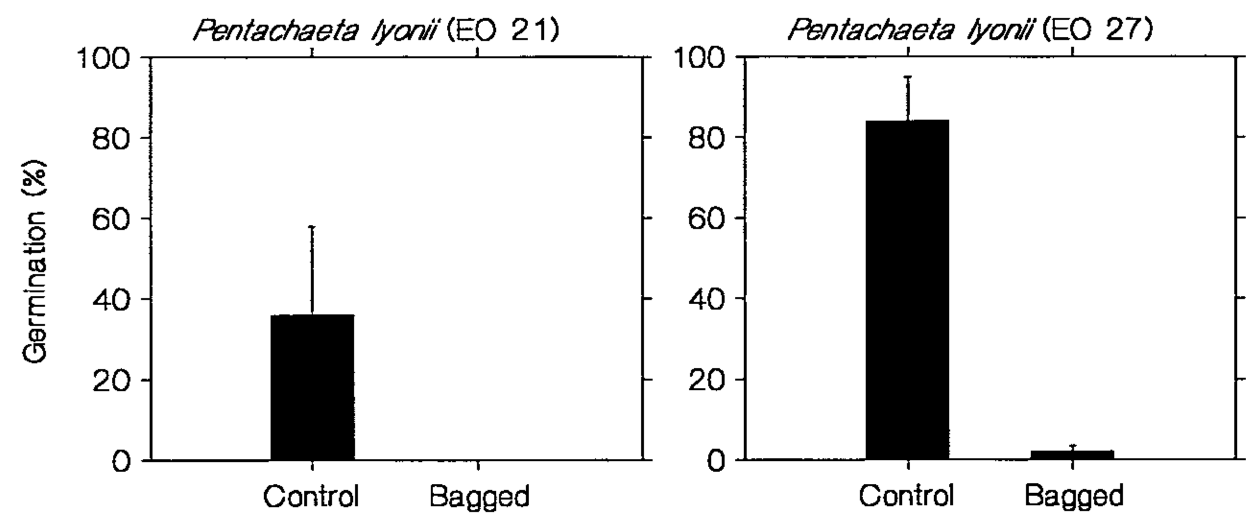
$r^2 = 0.26$
$P < 0.05$
100
80
60
40
20
0
0
5
10
15
20
25
Pentachaeta Density (#/m^2)
Soil Depth (cm)

Fig 7



Pentachaeta Density (#/m2)
125
75
25
-25
-75
-125
r2 = 0.46
P < 0.01
0
5
10
15
20
25
Soil Depth (cm)

Fig 8


Pentachaeta lyonii (EO 21)
Pentachaeta lyonii (EO 27)
Germination (%)
100
80
60
40
20
0
Control
Bagged