

THE CONSERVATION STATUS AND NATURAL
HISTORY OF *POGOGYNE FLORIBUNDA* IN OREGON

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SUMMARY

Pogogyne floribunda is a recently described (1992), annual mint species reported from an estimated six scattered sites in Oregon and one in western Idaho. It is otherwise restricted to a handful of locations in northeastern California on the Modoc Plateau, and is designated as a *sensitive species* by the BLM and a *species of concern* by the U.S. Fish and Wildlife Service. Populations are restricted to summer-dry playa lake beds and ephemeral channels in Great Basin silver sagebrush communities, and occur exclusively on public lands. The three year project described here was undertaken to evaluate the biology, taxonomic standing, and conservation status of the species in Oregon. Three Oregon populations were studied.

Pogogyne floribunda is highly autogamous yet has a mixed mating system. Greenhouse and field studies show that plants are predominantly self-pollinated, and although outcrossing via insect pollinators is probably infrequent, it can occur and is potentially important in maintaining and enhancing local genetic variation. Accordingly, it may play a role in any evolutionary diversification of populations. Plants are typically highly fecund and tend to be prolific seed producers, which is significant since the species depends on seed banks to maintain populations. Seed germination is variable – some seeds are germinable when dispersed, while others are dormant and move into the seed pool. In dry years, the species may not appear at all, though it is important to recognize that populations are still viable below the surface. It is therefore imperative to protect known habitat and document the boundaries of populations, to ensure conservation of the cryptic but important seed banks. The species appears to have limited susceptibility to foliar and flower predation in the wild – predators that infest cultivated mint fields may actually be the greatest insect threat to the species, at least in areas where mint farming and wild populations of *Pogogyne* coincide. Plants have no known mycorrhizal or other symbiotic associations, and are readily cultivated in a greenhouse setting. Large numbers of seeds can be produced quickly and efficiently for artificial seed banking, population augmentation, or other conservation purposes.

Cattle are common components of the playa ecosystems favored by *Pogogyne* populations in Oregon. Exotic weed species are not presently a significant competitive threat, though continued trampling of *Pogogyne* sites by livestock may ultimately change this dynamic if weeds are able to invade the playas as a result of the disturbance. The large population occurring on the Klamath Resource Area, near Dog Hollow Reservoir (the largest site for the genus in Oregon), appears capable of withstanding modest grazing impacts, though specific and broader assessments are needed to evaluate the effects of long-term grazing and trampling. The two disjunct populations studied here, from the Vale and Lakeview Districts (i.e., at Bull Flat and Foley Lake RNA), also need explicit study regarding grazing impacts – their smaller size, scattered population structure, and exposure to denser livestock concentrations suggest that the *Pogogyne* plants occurring here probably face the most serious threats from cattle. Soil moisture is a critical factor governing the distribution and survival of *Pogogyne* populations, with plants preferring intermediate soil moisture zones on the playas. Management actions that either dry out playas or increase the duration and extent of flooding can both be destructive influences.

Populations that occur at the outer boundaries of a species' range can exhibit unique qualities, and are often of interest to geneticists and conservationists. A goal of this study was to determine if the peripheral and disjunct Oregon populations of *P. floribunda* are comparable to those growing on the nearby Modoc Plateau area of California (i.e., those populations centered around the type locality). Morphometric and chloroplast DNA evaluation indicate the plants from the large Dog Hollow site are indeed typical for the species, while those from the highly disjunct Bull Flat and Foley Lake RNA populations are not. The latter populations are significantly divergent from typical *P. floribunda*, with the nucleotide data suggesting they have been potentially separated from the Modoc Plateau phenotype for perhaps tens of thousands of years. Moreover, the plants at Foley Lake may in fact be more closely related to a sister species, *P. zizyphoroides*, which otherwise occurs west of the Cascade-Sierran axis in low elevation valleys from extreme southwest Oregon to north-central California. While the disjunct Oregon populations are very interesting and may ultimately be worthy of formal taxonomic recognition, such a decision awaits further sequencing work, to place the divergence measured thus far into context within the genus. Formal taxonomic recognition would likely carry strong potential for *listing under the federal ESA*. In the meantime, it is recommended that *P. floribunda* sites continue to be protected by BLM, considering they plainly represent an evolutionarily significant genetic resource.

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INTRODUCTION

The rare annual mint *Pogogyne floribunda* was, until recently, considered endemic to vernal pools and seasonally wet flats on the Modoc Plateau of northeastern California, with populations scattered among a few sites in Shasta, Lassen, and Modoc counties (Jokerst, 1992). Believed by earlier workers to be a sagebrush-zone variant of the more common *P. zizyphoroides*, which typically occurs to the west in cismontane lowland valleys, Jokerst (1992) based the segregation of *P. floribunda* on its high desert distribution, cold weather ecology, summer blooming, flower color, and various morphological traits. The distribution of *P. floribunda* is notable, in that no other *Pogogyne* species occurs outside the western valleys and foothills of California and extreme southwest Oregon. Recognizing its vulnerability, the U.S. Fish and Wildlife Service designated *P. floribunda* a federal Species of Concern, and is considering it for formal listing under the Endangered Species Act.

Since the relatively recent description of *P. floribunda*, and its identification as a potentially endangered species, populations considered to be this taxon have been discovered in several remote areas of southeastern Oregon. Jokerst (1992) predicted this range extension, based on the known similarity of habitats across the Modoc Plateau and adjacent Lake County, Oregon. One of the new sites consists of a series of patches occurring along seasonal drainages near Foley Lake, east of Lake Abert. Four additional localities were discovered in ephemeral lakebeds in the Gerber Valley east of Bonanza, in habitat similar to sites on the nearby Modoc Plateau. And two well separated *Pogogyne* populations have since been observed farther east, one in extreme southeast Malheur County near the Idaho border, and the other in Idaho just southwest of Boise. It is remarkable this genus was not known before from the Great Basin proper, and now several sites have been located here in the last few years. Intensified surveys of sensitive habitats on public lands are clearly paying dividends.

The genus *Pogogyne*, collectively known as the *mesa mints*, is small, with only seven described species whose diminutive plants are frequently overlooked (unless stepped on, when their strong mint smell becomes evident). Additional rare species of *Pogogyne* are found farther south in California, where the genus is primarily distributed. All of these are narrow endemics, occurring in drying streambeds or vernal pools, with two restricted to natural depressions on the tops of coastal mesas. Other species (such as *P. zizyphoroides*, *P. serpylloides*, and *P. douglasii*) are more extensively distributed and, even though also restricted to vernal wet habitats, tend to be fairly common on the whole. *Pogogyne floribunda* appears unique in the genus in being geographically widespread yet extremely uncommon, occurring from western Idaho to northern California but represented by only a few populations.

The California endemic species have been given considerable conservation attention, especially those in the heavily urbanized southern part of the state. *Pogogyne abramsii* and its habitat, in particular, have been the subject of recurrent study in recent years (Scheidlinger, 1981; Bauder, 1989; Zammit and Zedler, 1990; Schiller et al., 2000). *Pogogyne floribunda*,

from the sparsely populated northeast corner of California, has received far less notice. Outside the work that led to the description of the species a few years ago (which was based solely on the Modoc Plateau populations), and a few floristic surveys sponsored by BLM (all known populations are on BLM land), very little has been reported regarding the ecological requirements or conservation status of *P. floribunda*. Information on breeding system, demography, seed production, germination requirements, seed banks, habitat condition, etc., and how these all may relate to conservation, is sketchy at best.

Potential variation among the disjunct populations of the species is also of interest. While the other rare members of the genus (such as *P. abramsii* and *P. clareana*) typically have localized and closely clustered occurrences, *P. floribunda* (especially in Oregon) is comprised of far-flung, highly isolated populations that have no realistic opportunity for genetic exchange. The vast distances between them (and the inhospitable terrain in between) suggest they may have been secluded for many years, providing opportunity for evolutionary divergence. How they arrived at these sites is unknown. Not surprisingly, preliminary field observations have hinted that morphological discrepancies may exist among the populations, indicating potential for taxonomic level differences within what has collectively been called *P. floribunda* in Oregon. Even in lieu of any *taxonomic* distinctions, the likelihood of *evolutionarily significant* genetic variation between the populations is high. If this is the case, the unique and scattered *Pogogyne* populations in eastern Oregon may very well merit enhanced conservation efforts.

Initiated in 2003, this project was originally intended to provide a natural history overview of *Pogogyne floribunda*, with an overall objective of developing a range-wide conservation strategy for the species in Oregon. Ideally we would have liked to include the single Idaho population as well, but that was not possible – hopefully this can be addressed in follow-up work. Towards this end, specific investigations were designed to focus on pollination biology, seed production, germination ecology, the identification of any foliar or seed predators, and cultivation requirements. Population level evaluations were also planned, including demographic measurements (through permanent plots) and conservation assessments of site quality (the latter focusing on substrate disturbances and the presence of exotics or other potentially competing vegetation). Finally, populations were also evaluated in terms of their uniqueness relative to each other, to assess any taxonomic or genetic differences that could impact the conservation significance of given sites. Initially, the taxonomic analyses were to have simply focused on the Oregon vs. California *P. floribunda* populations. As it turned out, the more interesting question appeared to be how much variation potentially exists between the populations *within* Oregon, which includes the most isolated and unusual sites for the species.

STUDY POPULATIONS

Three *Pogogyne* study sites were selected for various aspects of the study. Mapped locations of these are shown in Fig. 1, along with the approximate distributions of *P. floribunda* in California and Idaho. Also shown is the northern distribution of *P. zizyphoroides*, believed to be the closest relative of *P. floribunda* (Jokerst, 1992).

The study site near Dog Hollow Reservoir represents one of four *Pogogyne floribunda* populations known from the Klamath Falls Resource Area (Lakeview BLM District). This population is by far the most substantial, and is densely scattered across portions of an unnamed summer-dry playa (Fig. 2), about 0.5 miles due north of Dog Hollow Reservoir and 2.6 miles from the south end of Gerber Reservoir (coordinates are given in the caption for Fig. 1). A berm is present at the southern drainage end of the playa, helping to impound the site in

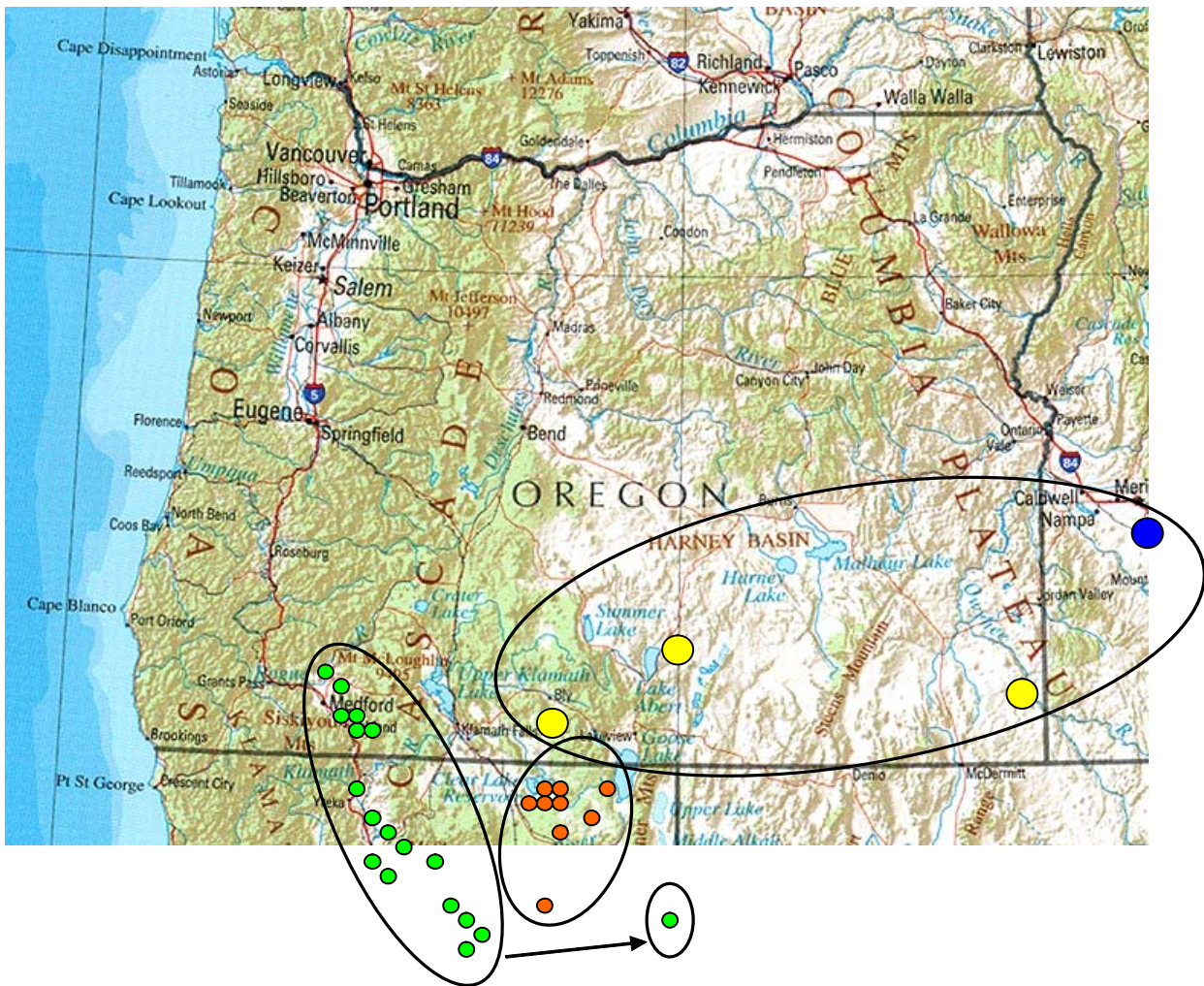


Fig. 1. Distribution of reported *Pogogyne floribunda* populations in Oregon (relative to California populations of the species, and populations of *P. zizyphoroides*). The yellow circles represent the three study sites for this project – from left to right, these are: Dog Hollow Reservoir (the site is actually in an unnamed ephemeral lakebed 0.5 miles north of Dog Hollow Reservoir at N 42 7.719' W 121 6.483'); Foley Lake RNA (N 42 40.713' W 120 1.464'); and Bull Flat (N 42 20.462' W 117 6.124'). Map coordinates were centrally chosen for general relocation purposes, as the populations were scattered over several acres. The blue circle represents the lone Idaho population of *P. floribunda*, which was not included in the study. The orange dots outline the approximate range of *P. floribunda* in California – these are based on Jokerst (1992) and are not intended to depict all current sites for the species. The green dots represent the northern fringe (also generalized) of the known range for *P. zizyphoroides*, considered by Jokerst (1992) to be the closest relative of *P. floribunda*. Earlier California floristic works (e.g., Munz, 1959) considered *P. floribunda* to be conspecific with *P. zizyphoroides*. The summer-flowering, disjunct population of *P. zizyphoroides* (indicated by the arrow) was considered “exceptional” by Jokerst (1992), in that it occurred in silver sage flats distinctly within the range (geographically and ecologically) of *P. floribunda*. All other populations of *P. zizyphoroides* exist well to the west and south, at lower elevations much less subject to severe winter conditions.

the winter. Moreover, the lakebed itself forms a shallow basin, and water collects readily and recedes slowly most years. As a result, the population here was consistently large, with 300,000 to 500,000+ plants present each growing season. The three other known populations in the area (each with significantly fewer plants) occur on smaller playas in the immediate vicinity, and were not included in the project.

The second study site is located east of Abert Rim, roughly 6.9 miles due east of the north end of Lake Abert (Fig. 1). It occurs within the Foley Lake Research Natural Area (RNA), and comprises a number of scattered *Pogogyne* subpopulations in meandering channels about 0.3 miles south of the Foley Lake playa margin (which varies somewhat according to yearly precipitation). These shallow waterways form a braided network of drying puddles in late spring that support a wide range of ephemeral species characteristic of Great Basin vernal pool environments. *Pogogyne* plants were not consistently present here each year, and in 2004 were essentially absent due to drought. They were moderately abundant in 2003 and 2005 (an estimated 3,000-6,000 plants were noted each year). The population may also extend along the edges of a small stock pond fed by the channels (Fig. 3) – this largely depends on winter rainfall levels as well as the extent of spring disturbance by cattle, which are prevalent here.

The third study location, at Bull Flat (Fig.4), is situated in southeast Malheur County, 3.8 miles west of the Idaho border and 2.1 miles west of the Owyhee Canyon (see Fig. 1 for location and coordinates). The area is very isolated, requiring nearly four hours by gravel and dirt track to access (after heading east from U.S. Hwy 95). In good years, *Pogogyne* plants are plentiful in the vernal wet silver sage (*Artemisia cana*) playa and occur with numerous other annuals. Unlike the Dog Hollow Reservoir site, but similar to the Foley Lake population, the yearly appearance of the species at Bull Flat appears closely tied to spring moisture levels. Plants were virtually non-existent in 2004 but locally abundant (20,000+) in 2005.

METHODS

The current project, extending over three summer field seasons (2003 through 2005), had multiple goals. Gathering data on the natural history of *Pogogyne floribunda*, with a focus on reproductive biology, seed ecology, cultivation potential, predation impacts, habitat quality, and population characteristics, was a primary objective for the study. The idea was to incorporate biological information into a general conservation strategy, designed to help federal land managers determine if current range management practices in southeast Oregon were sufficiently taking *P. floribunda* populations into account.

Also related to the conservation of the species are the issues of evolution and taxonomy. Geographic isolation of populations, especially of rapid-cycling annual taxa such as *Pogogyne*, can potentially be a precursor to speciation through genetic drift (Stebbins, 1971; Ellstrand and Elam, 1993; Elam, 1998). Initial field observations suggested that this might be an issue for *P. floribunda* in Oregon. If the Oregon plants, for example, were found to differ substantially from those in California, or from each other the conservation implications could be important. In 2003, the plan was to simply determine if the populations from the Klamath Falls Resource Area were comparable to or distinct from those in nearby California. At this point only the Klamath Falls Resource Area was sponsoring the project. However, as the Lakeview Resource Area and the Vale District became involved in supporting the work in 2004, the sampling scheme was expanded to include plants from the highly disjunct Foley Lake and Bull Flat areas, as well. The extension of the work to include the wider range of Oregon sites made the project more relevant, considering the even greater likelihood of gene flow barriers affecting these additional populations.

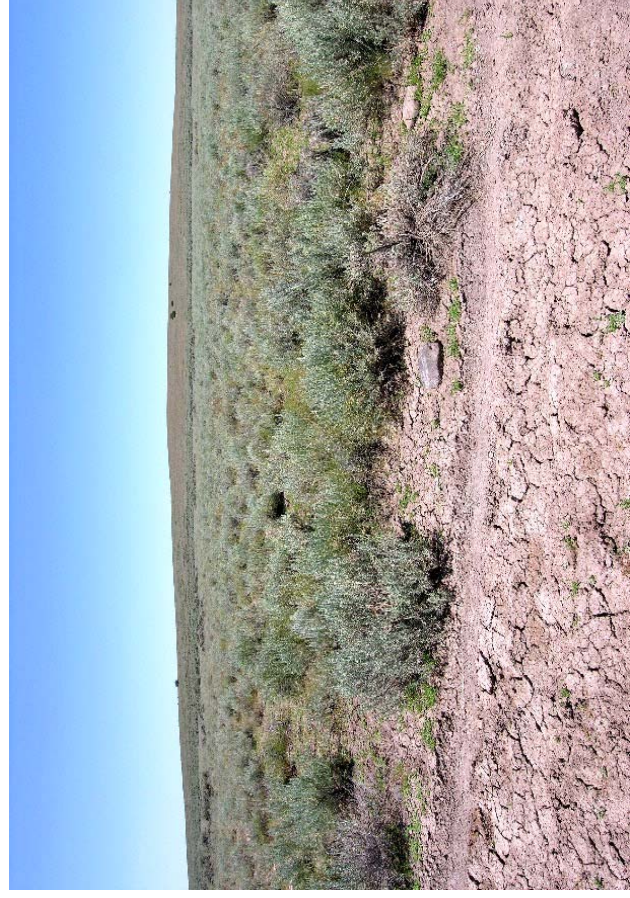


Fig. 2. (Above) Study site near Dog Hollow Reservoir in late July, 2003. **Fig. 3.** (Upper right) Small impoundment at Foley Lake RNA study site, mid-July, 2005. Most *Pogogyne* plants occur in temporary stream beds that feed this small pond. **Fig. 4.** (Lower right) Silver sage playa at Bull Flat study site in Malheur County, mid-July, 2005.

Greenhouse Protocol. All greenhouse studies were completed at Oregon State University. Due to the habitat specificity of *Pogogyne* populations, and the potential for edaphic endemism, plants for the following studies were grown in native soil collected at the study sites. Any seedlings that germinated other than the study species were removed, so that only *Pogogyne* plants were contained in the flats or pots. Unless otherwise noted, plants were grown under long-day photoperiods and watered, as needed, to keep the soil continuously moist but not completely saturated. A single fertilizer treatment (at three to four weeks) was added.

Reproductive Biology. The genus *Pogogyne* is divided into two subgenera (Howell, 1931), one (*Pogogyne*) characterized by striking, relatively large flowers and four fertile stamens, with the other (*Hedimoides*) having inconspicuous flowers possessing only two functional anthers. Jokerst (1992) appropriately assigned *P. floribunda* to *Hedimoides* based on floral morphology. While many plant species with tiny flowers are highly self-pollinated, others may rely wholly or partially on insects to facilitate pollen transfer despite their small corollas. For rare species that depend on floral visitors to mediate gene flow, habitat disturbances may disrupt pollination dynamics, something for land managers to consider.

The significance of self-pollination versus insect pollination as a means of seed production was evaluated in the field and greenhouse. *Pogogyne* seeds and/or live seedlings were collected from each study site and cultivated in four-inch plastic pots at OSU (during the summers of 2003, 2004, and 2005). Plants were grown to initial flowering (taking from five to seven weeks), four to six per four-inch pot, and then allowed to continuously flower and set fruit in a pollinator-free greenhouse environment for up to eight additional weeks. To determine the *potential* for autogamy, flowers from the dog Hollow site were examined at set intervals after corolla expansion to determine the timing of stigma and anther maturation and pollen release. Data was also taken in the greenhouse on the number of *flowers* produced per plant (20 plants per study population). The number of *seeds* (technically one-seeded nutlets) produced per flower via *autogamy* and the number of seeds produced per flower after *pollen supplementation* were also measured. The latter was effected in two ways, (1) by rubbing stigmas of recently opened flowers with pollen-laden anthers from *another* plant, and (2) by manually selfing flowers with pollen from the *same* plant. Means derived from 10 flowers from each of 20 plants (per study site) were used for the autogamy and supplementation analyses. It was very difficult to effectively emasculate the tiny flowers of *Pogogyne* in advance of pollen release, so a strict outcrossing treatment was not attempted. Finally, whole plants (90% or more in fruit) were harvested from the field and brought back to the lab, where seeds produced per flower for open-pollinated plants were counted (mean seed set from 10 flowers for each of 20 plants per site, as above). This was done to (1) estimate the potential for pollinator-limitation in nature, and (2) assess the effectiveness of autogamy (by comparing the seed sets of open field-pollinated versus greenhouse-selfed flowers).

Pollinators. To evaluate the potential role of insects in effecting reproduction, observations of floral visitors were made at each study site on sunny or partly cloudy days (between 1100 and 1600 hours, with temperatures ranging from about 20° to 30°C). Over several days between 2003 and 2005, 15 hours were spent in pollinator observation at the Dog Hollow site, 10 hours at Foley Lake, and 3½ hours at Bull Flat.

Germination Ecology. Most desert annuals occur in variable environments, where the timing and amount of precipitation over any given growing season is unpredictable. To compensate, many possess a seed dormancy mechanism, generally considered a defense against untimely germination (such as after a cloudburst in the heat of summer) that could result in catastrophic seedling losses (Venable and Brown, 1988; Pake and Venable, 1996; Tielbörger and Valleriani, 2005). Accordingly, it was hypothesized that *Pogogyne floribunda* would

produce dormant seeds, and that populations would be capable of maintaining a multi-year seed bank in nature as a means of evading drought years. It was also speculated that *P. floribunda* may have a comparatively more effective means of seed dispersal. Unlike most other species in the genus, which typically occur within the comparatively tight confines of vernal pools or small depressions, *P. floribunda* often grows in more open expanses, i.e., larger basins created by playa lakes or on broad, sparsely vegetated flats associated with silver sage. The capability of long-distance dispersal here may be an advantage as opposed to the narrowly delineated pools, where traits that facilitate mass movement of seeds outside the pool environments could be a drawback.

To evaluate germination behavior, ripe seeds from the three study sites were collected while still on parent plants (in mid-June and July of 2003 or 2005) and brought back to the lab for cleaning and sorting. Seeds from the Bull Flat site were partially obtained from greenhouse plants grown from seedlings collected on-site in 2005. Filled seeds (i.e., those that appeared plump and viable and were not overtly shriveled) were immersed in 5 mm of water in sterile petri dishes, and either (1) stored at 3-4°C for eight weeks and then exposed to ambient conditions (typically 18° to 22°C); (2) stored at 3-4°C continuously; or (3) maintained at ambient temperatures without any refrigeration. Percent germination by dish was recorded weekly (beginning four or five days after the first seed in a treatment had germinated). The experiment terminated after 15 weeks for the first two treatments, and after seven weeks for the last treatment. A random mix of twenty seeds from different parents was placed in each of 10 petri dishes per treatment. Comparisons were made between treatments and study sites.

Dispersal and Seed Bank Considerations. To learn more about *Pogogyne* dispersal and recruitment strategies, 30 plants from the Foley Lake and Dog Hollow sites were grown in separate flats beginning in July, 2003. Plants were raised to reproductive maturity for 40 days under semi-saturated conditions, and then allowed to fully senesce (by eliminating further watering) over the following 30 days. At this point counts were made of the number of seeds produced by individual plants, and the flats with the dead plants were then set outside in the greenhouse yard where they were exposed to wind and fall rains. After 60 days, the proportion of seeds that had dispersed was determined.

To assess the potential for a seed bank to exist in nature, about six liters of topsoil from each of three locations were collected within the perimeter of the Dog Hollow playa *Pogogyne* population in August, 2003. The soil was mixed and then divided equally among six standard greenhouse flats. Three of these were watered and placed outside (in Corvallis) in October. The number of *Pogogyne* seedlings appearing that fall and the following spring were counted and removed prior to flowering. These three flats were then retained, allowed to dry out over the summer, and the procedure was repeated with the same soil over the fall and winter of 2004-2005. The other three flats were left dry for the first year, and then similarly saturated 12 months later, placed outside in September, 2004, and examined for seedlings that fall through the following spring. All flats were soaked periodically over the winter to keep them wet.

Foliar and Floral Predation. Predation of leaves, flowers, and fruits can limit reproduction, negatively influence recruitment, and seriously affect the dynamics of plant populations (Janzen, 1971; Louda, 1982; Louda and Potvin, 1995). This can be an issue in natural populations, as well as a potential problem in cultivation settings where plants are being grown for research or conservation purposes. Pressed collections of *Pogogyne* plants from the three study sites were made in 2003, 2004, and 2005, and assessed (after drying) for foliar and floral damage caused by predators. Seed samples (from collections discussed in the previous section) were also evaluated for damage by pre-dispersal predators. Any adult insects or larvae encountered during the examinations were identified to the degree possible.

Cultivation. Reintroduction is becoming an increasingly used conservation tool for many endangered plant species (Maunder, 1992; Falk et al., 1996). Understanding the growth requirements of a target species is prerequisite to accomplishing a successful re-introduction project, something that in practice has been relatively infrequent (Allen, 1994; Pavlik, 1996). An important goal of this study was to describe the best protocol, based on available life history information, for growing *Pogogyne* plants in cultivation, which could be used for (1) producing greenhouse seed crops that could be stored cryogenically for future recovery efforts, or (2) growing plants for direct translocation to field sites.

Population Dynamics and Monitoring. Annual species, especially those believed to have persistent seed banks, are difficult to evaluate demographically without long-term field studies (Menges, 2000; Doak et al., 2002). No attempt was made here to predict *Pogogyne* population growth or survival using viability analysis or any other modeling technique. However, a series of plots were established at study sites to assess the degree plant distribution

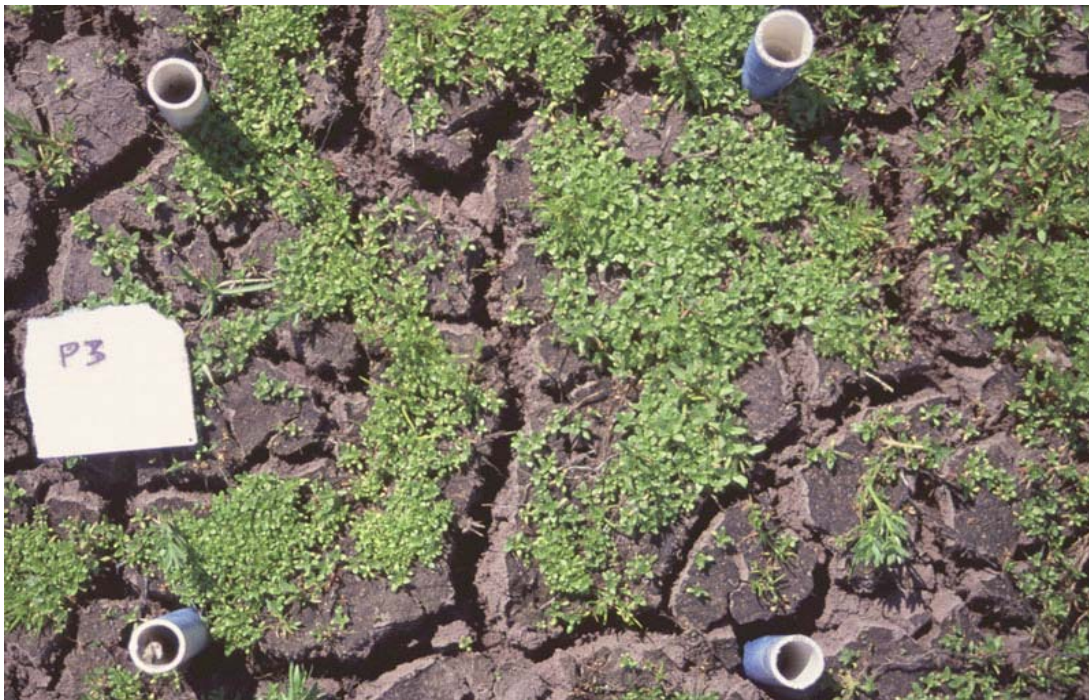


Fig. 5. Example of microplot set up at the Dog Hollow study site to gather annual cover estimates for *Pogogyne* plants and associated species. *Pogogyne* cover for this plot was estimated at 55%.

remained constant within the populations. In late May, 2003, two sets of 10 plots (3 x 3 dm each; see Figs. 5 and 20-22) were set up near the southwest edge of the playa at the Dog Hollow site. Each was arranged perpendicular to the existing moisture gradient and parallel to each other, extending about 120 m from the shallow edge of the drying lake bed (where *Pogogyne* first appears), into the center of the population where plants were most abundant, and then on towards the muddy center of the playa where silver sage dominates but winter water depth limits annual plant growth. Plot data were recorded from 2003 to 2005 (mid-July), and included the cover of (1) *P. floribunda*, (2) any associated native annuals, e.g., *Downingia*, *Plagiobothrys*, etc. (tallied collectively), and (3) any exotic associate species (also recorded collectively). The amount of substrate disturbed by cattle was noted, and in 2003, soil moisture was also measured in each plot (see Fig. 20). Comparisons were made between plots and between years. Some of the PVC markers (Fig. 5) were destroyed by cattle activity during and

after 2003, but usually at least two or three remained for a given plot, facilitating the reestablishment of plots when necessary.

Reference points were also established within the *Pogogyne* populations at Foley Lake RNA (in 2003) and Bull Flat (in 2004). At Foley Lake, single stakes were placed at eight scattered locations where clusters of plants were observed in June, 2003. The stakes marked the center of 2 x 2 meter plots. Few plants were located in 2004 at Bull Flat, presumably due to drought that year, but plots were established based on explicit GPS coordinates of 2003 *Pogogyne* patches provided by Don Mansfield (Albertson College of Idaho). Plots at both sites were re-visited in mid-July, 2005. The purpose of the Foley Lake and Bull Flat plots was simply to assess annual fluctuations in relation to yearly precipitation patterns in the area, and then to contrast population trends among the three sites. Since *Pogogyne* plants at these two study sites were much less densely distributed than those at the Dog Hollow locality, they were individually counted within plots. Estimates of cattle impact were also recorded from the Foley Lake and Bull Flat plots (measured as the percent cover of trampled substrate).

Measuring Divergence Among Populations. Geographic isolation is a well known stimulus for speciation in plants (Clausen, 1951; Grant, 1971; Stebbins, 1977). Consequently, disjunct and localized peripheral populations are often of conservation interest. *Pogogyne floribunda* is geographically and ecologically separated from *P. zizyphoroides*, and this clearly played a role in the partitioning of these two taxa (Jokerst, 1992). Could isolated populations within *P. floribunda* also show evolutionary trends associated with geography?

With this in mind, an original goal of the current project was to compare the California populations described by Jokerst (1992) with those recently discovered in the Dog Hollow Reservoir area of Oregon, to determine if any differences could be detected. However, it became obvious soon after the start of the work that these populations are not as separated as once thought. The populations on California's Modoc Plateau are geographically adjacent to and ecologically equivalent with those now known from across the line in Oregon, and it was apparent the plants and habitat from both areas were very similar. However, the isolated populations at Bull Flat and Foley Lake RNA were another matter. Both are well separated from the core area for the species, and occur deep into the Great Basin proper. cursory review suggested these populations may in fact have unique morphological traits, so the comparative work was expanded to take in representatives from all three areas inhabited by the species in Oregon (Fig. 1), as well as collections from near the type locality in Modoc County (used in the PCA only, see below). Included in both the morphometric *and* DNA work were collections of *P. zizyphoroides* from the Rogue Valley in southwest Oregon, for comparison. The site reported for *P. floribunda* in western Idaho could not be included in the present study.

Morphometric evaluation. Plants from the Oregon populations described above were grown in the greenhouse from wild-collected seed. Seedlings were thinned and cultivated in flats (temperature ranging from 17°C to 25°C min/max) under lighting set to a 15 hour photoperiod, and maintained for 16 weeks. Twenty-three morphological traits (see Fig. 30) considered valuable for taxonomic interpretation of *Pogogyne floribunda* and *P. zizyphoroides* (based on Howell, 1931, Jokerst, 1992, and general observation) were measured for 20 randomly selected plants per population. Greenhouse plants at this point were 80% or more in fruit but retained corollas at upper nodes, and were phenologically comparable to the herbarium collections. A Principle Components Analysis (PCA) was performed on the resulting data set, to evaluate the phenetic similarity of the individuals and populations. Results were graphically depicted to assess relatedness among groups and to evaluate important diagnostic features.

DNA sequencing. In the first known attempt to isolate and sequence DNA of any *Pogogyne* species, chloroplast DNA was obtained from fresh plant material grown in the

greenhouse (see above). For additional comparison, *P. zizyphoroides* was employed as an out group, using fresh plants collected from a site near Medford, Oregon. For each population, approximately 50 mg of leaf material was used to extract DNA, using a DNeasy Plant Mini kit (Qiagen, Valencia, CA). Polymerase chain reactions for plasmid DNA were performed in 20 μ l reaction volumes which contained 3.0 mM MgCl₂ (Promega, Madison, WI), 10X Promega Buffer A, 0.1 μ M each dATP, dCTP, dGTP, and dTTP (Epicentre, Madison, WI), 10 pmol of each primer (Taberlet et al. 1991), 1X BSA, 1 unit of *Taq* polymerase (Promega), and 2.0 μ l DNA template. The reactions, overlaid with approximately 10 μ l of mineral oil, were placed in an MJ research programmable thermal controller programmed as follows: 5 min at 95 °C, 25 cycles of 1 min at 95 °C, 4 min at 65 °C, with a 10 min final extension at 65 °C. Following PCR, products were purified using a QIAquick PCR purification kit (Qiagen, Valencia, CA). As a result of low DNA yields, the 50 μ l elutions were concentrated to 5 μ l using a LABCONCO centrivap-concentrator. Sequences were obtained from Northwoods DNA (in Solway, MN), were aligned "by eye," and analyzed using BioEdit for Windows 95/98/NT.

RESULTS AND DISCUSSION

Reproductive Biology. The intricate structure of the flowers and the timing of pollen release in *P. floribunda* (Fig. 6) imply that the potential for autogamy is extremely high. The data do not provide any evidence for routine delayed selfing, commonly seen in larger flowered

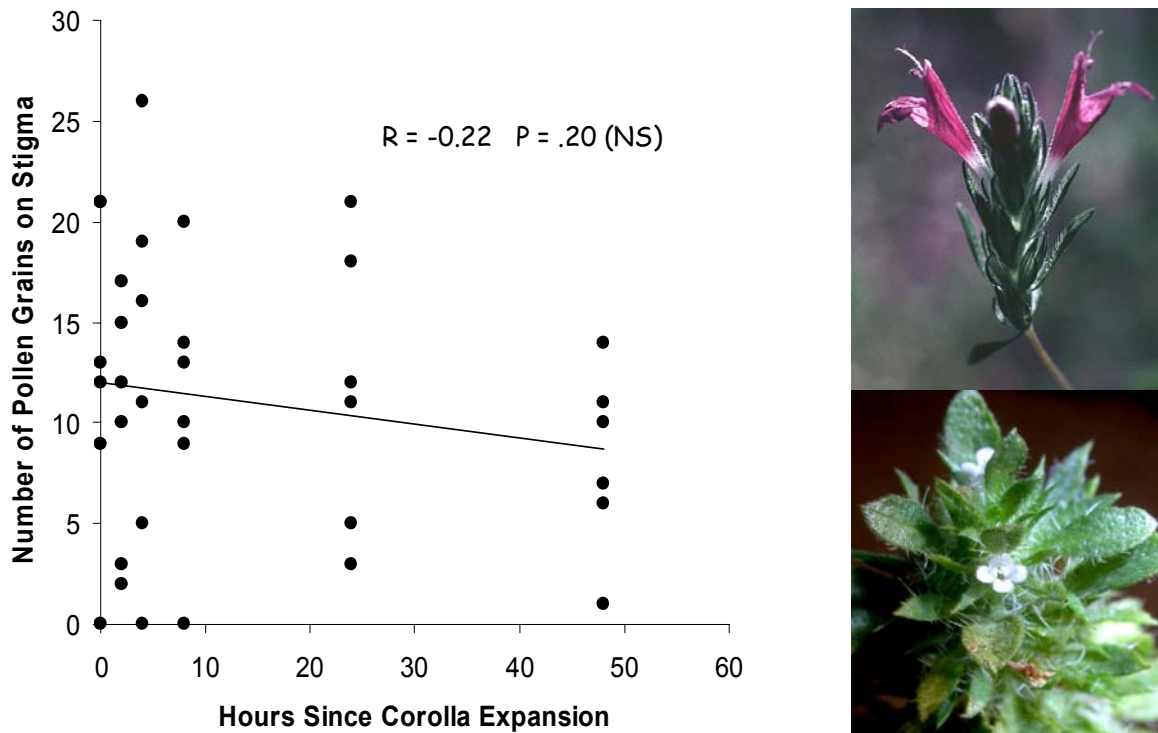


Fig. 6. Number of *P. floribunda* pollen grains on selfed stigmas when corollas first expand (0 hrs), and then at 2, 4, 8, 24, and 48 hrs after expansion (n=6 per time interval). Larger flowered species of *Pogogyne* (such as *P. clareana*, top right) have anthers and stigmas separate at anthesis, providing ample opportunity for outcrossing, while the small flowers of *P. floribunda* (below) show little if any separation between the floral organs. As expected, the data indicate limited chances for outcrossing in *P. floribunda* (see text), with most flowers shedding some pollen onto stigmas at or about the time corollas open. However, 25% of the stigmas sampled had 5 or fewer grains, suggesting that outcrossing is possible.

mixed-mating system species (Dole, 1990; Klips and Snow, 1997), since the correlation between time after corolla expansion and amount of pollen on stigmas is not significant and trends negative. Although relatively few grains overall were deposited on unmanipulated greenhouse flowers, they are probably adequate for a species that produces only four ovules per flower. Anthers of the species are very small and reduced to two (unusual in Lamiaceae), and species with highly reduced, autogamous flowers often have low pollen-to-ovule ratios (Cruden, 1977). It is worth noting, however, that outcrossing is apparently possible in *P. floribunda*, as several sampled greenhouse flowers had few (or even zero) grains deposited on stigmas up to several hours after corolla expansion, suggesting a brief window of opportunity potentially exists for cross-pollination. Plants used for these measurements were all from the Dog Hollow Reservoir playa population, grown in the greenhouse.

A one-way ANOVA indicates that the 20 plants from Dog Hollow Reservoir produced significantly more flowers than the plants from the other two study sites (Fig. 7) when grown under identical conditions in the greenhouse ($F=11.2994$, $P<.0001$). A Tukey-Kramer post-hoc test of mean differences showed that Dog Hollow plants differed from Foley Lake and Bull Flat ($q=4.223$, $P<.01$; and $q=6.626$, $P<.001$, respectively), while the Foley Lake and Bull Flat plants did not differ significantly.

The *Pogogyne* plants examined during this study are prolific seed producers – out of the 240 plants and 2,400 flowers examined during the pollination treatments, the total seed set was approximately 92%. And as Fig. 6 predicted, the level of autogamy in the Great Basin study populations is extremely high. Plants from the three study sites were not identical in this regard, however.

Those from the large population at the Dog Hollow Reservoir playa are not only more floriferous

than plants from the other sites (Fig. 7), they also tend to produce more seed per flower in the greenhouse (Fig. 8). The trend is clear, even though the differences between this population and the other two are not quite significant for autogamous plants ($P=0.0662$, one-way ANOVA), or the supplemental selfing ($P=0.4935$, Kruskal-Wallis) or supplemental outcrossing ($P=0.1835$, Kruskal-Wallis) treatments. The addition of pollen to recently opened greenhouse flowers did manage to increase seed set over strict autogamy in two instances (Fig. 8) – greenhouse-grown plants from Foley Lake and Bull Flat produced significantly more seed when supplemented with *self* pollen than when left alone ($P<.01$ and $P<.05$, respectively; Kruskal-Wallis followed by Dunn's Multiple Comparison Test). Adding *outcross* pollen also improved seed set, but not significantly in between-study site comparisons ($P>.05$, Kruskal-Wallis). And as expected, *Pogogyne* plants are not pollinator-limited. Seed set measured for

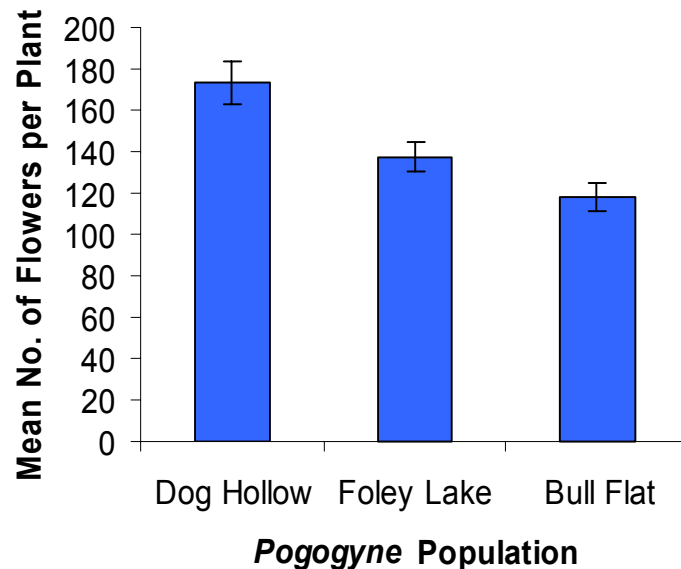


Fig. 7. Average number of flowers per plant for each of the three study populations ($n=20$). (Measured from greenhouse-grown plants – see text).

open-pollinated field plants did not differ from greenhouse autogamous flowers ($P=0.2596$, Kruskal-Wallis), so there was no apparent seed production advantage to being exposed to potential pollinators in nature versus sitting in the greenhouse.

While the evidence suggests that the *Pogogyne* plants are reproducing near to full capacity, Fig. 8 does demonstrate that under some circumstances adding pollen to flowers after they open can improve seed set. This is consistent with the data in Fig. 6, which indicate that not every flower has a full stigma load at anthesis. So even though plants are likely to be

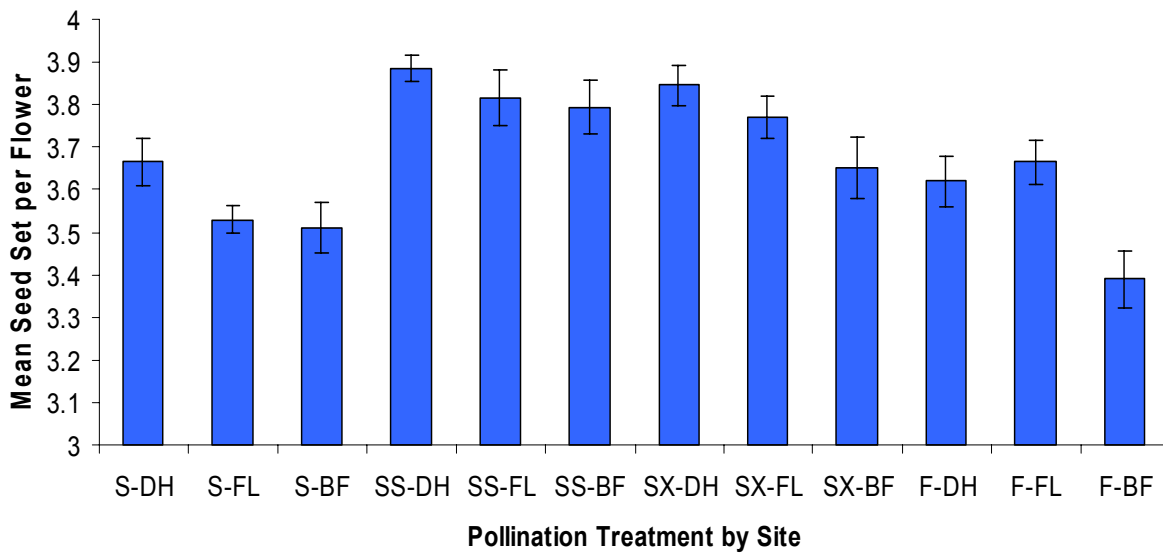


Fig. 8. Seed production in *Pogogyne* by study site and treatment. S=autogamous self-pollination; SS=self-pollination manually supplemented with pollen from the same flower; SX=self-pollination manually supplemented by pollen from another plant; and F=open-pollinated in the field. DH=Dog Hollow population; FL=Foley Lake population, and BF=Bull Flat population. Adding pollen to the stigmas of recently opened flowers that had already selfed in the greenhouse resulted in a small but measurable increase in seed production over unmanipulated flowers (the increase was apparent for both self and outcross pollen, but *significant* only in S-FL vs. SS-FL, and S-BF vs. SS-BF – see text). Open-pollinated flowers from the field did not produce any more seed than autogamously pollinated flowers in the greenhouse.

highly inbred overall, the potential exists for some stigmas to be available for pollinators to add outcross pollen, even though this was not measured here. This may be genetically important in the long run, especially for peripheral populations such as these, where maintaining diversity through outcrossing may be desirable for adapting to changing environments.

An interesting observation that came out of the reproductive data from Fig. 7 was the relationship between floral fecundity and plant size. For each of the three study populations, there was a significant inverse relationship between plant size (as inferred from the number of flowers produced by an individual) and the number of seeds developed per flower (Fig. 9). Although the results are statistically significant, they may or may not be particularly significant from a demographic standpoint, inasmuch as all plants (regardless of size) had consistently high seed sets. But this again relates to the idea that even though plants are highly autogamous overall, settings do exist where outbreeding can potentially still occur (i.e., not all ovules are fertilized by selfing, leaving some of them theoretically available for outcrossing). But what conditions are likely to promote scenarios conducive to outcrossing in the species? And why

would larger plants end up with fewer seeds per flower in the greenhouse, where resources (i.e., water and fertilizer) were plentiful and competition limited? A possible explanation for the latter has to do with flower size and positioning of floral organs. Measurements of 40 flowers

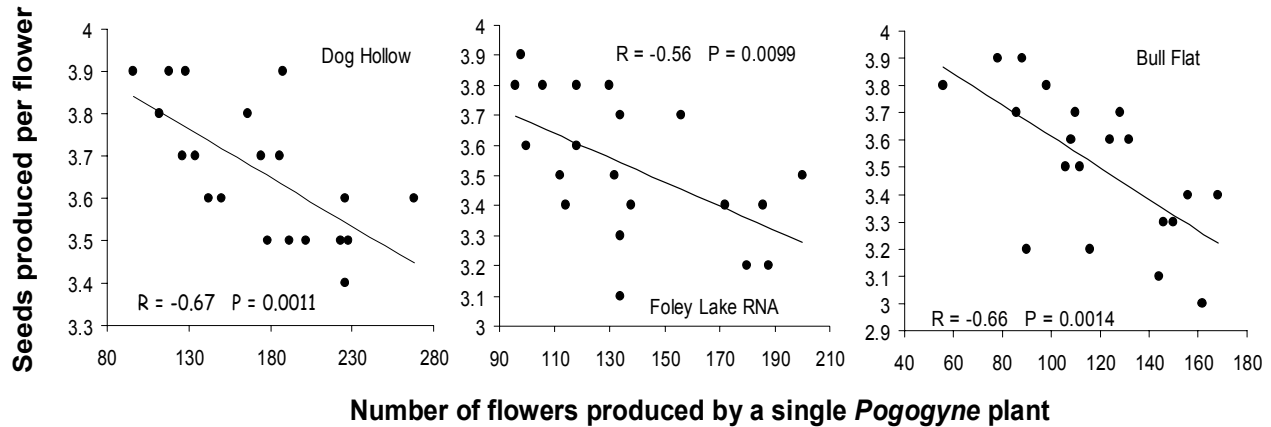


Fig. 9. The relationship between plant size and mean seed production per flower. *Plant size* in this case is assumed to be related to the number of flowers produced, i.e., the more flowers on a plant the greater its biomass. On the Y axis, each data point represents the average number of seed produced by ten randomly selected flowers from a single plant, while on the X axis each point represents the total flowers counted for one plant. The plants measured were grown in the greenhouse in the absence of pollinators (these are the same data depicted in Fig. 7, and in S-DH, S-FL, and S-BF in Fig. 8). Plants from each of the three study sites (Dog Hollow Reservoir, Foley Lake, and Bull Flat) showed comparable significant responses, with a lower overall seed set per flower correlated with an increase in plant size. (R=Pearson product-moment correlation coefficient)

from 20 plants from the Dog Hollow population showed variation in the relative positions of anthers and stigmas (Fig. 10). The variation was not random, however, as once flowers approached 8 mm in length they tended to exhibit significantly more separation between anthers and stigmas (presumably due to the extra “space” inside their corollas).

Although the separation was not great, even for the largest flowers (no separation was greater than 2 mm!), it may still be enough to slightly decrease levels of self-pollination by reducing opportunities for autogamous pollen transfer. This could account for those stigmas depicted in Fig. 6 that received comparatively fewer pollen grains via autogamy. So this appears to tell us that plants with larger flowers and greater floral displays may play a role in assuring that *Pogogyne* populations can also occasionally outcross, thereby potentially increasing genetic diversity within populations and improving chances for adaptation over time.

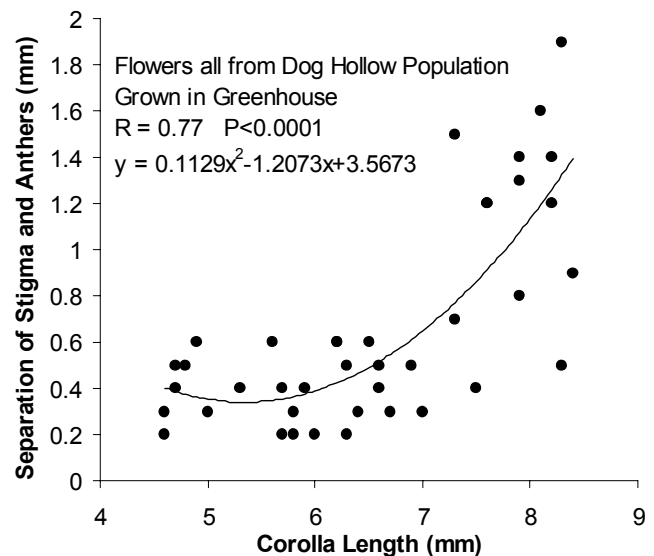


Fig. 10. The larger *Pogogyne* flowers become, the more separation tends to develop between anthers and stigma lobes. The rate of autogamy is potentially impacted as plants grow larger – see text.

For populations that occur in challenging environments (such as vernal pools and playas in the Great Basin), the adaptability factor is undoubtedly important as plants struggle in marginal habitats. Seeds are also potentially subject to long-distance dispersal (possibly via waterfowl), considering the insular and scattered nature of suitable *Pogogyne* habitat across the Great Basin. The fact that the plants at Foley Lake and Bull Flat exist is support for the perception that long-distance dispersal events can lead to the establishment of unique populations, providing the founding members are able to adapt and adjust to their new environment. Maintaining within-population genetic diversity increases these odds.

Pollinators. None of the previous discussion about self- versus cross-pollination has much meaning if pollinating insects never visit *Pogogyne floribunda* flowers. Pollinators for *Pogogyne abramsii* are well-documented (Schiller et al., 2000), and the floral morphology of the other larger-flowered species in the subgenus *Pogogyne* (see example in Fig. 6), with exerted and well separated stigmas and anthers, certainly seem designed for insect. However, primarily autogamous species seldom attract many visitors, due to their typically reduced flower size and negligible rewards for foraging insects, and it was expected that locating pollinators on *P. floribunda* flowers would be a challenge.

So it was a bit surprising when a number of insect visitors were noted at all three study sites (Table 1). Nectar was not detected in any flowers, but a small amount of pollen was available on most flowers immediately after corollas opened. The larger visitors (honeybees and bumblebees) seemed transient and their wallowing across and among *Pogogyne* patches appeared haphazard and accidental. The solitary bees, although seen infrequently, did actively forage for pollen. While the number of visits recorded was small for all classes of floral visitors, particularly when compared with the larger flowered *P. abramsii* (Schiller et al., 2000), the bees observed are clearly capable of transferring pollen from flower to flower. Based on these observations, and the previously discussed data, it appears likely that *P. floribunda* is a highly self-pollinated species that sustains the ability to occasionally outcross.

Table 1. Floral visitors (all were bees) recorded for *Pogogyne* populations at the three study sites. Observations consisted of watching small patches (15-30 plants) for an hour at a time, and then shifting to another spot at least 20 m away. The numbers below denote different pollinators that were followed in the patches, and not individual floral visits (which were impractical to track). Dog Hollow observations were made in 2003 and 2005 (15 hours total), Foley Lake in 2003 and 2006 (10 hours), and Bull Flat in 2004 and 2005 (3½ hours). Honey-bees (*Apis*) and bumblebees (*Bombus*), potential long-distant dispersers, were the most common at the Dog Hollow Playa population. Solitary bees (Megachilids and Halictids) were dominant at the more remote sites at Foley Lake and Bull Flat.

Floral Visitor	Dog Hollow	Foley Lake RNA	Bull Flat
<i>Apis</i>	27		
<i>Bombus</i>	8	2	
Megachilidae	1		6
Halictidae	16	17	4

Conservation issues. The data here indicate that in years favorable for the growth of larger *Pogogyne* plants, not only is more seed likely to be available for the seed bank in general, but significantly more of this seed may be outcrossed. Protecting large plants and the favorable habitat they occur in should be a priority of public land managers. Accordingly, special care should be taken to reduce or eliminate grazing and other disturbances during the

short period when *Pogogyne* plants are flowering and setting seed, and pollinators are active, particularly in wet years when larger plants are likely to be more plentiful.

Germination Ecology. Seed germination data for the *Pogogyne* study areas are summarized in Fig. 11. The immediate impression is that there are no apparent differences in germination behavior between plants from the three disjunct populations. Although not necessarily expected, if the sites have been isolated for some time, the potential exists for variation in germination behavior to arise among the populations, as has been shown for other desert annuals and some vernal pool taxa (Silvertown, 1984; Phillipi, 1993; Elam, 1998). Yet on the other hand, any genetic changes due to drift or mutation that affect the established germination ecology of a vernal pool annual would likely be detrimental, or may even prove lethal, inasmuch as the species probably already possesses a germination strategy that facilitates survival in a harsh environment. Such changes would likely be selected against.

Not surprisingly, seeds that were kept chilled for 15 straight weeks remained dormant, while those that were chilled and then released from chilling after eight weeks showed a burst of germination at that time (a pattern commonly seen in spring annuals occurring in areas with

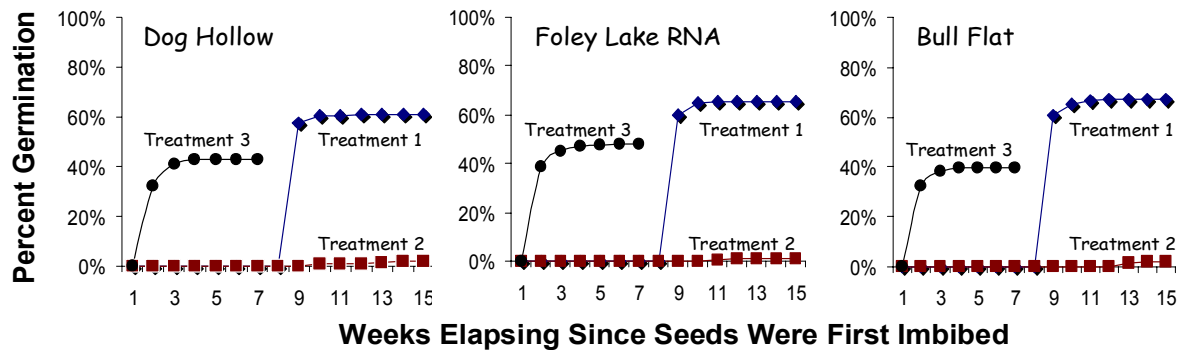


Fig. 11. Mean seed germination data for *Pogogyne* populations at the three study sites. Treatments were as follows: data represented by diamonds (◆) are for seeds stratified at 3–4°C for 8 weeks prior to being exposed to ambient conditions (~18–22°C); squares (■) represent data for seeds stratified at 3–4°C for the duration of the experiment; and circles (●) are for seeds that were allowed to germinate under ambient conditions without ever being chilled (see Methods for more details). Clear differences existed within populations based on treatment. Seeds chilled for the entire 15 weeks (*Treatment 2*) scarcely germinated at all (under 1%), while seeds that were not chilled (*Treatment 3*) and seeds that were chilled and then later exposed to ambient temperatures (*Treatment 1*) readily germinated. There were significant mean differences between the latter two treatments at the end of the experiment within populations (repeated measures ANOVA, $F=25.014$, $P<0.001$ – Tukey-Kramer post-hoc comparison test: $q_{(\text{Dog Hollow})} = 7.853$; $q_{(\text{Foley Lake})} = 8.031$; $q_{(\text{Bull Flat})} = 12.043$; all $P<0.001$), indicating a modest germination advantage for seeds that undergo a period of moist chilling (simulating overwintering temperatures in nature). However, there were no significant differences between like treatments among the three study populations under any of the treatments (repeated measures ANOVA followed by Tukey-Kramer test). Percentage data were arcsine-transformed prior to analyses.

dry or cold winters). However, a somewhat smaller percentage of the overall seed crop did not seem to require any chilling, and these seeds germinated soon after being placed in water (Fig. 11). As with the chilled seeds, these responded rapidly, with most germinating in the first few days. While seemingly a risky strategy for a desert annual like *P. floribunda*, this is in line with so-called “bet-hedging” theory (Silvertown, 1984; Pake and Venable, 1996; Clausen and Venable, 2000), where in this case both dormant and non-dormant seeds are dispersed simultaneously. Initially, this gives the species the “option” of taking advantage of pooled

precipitation during the hot summer, should it occur, while retaining a larger portion of its seed for germination later under more amenable circumstances. Greenhouse work has demonstrated that *Pogogyne* plants are capable of reproducing very quickly after germination, especially if drought-stressed (Bauder, 1989 has also shown this to be true in *P. abramsii* in California) – if habitat is inundated after a summer thunderstorm, enough moisture may temporarily accumulate for a seed to germinate, flower, and produce selfed seeds before drying up. Germination at this time is risky, but it pays off if the summer-germinating plant can survive to reproduce and contribute even a few propagules to the seed pool. If summer precipitation is lacking, the non-dormant fraction of the seed crop sits, and may then be available for fall germination (assuming these seeds did not acquire dormancy later in the season due to environmental or age-related effects).

While the potential relationships of seed age or post-dispersal environment and acquired dormancy were not explicitly evaluated in the study, informal trials showed that many *P. floribunda* seeds retained their non-dormant state for at least a year or more while in dry storage, demonstrating they could be potentially available for germination the fall after dispersal. The inherently dormant portion of the seed crop would then presumably require chilling prior to germinating the following spring, allowing the species to further “hedge its bet” by producing seedling cohorts at two different times of the year (in addition to the sporadic appearance of summer germinants). Consistent with this thought, the study sites routinely exhibited plants of strikingly different size classes. While this could simply be the result of same-season competition or variation in habitat quality at the microsite level, it may also be at least partially explained by the species having both fall and spring germination times.

But what about the significant portion of tested seed that never germinated at all (Fig. 11)? For each of the three study populations, 30-40% of the seed did not sprout under any treatment. It’s possible that these ungerminated seeds were simply not viable, even though every effort was made to choose test subjects from a pool of seeds that were pre-selected for their “germinable” appearance (i.e., plump, undamaged, uniform in appearance). However, viability tests (such as a tetrazolium assay) were not employed, so it’s impossible to say with certainty that a large group of dead or otherwise inviable seeds were not inadvertently included in the study. But there are other potential explanations. First, it’s possible that added chilling (beyond the eight weeks provided here) might trigger further germination – considering that cold weather in the Great Basin lasts longer than two months, at least some seeds may require longer stratification. Another possibility is that the tough seed coat common to all *Pogogyne* species is serving to inhibit the germination of selected seeds, something often seen in legumes and other hard-seeded taxa (Kelly et al., 1992). Zammit and Zedler (1990) demonstrated that the simple nicking of the seed coat after imbibition in *Pogogyne abramsii* improved germination from 75% to 98%, and it is possible a similar inhibitory mechanism affects *P. floribunda*. It may be that the ungerminated *P. floribunda* seeds during these tests were simply impermeable to water, and in nature would require weathering or mechanical abrasion of the seed coat, in addition to favorable temperature and soil moisture, to break dormancy.

The wide variability in response by the tested seeds is very interesting. Zammit and Zedler (1990) identified a range of attributes in *P. abramsii* (such as seed weight, parental plant fecundity, and plant biomass) that affected germinability as well as the proportion of dormant versus non-dormant seeds produced per plant, and any of these could potentially apply to *P. floribunda*. In reviewing the literature it was interesting to learn how much apparent similarity in germination ecology exists between *P. floribunda*, a high desert species, and *P. abramsii*, a coastal southern California mesa endemic. Despite the considerable climatic differences that characterize the regions inhabited by the two species, the common vernal pool habitat, with its

consistent winter-wet and summer-xeric environments, may be the overriding factor in determining germination patterns.

Dispersal and Seed Bank Considerations. After 70 days of growth the 60 plants (30 each from the Dog Hollow playa and Foley Lake RNA sites, with watering stopped after 40 days) had ceased flowering and were fully in fruit. Most plants had died but were still stiffly erect in the flats. Reflecting the results of Fig. 7, Dog Hollow plants produced significantly more seed individually than Foley Lake plants ($\bar{x}_{(\text{Dog Hollow})} = 411.13$, $\bar{x}_{(\text{Foley Lake})} = 370.33$; $t=2.285$, two-tailed $P=0.0307$).

After 60 days outside in the elements, a surprising number of seeds remained within calyces on the dried plants, which for the most part remained standing. The mean difference for retained seed between the populations was highly significant ($\bar{x}_{(\text{Dog Hollow})} = 209.13$, $\bar{x}_{(\text{Foley Lake})} = 131.87$; $t=3.943$, two-tailed $P=0.0005$). This may be due in part to the less open, more crowded inflorescences that characterize the Dog Hollow plants (Fig. 12). Dog Hollow individuals, when compared to the other two populations, often grow in large, highly congested patches. The fact they retain more seeds on plants long after senescence may facilitate *en masse* germination, although the Foley Lake plants do retain ample seed as well. In the related *Pogogyne abramsii*, seeds are evidently also retained in calyces well after maturation, being released as plants collapse and fall to the surface with autumn rains (Schilling et al., 2000). This may also happen with *P. floribunda* in nature, although it was not observed in the greenhouse flats. Seeds of *P. floribunda* are similarly held in the fruiting calyces, but at least some of these disarticulate as standing plants dry out prior to fall rains, allowing them to serve as wind blown dispersal units during the dry summer. This feature was more prevalent in the Foley Lake plants.



Fig. 12. Congested inflorescence branch from *Pogogyne* plant growing at the Dog Hollow playa population, Klamath County.

The earlier speculation about the existence of a soil seed bank for *Pogogyne floribunda* is confirmed in Fig. 13. Native soil collected from the Dog Hollow study site in August, 2003 did contain *P. floribunda* seeds that germinated after being watered. Most seeds germinated in the spring after overwintering outside, with an initial flush of germination also occurring in the fall. The former seeds were presumably dormant when initially dispersed, eventually germinating in response to the cold winter temperatures or the degrading of impermeable seed coats over the winter. The majority of the germination recorded for seeds placed out in the fall

Conservation Status and Natural History of Great Basin *Pogogyne*

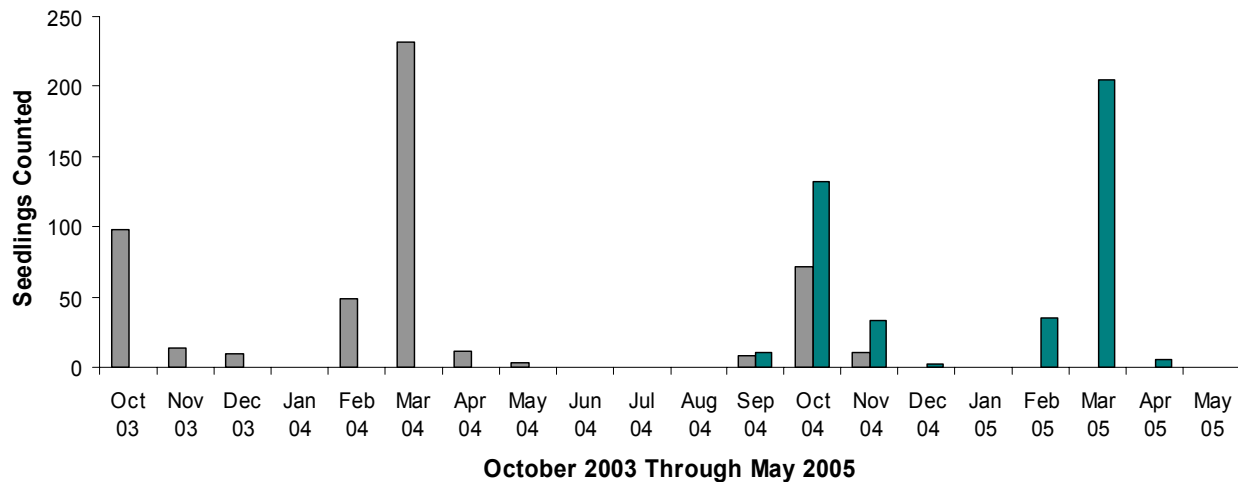


Fig. 13. *Pogogyne floribunda* seedling counts from topsoil collected at the Dog Hollow playa study site in August, 2003. The gray bars represent seedlings emerging from flats placed outside and watered regularly over the winter, allowed to dry out in the summer of 2004, and then watered again (while still outside) the following fall and winter. The green bars represent seedling emergence data for flats of soil that were left inside and dry for 12 months after collection, and then placed outside and watered starting at the beginning of September, 2004. The data support the notion that *P. floribunda* can and does maintain a soil seed bank in nature. It also supports the concept of a bimodal germination strategy, with some seeds germinating in the fall, and an additional fraction germinating the following spring after being exposed to cold fall and winter temperatures. The data additionally show that *P. floribunda* seeds can survive a minimum of 12 months in the soil and germinate the following year when exposed to favorable conditions. A total of 925 seeds had germinated by April, 2005.

of 2003 took place in the first six months, with a small amount of carryover into fall, 2004 (Fig. 13). For both the 2003 and 2004 cohorts, spring germination outpaced fall emergence, in line with what might be expected based on Fig. 11, where innately dormant seeds were more prevalent than non-dormant seeds in bulked samples.

Conservation issues. Even if the ungerminated seeds identified in this study (see Fig. 11) were not viable (which is unlikely based on Fig. 13), *Pogogyne floribunda* populations still produce a large quantity of viable seeds in favorable years, some of which may germinate immediately, and some which are dormant and may become part of a persistent seed bank (Fig. 13). Even in years when above ground *Pogogyne* populations are small or absent (as in 2004), known or suspected sites for the species should still be protected due to the likely presence of dormant seeds. And the apparent disappearance of a population for one or even several years should not result in the assumption that the site is no longer viable. Black and Zedler (1998) have observed that seeds of the rare *P. abramsii* can remain alive in the soil for up to seven years – the lack of *Pogogyne* plants at Foley Lake in 2004 followed by the thousands appearing in 2005 are similar testament to the importance of a seed bank for *P. floribunda*.

Management for the species also needs to take into account the fact that germination may occur in spring *or* fall. Activities in sites during the fall may directly affect the health of populations the following spring and summer, or for years to come if the seed bank is destroyed or damaged. *Pogogyne floribunda*, similar to other vernal pool species (Schiller et al., 2000), tolerates inundation and behaves as an aquatic for the early portion of its life cycle, becoming terrestrial and reproductive as pools or playas dry out. Trampling playas, draining pools, or allowing cattle watering (observed at Foley Lake in 2005 and at Dog Hollow every year of the study) can be disruptive to population dynamics, especially in years with comparatively few plants. The length of time seeds can remain alive in the soil is unknown for *P. floribunda* and

repeated grazing of pools and playas (especially for small populations such as Foley Lake or Bull Flat) may compromise the ability of populations to recover from natural droughts.

Foliar and Seed Predation. Pre-dispersal seed predation for *Pogogyne floribunda* was very limited among the samples examined. Sixty fruiting calyces per population (from a minimum of 20 plants each) were randomly selected in the field and examined for evidence of herbivory. Sepals were still slightly green when gathered, and contained fully developed fruit. Out of the 619 nutlets examined, only 21 showed any indication of insect damage, and only eight of these were clearly destroyed, a remarkably small number. Examination of herbarium collections showed a similar paucity of damaged specimens. Out of 120 pressed plants (40 from each study site) only 14 exhibited any foliar or floral predation, and none had more than 20% loss of biomass. Outbreaks of insect predators are often cyclic, and the fact that herbivory was not an important issue for *Pogogyne* during this study is not assurance it won't be at some other point. But from 2003 to 2006, seed and foliar predation in nature were minor problems, and did not significantly impact seed production or plant growth. Oddly enough, it was a different story for the cultivated plants. The non-field component of this study took place in Corvallis, with many plants being grown either in local greenhouses or outdoors during the warm summer months. In 2003, during the initial grow-outs for *Pogogyne*, outside plants were repeatedly attacked by a floral and leaf predator (Fig. 14) that, if left unmolested, could destroy dozens of flower buds and strip plants of their leaves.

Examples of the larvae were collected, allowed to pupate and hatch, and the adults were then examined by Richard Worth at the Oregon Department of Agriculture (ODA). The culprit was identified as *Pyrausta californicalis* (Figs. 15-17), a native moth in the family Pyralidae that is closely related to the European corn borer, a major agricultural pest in the United States. *Pyrausta californicalis* has been similarly reported as a crop pest, with the host (perhaps not surprisingly) being cultivated mint!

Peppermint (*Mentha piperita*) is commonly grown in the mid-Willamette Valley, but according to ODA, *Pyrausta* has not been reported as a serious problem to date. However a related species, the mint root borer moth (*P. fumalis*), is evidently a concern in western Oregon (Berry, 1974). *Pyrausta californicalis* has been intermittently collected from British Columbia to California, but never east of the Cascades, so it appears unlikely that natural populations of *P. floribunda* would be affected. The Willamette Valley infestation on *Pogogyne* was unexpected and initially caused serious damage to plants being used in the project. However, once the situation presented itself, it was easy enough to watch for the larvae and pick them off or just go ahead and spray flats to eliminate the problem. The moth did not reappear in 2004 or 2005.



Fig. 14. Larva of the moth *Pyrausta californicalis* feeding on a cultivated *Pogogyne floribunda* plant from The Dog Hollow playa population (grown at Oregon State University, Corvallis).



Figs. 15-17. Life history phases of *Pyrausta californicalis*: larva (upper left), pupa (upper right), and adult (below). Larvae were collected from *Pogogyne floribunda* plants (Dog Hollow playa population) that were being grown at OSU, and then switched to *Mentha* foliage to produce pupa and adults.

Conservation issues. The primary concern at this point is keeping *Pogogyne* plants being grown in cultivation free of *Pyrausta* infestation. This could be an issue if plants were being grown outside in areas where cultivated mint fields were common. *Pogogyne* grows equally well or better in the greenhouse, and if the purpose was to grow plants to produce seed for conservation purposes (artificial seed banking, creating new wild populations, etc.), then it would be prudent to do this indoors and away from potential pests, at least in western Oregon.

Should mint fields occur or be established in any area near native *Pogogyne* populations in Oregon or Idaho, occasional monitoring for pest outbreaks is recommended. Although *Pyrausta californicalis* has not been recorded east of the Cascades, *P. orphisalis* (the orange mint moth) has been found in mint fields there. While it has not been considered a serious pest of cultivated mints (Pike et al., 1987), its potential to infest and damage *Pogogyne* is unknown. Mint aphids (*Ovatus crataegarius*) are prevalent in mint fields east of the Cascades, have been reported as a serious pest in Idaho (<http://pestdata.ncsu.edu/cropprofiles/docs/IDMint.html>), and could in theory transfer to *Pogogyne* from infected fields. Two other potentially serious pests in mint fields, *Pseudobaris nigrina* (the mint stem borer, a weevil) and *Longitarsus waterhousei* (the mint flea beetle), also occur east of the Cascades (C. Baird, unpubl.). Both infect the lower stems of *Mentha* plants, which are much thicker and sturdier than those of *Pogogyne*, so these beetles may not be much of a threat. Finally, all the insects listed here overwinter (either as eggs, pupa, or adults, depending on the species) in the soil or among dead plant debris. Since *Pogogyne* habitat is usually inundated in the winter, it may not be possible for these pests to actually establish local populations in *Pogogyne* patches; however, short-term infestations are clearly feasible based on the experience with *Pyrausta californicalis*.

Cultivation. The information presented here is limited to plants from Foley Lake RNA and the Dog Hollow playa study populations. *Pogogyne* plants from all three study sites were cultivated for a variety of uses from 2003 to 2005, and as stated earlier, were grown in native soil gathered from the field. It was not difficult to raise numerous plants this way, which produced prolific amounts of seed through self-pollination (as described earlier). However, recognizing that gathering native soil for cultivation work may not always be an option (or convenient), a comparison was made towards the end of the project of the relative performance of *Pogogyne* plants grown in soil collected from the field versus plants grown in a standard potting mix. While the data in Fig. 18 do show measurable fitness differences, none of these are statistically significant. Plants from the Dog Hollow site grown in potting soil (Fig. 19) actually seemed to do better than those in native soils (even if not significantly so), so using a greenhouse potting medium is probably perfectly acceptable in any future grow-out.

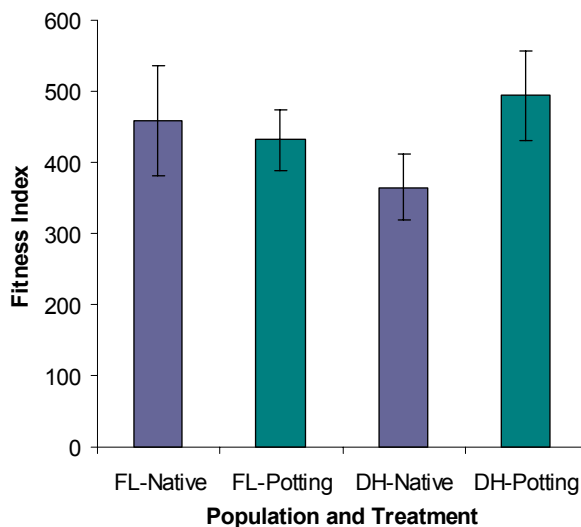


Fig. 18. Comparison of Foley Lake (FL) and Dog Hollow (DH) *Pogogyne* plants (n=10 per treatment) grown in native versus potting soil. Plants were germinated in pots and then grown for 70 days, after which a *fitness index* was developed for each, consisting of plant height *times* the number of flowering stems initiated *times* the number of floral whorls on the main stem axis. Although there was an observable difference between the index means for the potting versus native soil treatment for both study populations, the variation was not significant (for FL, 2-tailed P=0.7710, t=0.2955, and for DH, 2-tailed P=0.1181, t=0.1641; 18 d.f.).



Fig. 19. Young *Pogogyne floribunda* plants (about 40 to 45 days old) from the Dog Hollow playa population being cultivated in a greenhouse potting mix in Corvallis. As long as watering was kept constant, plants remained healthy (and fared no worse reproductively) when grown in commercial potting soil than when grown in the native vertisol topsoil from the study sites.

Conservation issues. Many rare species, such as *Astragalus applegatei* (M. Carlson, pers. comm.), have very exacting cultivation requirements. They may require a specific soil chemistry, precise greenhouse temperature or humidity, or particular soil symbionts (e.g., *Rhizobium* species or various mycorrhizal fungi). Other species may be far less finicky, but that information is seldom available for most rare plants when studies are being planned. Since *Pogogyne floribunda* populations occur naturally under what appear to be rather specific edaphic conditions (i.e., clay pans in silver sage dominated vernal pools and playas), it was initially decided that using native soil for cultivating the species would be the prudent course. It ultimately appears this may have been unnecessary. As long as the soil was kept saturated, plants did equally well in a standard potting mix available from any nursery. This certainly makes it easier to produce large quantities of plants for seed collection without impacting wild populations or their habitats, which can then be used for a range of conservation and recovery actions. The seeds germinate so readily and the plants grow so well that maintaining a cultivation program for this species, should it be required, would be a relatively easy matter.

Population Dynamics and Monitoring. Demographic and cover plot data recorded for the Dog Hollow playa study site are illustrated in Figs. 20-22. Visits to the two permanent transects spanned three consecutive years, beginning in the spring and summer of 2003. The Dog Hollow site represents by far the largest known *Pogogyne* population in Oregon, and the species was consistently present and well distributed on the playa all three years. A visit to the

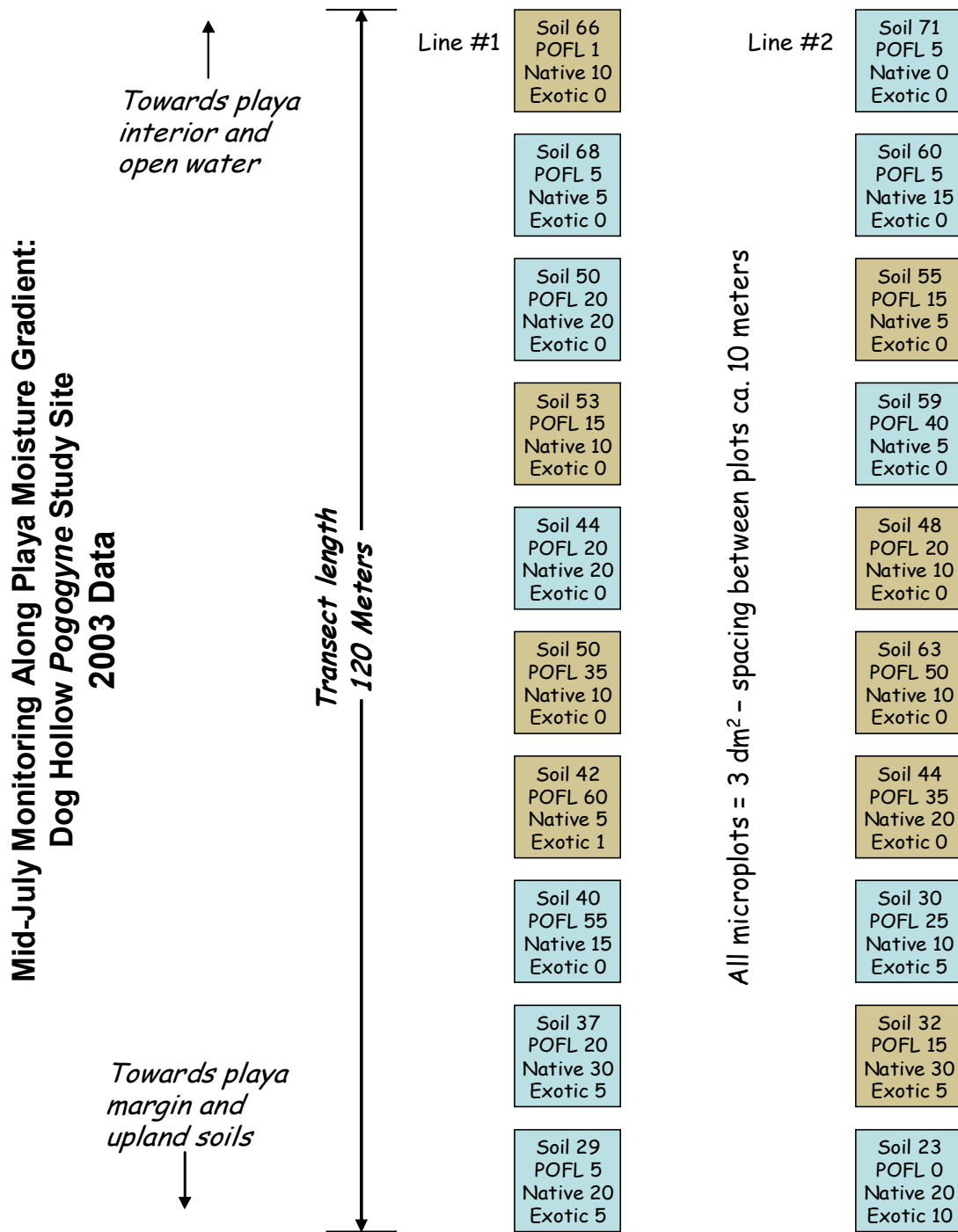


Fig. 20. Stylized diagram of plot layout along moisture gradient at the Dog Hollow playa site, with 2003 data. Each column of 10 boxes represents the transect line for a given year, and includes (for each plot) soil moisture data, and percent cover of *Pogogyne* plants, native species (collectively), and exotic taxa (also collectively). Soil data (for 2003 only) were calculated by collecting about 20 g of soil from each plot (from 3 cm deep) and weighing each of these wet (w_w). After thorough drying, the samples were weighed dry (d_w), and the percent soil moisture was calculated by: $\frac{w_w - d_w}{w_w} (100)$. Brown boxes represent plots that were 25% or more impacted by cattle grazing (primarily from soil compaction by trampling).

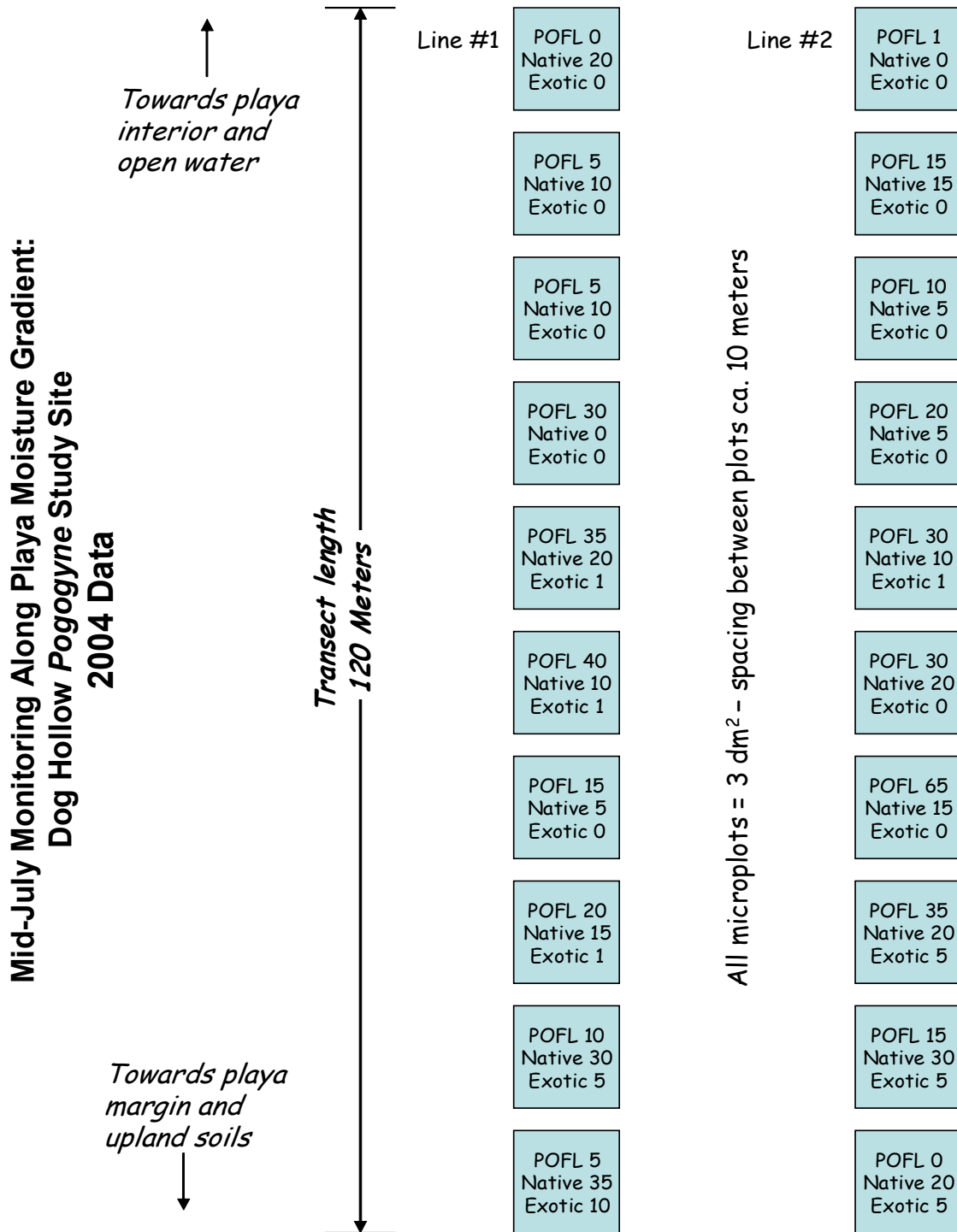


Fig. 21. Stylized diagram of plot layout along moisture gradient at the Dog Hollow playa site, with 2004 data. Each column of 10 boxes represents the transect line for a given year, and includes (for each plot) percent cover of *Pogogyne* plants, native species (collectively), and exotic taxa (also collectively). Though present on the playa in June and July, cattle did not impact any plots in 2004.

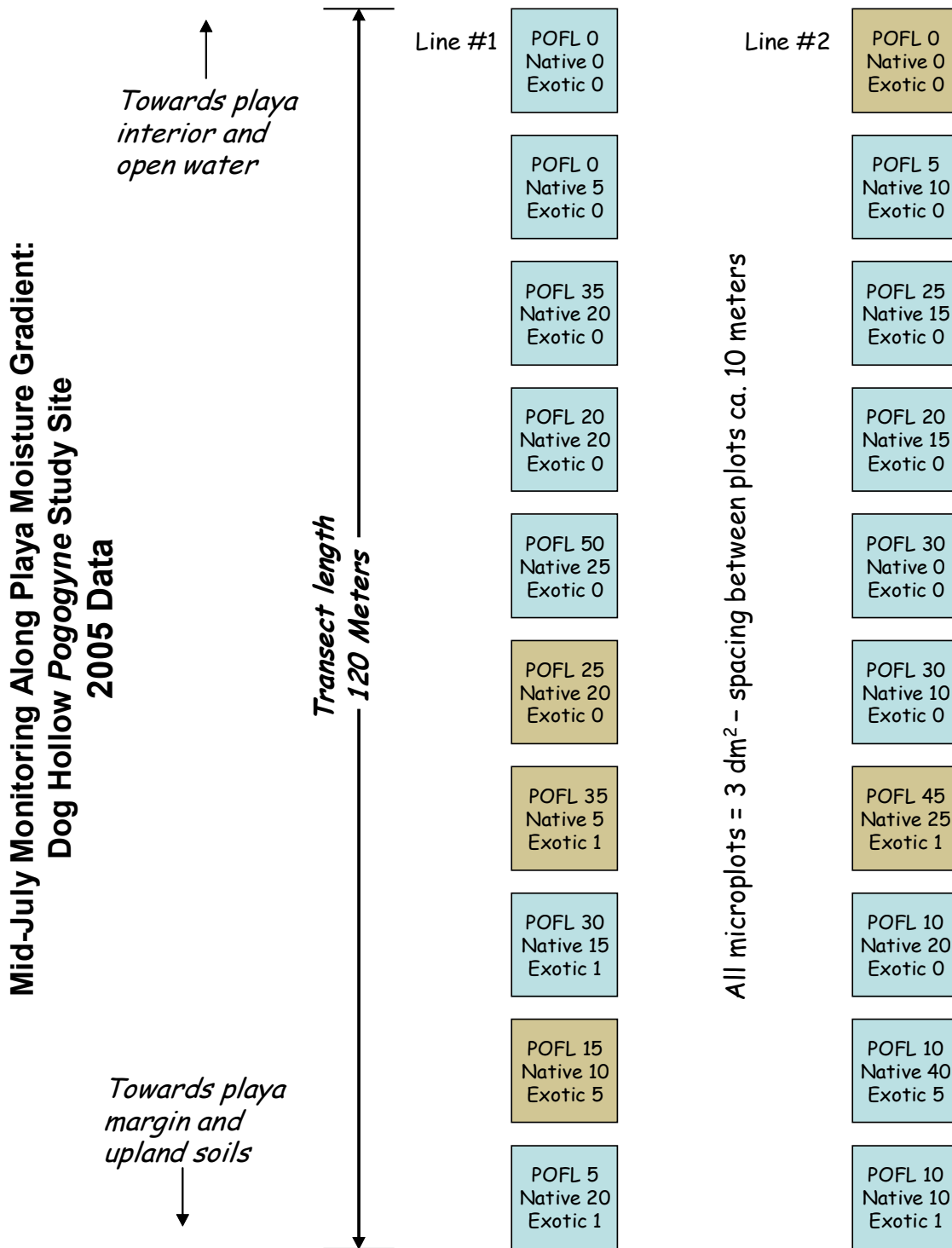


Fig. 22. Stylized diagram of plot layout along moisture gradient at the Dog Hollow playa site, with 2005 data. Each column of 10 boxes represents the transect line for a given year, and includes (for each plot) percent cover of *Pogogyne* plants, native species (collectively), and exotic taxa (also collectively). Brown boxes represent plots that were 25% or more impacted by cattle grazing (primarily from soil compaction by trampling).

area in 2006, although not formally part of the study, showed the *Pogogyne* population continuing to do well. *Pogogyne floribunda* is well established at this site and the extent of the species across the playa is impressive. Despite what would seem to be strong potential for the population to ebb and flow across the playa landscape, due to factors such as annual habit and

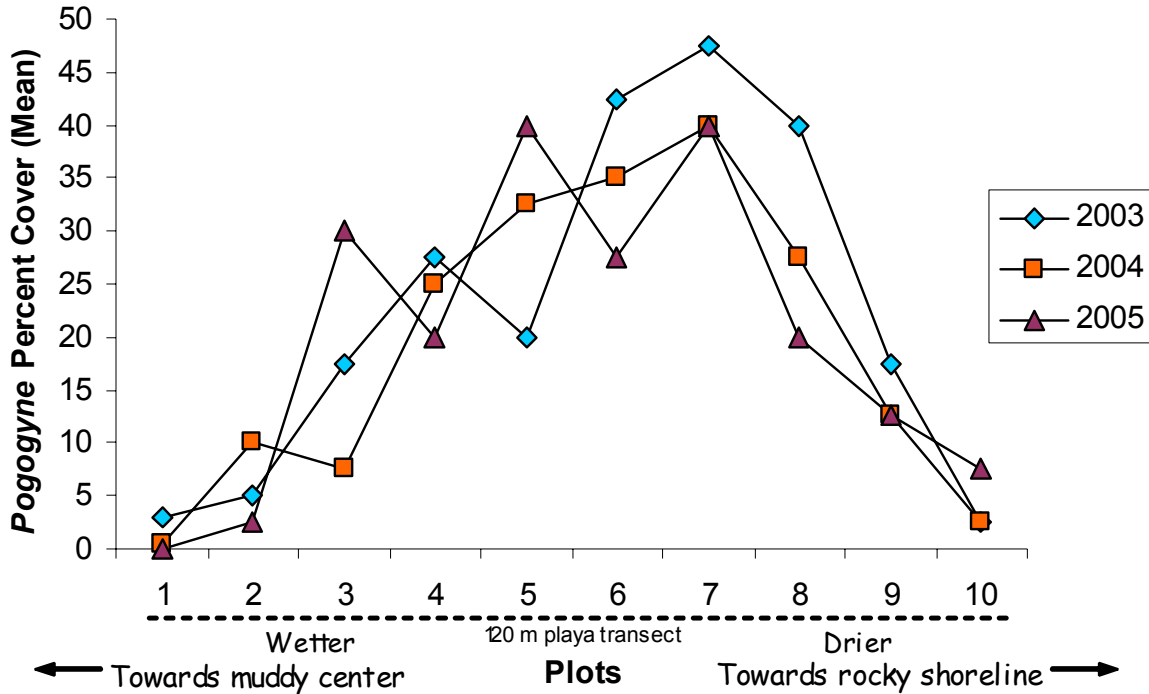


Fig. 23. Percent cover of *Pogogyne* plants in 20 microplots at the Dog Hollow study site (see Figs. 20-22 and Methods for set-up details) for each of three sampling years (recorded in mid-July, when plants were fully developed). Data for each year are averaged by plot position (i.e., Plot 1 on the X axis represents the mean of the cover measurements for Plot 1 on both transects – the two transects were laid out parallel to each other, so like plot numbers on each transect line were comparably positioned along the moisture gradient of the playa). Mean differences in overall percent cover between the three sample years was not significantly different using a one-way ANOVA ($P=0.8991$).

yearly fluctuations in precipitation, the mean percent cover differences for the species between the three years was not significantly different (Fig. 23). The fact that *Pogogyne* plants returned yearly and in the same numbers (more or less) to such small plots suggests that plant numbers at this site tend to be constant and the population does not shift around very much. The playa habitat here is well-defined, especially at the western edge, and *Pogogyne* plants seem to occupy most of the available habitat. The seed bank is unquestionably extensive, and the basin-like topography of the playa that inhibits run-off presumably facilitates the soaking of seeds every winter, ensuring consistent recruitment most years.

While drought will always be a potential dilemma for an annual species like *Pogogyne floribunda*, even on playa habitats such as the Dog Hollow study site, too much water may also pose a problem. The cover data in Fig. 23 suggest that plants do best in areas of the playa that received intermediate levels of inundation, which is perhaps not too surprising. Soils that drain quickly do not support the species, but soil that remains heavily saturated or under water for too long a period is likewise problematic. This observation is corroborated in Fig. 24, where a

polynomial regression reveals a significant relationship between the *percent soil moisture* measured in each of the 20 sample plots and the *percent cover* of *Pogogyne* as recorded in mid-July, 2003. Plant distribution appears not only limited by droughty conditions, but by excessive soil moisture as well. Evidently, even species that generally thrive in a seasonally aquatic environment can get too much of a good thing.

Competition was considered another potential problem for *Pogogyne* populations. However, Figs. 20-22 indicate that the cover of exotic species was very low overall in *Pogogyne* habitat, with only minimal weedy incursions at the dry edge of the moisture gradient. Numerous weedy species are found in the drier upland sites adjoining the lakebed, but these are in general not adapted to the extreme wet-dry moisture regime of the playa. But could indigenous annuals potentially compete with *Pogogyne*? Species of *Downingia*, *Plagiobothrys*, *Psilocarphus*, *Naverretia*, and additional genera do form thick carpets across the playa in some years. Perhaps high densities of these or other native annuals could negatively impact *Pogogyne* populations, and affect their ability to persist at a site or successfully immigrate to new localities. The data in Fig. 25 do not support this, however.

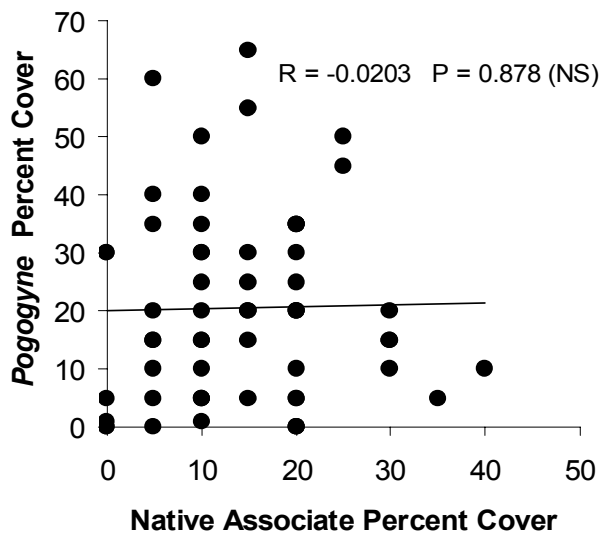


Fig. 25. Percent cover of *Pogogyne* plants as a function of the cover of other native annuals in the plots. More than one data point may occupy the same x-y coordinate on the graph. Data is for all three study years combined (= 60 plot readings). There was no significant relationship between the variables.

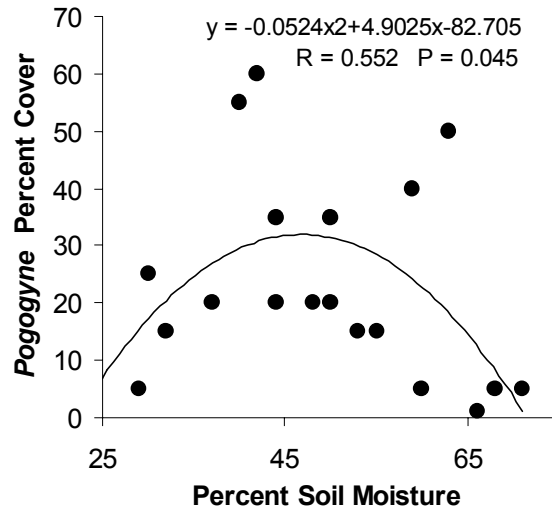


Fig. 24. Percent cover of *Pogogyne* plants as a function of soil moisture in the 20 permanent study plots. Cover was significantly higher in areas with intermediate levels of soil moisture. Data is from July, 2003 only.

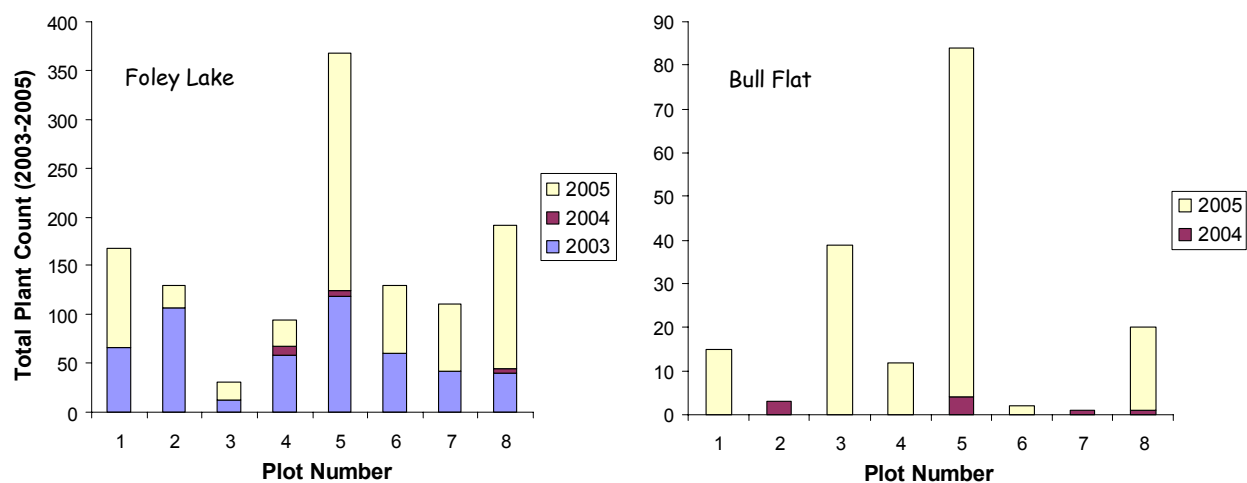
Pogogyne plants in the sample plots were virtually unaffected by the cover of associate native species, implying they are well adapted to growing and competing with other playa annuals.

The habitat at the Dog Hollow playa study area is dissimilar from the Foley Lake RNA and Bull Flat sites. While plant communities at the three locations certainly have components in common, most notably silver sage, the floras are by no means identical. In addition, aspects of microtopography and drainage patterns appear to differ substantially between the sites. The Dog Hollow population is perched on a shallowly depressed clay playa, a feature that promotes the temporary impoundment of winter precipitation. Assuming the water recedes on schedule in the spring, it is clearly an ideal locality for *P. floribunda*, which is thriving there.

Bull Flat is the most comparable to Dog Hollow of the other two sites. It also has

the qualities of a playa, but the drainage where *Pogogyne* occurs is clearly more diffuse, and the winter impoundment less pronounced – the associate flora reflects this by being more diverse (i.e., not all the herbaceous associate species growing with *Pogogyne* are vernal pool obligates, though most can be categorized as spring ephemerals). While the Dog Hollow playa population will probably do well even in years with less than average precipitation, the situation for the Bull Flat plants is probably a bit dicier, based on the habitat differences. The population at Bull Flat was virtually non-existent in 2004 yet very evident in 2005, while the population at Dog Hollow was well represented both years, despite similar rainfall patterns at the sites for those years. The Foley Lake RNA study site supported numerous plants in 2003, essentially none in 2004, and then many appeared again in 2005. This RNA has a very distinct playa lake, but *Pogogyne* for the most part does not occur there. Instead the species is distributed less than half a mile away along a series of natural channels leading into a stock pond (Fig. 3), in relatively light, clay-based soils subject to severe frost heave. What’s more, plants do not occur directly in the bottom of these seasonal drainages (where pooling occurs in wet years), but along their upper margins and occasionally near the drying edges of the catch basin in Fig. 3, typically under shrubs where soils remain moist into late spring but are seldom saturated. As at Bull Flat, the local distribution of *Pogogyne* here is scattered, even in “good” years, as compared to the dense patches that characterize the Dog Hollow playa study site.

The point here is not to formerly characterize or contrast the habitats of the various populations, but to emphasize the general features of the sites that may contribute to population stability. The observations and data collected since 2003 strongly imply that the Dog Hollow playa population is relatively stable, and should be expected to make a significant appearance most years assuming the habitat is not seriously degraded in the future. All things considered, it is probably less subject to the climatically-related hazards that often plague annual species occurring in arid environments. And if worse comes to worst, the population has a seed bank to fall back on in case of catastrophic drought. Based on their habitats, the Foley Lake and Bull Flat populations seem to exist under generally more tenuous circumstances. When precipitation is lacking, as it may have been (at least locally) before and during the 2004 field season, *Pogogyne* seeds at these sites may not germinate or seedlings may die prematurely (Figs. 26 and 27). Seed banks exist at Bull Flat and Foley Lake as well, since populations seem



Figs. 26 (left) and **27** (right). Annual *Pogogyne* counts for each of eight 2 x 2 meter plots established in 2003 at the Foley Lake RNA study site, and in 2004 at Bull Flat (see Methods for details). Both sites produced very few plants in 2004, with numbers rebounding in 2005, emphasizing the significance of soil seed banks in replenishing populations. Counts were made in late June or early July.

capable of recurring after unfavorable years, the difference here being they may have to depend more regularly on their seed banks than the population at Dog Hollow playa.

Conservation Issues. Several management-related issues are apparent as a result of the monitoring work. Although readily apparent to anyone who visits the sites, the data presented confirm that at the Dog Hollow site at least (and probably the others), soil moisture is a critical limiting factor with respect to recruitment and survival in *Pogogyne*. Anything that would serve to alter the hydrology of the playas or channels where populations currently exist could do significant harm. While it would take some effort to ditch and drain these remote sites (not to mention there would be no point), it would be considerably easier to excavate and dam portions of them, with the goal of improving watering areas for livestock. Even if the impoundments dried up later in the summer, it's likely that the longer period of soil saturation and resulting sedimentation would negatively impact populations. The hydrologic balance currently in place at the sites should not be disrupted.

Changing the soil moisture regime through disturbance or sediment build-up may also affect the ability of exotics to establish in *Pogogyne* habitat. Due to their extreme hydrologies, intact playas and vernal pools are typically considered resistant to impacts by exotic species (Zedler and Black, 2004), and observations during this study support this tenet for the Dog Hollow, Foley Lake, and Bull Flat study sites. However, altering the substrate and changing the soil moisture regime would likely erode this resistance. Invasion by exotics would further complicate the scenario for *Pogogyne* populations by changing the competition dynamics for the species. While *Pogogyne* seems perfectly capable of holding its own against native annual species (Fig. 25), this competitive edge may very well be lost if the species had to simultaneously contend with a shift in the soil moisture balance concurrent with an invasion by exotics. In addition to hosting *Pogogyne* populations and other unique species, playas are important to a wide range of biological functions and are considered high priorities in wetland conservation (Haukos and Smith, 2003).

All three study sites are a magnet for livestock, particularly Dog Hollow playa and Foley Lake RNA. The Dog Hollow site clearly has a history of grazing, and features a small berm along the southwest edge that was evidently constructed to create a mini-reservoir (for cattle watering) in the past. Cows were observed within the *Pogogyne* population every year of the study, trampling sample plots in 2003 and again in 2005 (Figs. 20 and 22). Although cattle were not actually observed at Bull Flat, evidence of their visits was abundant. Probably due to the lack of summer water here (there is a small bulldozed berm adjacent to the road that bisects the site, but it was dry in July), livestock impacts at this site were comparatively light in 2004 and 2005. This may not be the case every year (see cattle trail in foreground of Fig. 4).

However, heavy cattle use was witnessed at the Foley Lake RNA in July, 2005, and considerable evidence of grazing was noted here during the previous two years of the study. The small catch basin at the site (Fig. 3), evidently resulting from past enlargement by BLM (or local ranchers) of a natural, playa-like depression into a waterhole, ensures continuing interest in the local area by livestock, which have now heavily damaged the immediate shoreline (Fig. 28). The Research Natural Areas (RNA) system (www.fsl.orst.edu/rna/about.htm) was set up to preserve a representative array of significant natural ecosystems and their inherent processes as baseline areas. While it's unclear if there is an official BLM policy regarding grazing in RNAs, the practice certainly seems incongruous with a management program developed to "help protect biological diversity at (the) genetic, species, and ecosystem scales," particularly so if the RNA in question was primarily designated to manage and conserve rare native plants and relatively pristine rangeland communities (in this case, *Pogogyne* and *Rorippa columbiae* populations, and silver and black sagebrush flats). Based on the description of the RNA

program provided at its federally maintained website (above), allowing focused grazing within the habitat of Bureau Sensitive species is clearly inconsistent with the stated goals of preserving and protecting genetic diversity and natural ecosystems. Even if the 2005 grazing impacts (in Fig. 28) were the result of an unauthorized trespass by local ranchers, BLM needs to work harder to safeguard the small fraction of public lands designated as RNAs.



Fig. 28. Catchment area at Foley Lake RNA, fed by the shallow, seasonal channels (not shown) that supports the bulk of the unique *Pogogyne* population in the area. The population extends down the meandering drainages and more or less terminates along the upper margins of the basin above (as observed in 2003, and also reported by Lakeview BLM staff for earlier years). Extensive trampling by cattle in 2005 (above), and perhaps in other years, has seriously degraded habitat that supports the species. No *Pogogyne* plants were observed along the shoreline area in 2005.

So is grazing completely incompatible with the long-term survival of *Pogogyne* populations in the Great Basin? One would be tempted to think so, based on observations made at the Foley Lake RNA and Bull Flat sites. Every one of the sample 4m² plots at these two sites showed some evidence of cattle activity in 2005, and the *Pogogyne* plants here are scattered and not particularly abundant (probably between 3,000-6,000 at each locality in 2005, encompassing a few acres). And at the Dog Hollow playa, 45% of the microplots showed 25% or more trampling impact from livestock in 2003 (Fig. 20), and 25% did in 2005 (Fig. 22).

Although an overall census was not attempted at Dog Hollow, a conservative estimate would place the *Pogogyne* population there at well over 500,000 plants in 2005, with many dense patches scattered across the playa. So considering the yearly presence of cattle here, how

do we explain the abundance of *Pogogyne* plants at the Dog Hollow site, even accounting for the fact that this site is physically larger than the other two? One point to consider would be grazing intensity. Although cows were present all three years of the study at Dog Hollow, they were never observed to occur in great numbers, or at least in very high densities. Considering the playa itself has minimal palatable forage, cows typically traverse the site mainly to drink, moving back and forth from the receding edge of the open water in spring and early summer. They probably seldom congregate within the *Pogogyne* population for any length of time, as they appear to do at the Foley Lake RNA site, for example (Fig. 28), where forage and water are in closer proximity. And then there is the question of substrate disturbance. While the soils supporting *Pogogyne* plants at Bull Flat and (especially) Foley Lake RNA are relatively loose and subject to compaction, the comparatively firmer substrate (when dry) characterizing the larger playa at the Dog Hollow site appears more resilient – even when trampled, the seasonal lakebed here seems less subject to degradation than the other study sites. This observation is subjective, of course, and no data are available that actually contrast the surface “compactability” of the three sites. So is there any hard evidence we can use to evaluate the impact of cattle on the microhabitat of *Pogogyne*?

As it turns out, cattle seriously trampled several plots (25-100% of the surface area) at the Dog Hollow playa in 2003 and 2005, but by coincidence they managed to miss all 20 plots in 2004. This provided an unplanned opportunity to compare the 2004 recruitment rates of plots that were disturbed by livestock in 2003 and those that were not. Admittedly, many factors may have played into the 2004 performance of the sample plots in addition to trampling, including 2003 plant density, the extent and timing of water levels on the playa, plot position,

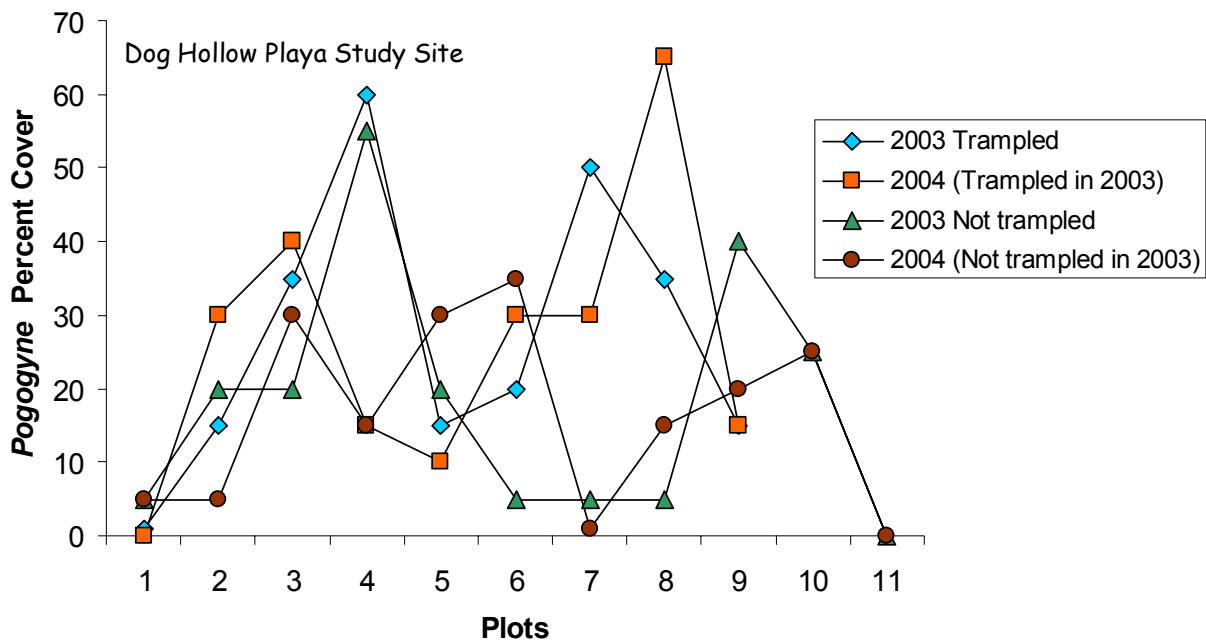


Fig. 29. Comparing the percent cover of trampled and untrampled *Pogogyne* plots on the Dog Hollow playa study site. Nine plots were trampled in 2003 and eleven plots were not (*Pogogyne* cover data from Figs. 20 and 21, recorded in July). There were no significant differences between the treatment means (one-way ANOVA, $P=0.3848$), indicating that soil disturbance by cattle did not influence overall recruitment the subsequent year for the same plots. Percent cover was estimated at 5% increments, so some data points overlap at the same x-y coordinates.

etc. But inasmuch as trampling is a serious (and controllable) perturbation it seemed worth a look. Interestingly, once the data were analyzed, there appeared to be little effect from trampling. Fig. 29 shows that not only was there no statistically significant difference between trampled and untrampled plots in 2003, there was no residual effect in 2004. While individual plot cover varied up or down, the overall mean differences in performance between years and treatments (measured by percent cover of *Pogogyne* in July) were not significant. For these plots, at least, being trampled in 2003 was not a precursor to poorer recruitment in 2004.

The data in Fig. 29 infer that *Pogogyne* at the Dog Hollow site is capable of withstanding moderate grazing within its habitat, and that perhaps the current grazing regime is not a serious threat to the species if the site is otherwise not disturbed. But clearly, a much broader study, taking into account a wider range of variables, would be necessary to effectively tease out the factors that govern reproduction and survival of *Pogogyne* plants on the playa relative to livestock use. And considering the habitat differences observed between the three Great Basin study sites, results from such a study at Dog Hollow would not necessarily be applicable to the populations at Bull Flat or Foley Lake RNA. The recommendation at this point would be to cautiously allow continued grazing at the Dog Hollow site, taking care to maintain the management status quo, while eliminating the heavy grazing at Foley Lake RNA which observations suggest is seriously degrading the site (not to mention being contrary to the RNA mission of BLM). The population structure at the Bull Flat site appears more vulnerable than Dog Hollow, and this site may also need to have livestock use curtailed, if possible. Additional study regarding the specific effects of grazing is required here as well.

Measuring Divergence Among Populations. Molecular systematics and genetic evaluations continue to make significant contributions towards clarifying the treatments and understanding the phylogeny of many plant groups, while morphological studies frequently form the pragmatic basis for classifications, and are necessary if the taxonomy being developed is to be put to practical use in the field or herbarium. Rarely does genetic or molecular research alone result in the description of new taxa, for example, and at least some phenotypic corroboration is considered essential to a robust classification scheme. Moreover, for unique plant populations to be protected under endangered species laws, they must actually be described and published as distinct taxa (see review in Mace, 2004), so morphologically-based taxonomic studies will continue to play an important role in conservation biology. Simple demonstration of genetic diversity is generally not enough for formal protection of plants under current legislation, unlike the situation with fish and wildlife.

Morphometric evaluation. The morphometric portion of the present study focused on key phenetic traits of (1) the three *Pogogyne floribunda* study populations from Oregon, (2) plants from the type locality for the species in California, and (3) populations of the (by all accounts) closely related *P. zizyphoroides* (using plants from the northern fringe of its range, in the Rogue Valley), to ascertain if measurable differences exist that might contribute to a taxonomic reassessment. The multivariate procedure Principal Components Analysis (PCA) was used to evaluate a selected group of quantitative and qualitative traits that were considered of potential taxonomic value. In this procedure, the investigator selects a range of characters for analysis, focusing on those believed important to the taxonomy of the group by earlier workers (in this case see Howell, 1931; Jokerst, 1992) as well as any important new traits that come to light during the course of preliminary review. Usually 15-20 characters are measured at a minimum, typically including reproductive as well as vegetative features. PCA is useful in studies attempting to distinguish taxonomic differences, because it avoids the need for preconceived assumptions about which populations are thought to represent which taxa. The procedure is good for sifting through dissimilarities between populations or species, based on a

suite of traits, even when the differences may not be readily apparent. Visit <http://ordination.okstate.edu/PCA.htm> for a review of the technique.

Statistically, PCA reduces the number of variables in the overall data set by forming linear combinations that explain most of the variability. That is, PCA is a type of multidimensional scaling (James and McCulloch, 1990) that reduces the dimensions of a set of variables by reconstructing them into uncorrelated combinations. The analysis combines the variables that account for the largest amount of variance to form the first principal component. The second principal component accounts for the next largest amount of variance, and so on, until the total sample variance is combined into component groups. Each successive component explains progressively smaller portions of the variance in the total sample. Often a very few components will account for the vast majority of the variance in an analysis, and these components are the ones used to plot the data. In general terms, the analysis is designed to identify those morphological traits most helpful in distinguishing potential taxonomic distinctions, and will group measured units as data points on a scatter plot. As applied in biology, plotted data points from PCA may represent groups or individual organisms, depending on the nature of the study and how the data is recorded. In the case of *Pogogyne*, individual plants from different populations were the units being evaluated.

Twenty-three morphological traits were used in the PCA (see caption for Fig. 30), with the results depicted on the following page. The graph in Fig. 30 reveals differences and similarities between the populations of *Pogogyne* sampled. Based on this data, the Dog Hollow population and *Pogogyne floribunda* plants from the type locality in California are essentially indistinguishable, while the Foley Lake RNA and Bull Flat populations are much more distinct. The data also suggests a relationship between the Foley Lake population and *P. zizyphoroides*. The first two principle components explained 79.5% of the variance in the data set, with the first three describing 96%. Characters that loaded heavily along the first axis that were the most useful in differentiating sampled plants included the length of the terminal inflorescence cluster, whether or not leaves persist in fruit, and the nature of the stems (i.e., erect versus lax and decumbent). Traits with potential taxonomic value along the second axis were corolla color (not surprising), corolla length, calyx length, the degree to which floral bracts are ciliated, how stout the stems are, and leaf base morphology (petioles decurrent and sharply angled versus more or less straight).

DNA sequencing. The DNA sequences also show specific differences between the four populations sampled (DNA was not extracted from type locality plants, but was taken from plants originating at the Dog Hollow playa, Foley Lake RNA, and Bull Flat sites, as well as from *P. zizyphoroides* plants that grew near Medford in the Rogue Valley – more detail is available in the Methods section). Based on the sequence data, the Foley Lake RNA plants as well as those from the Dog Hollow area appear closely related to *P. zizyphoroides*, but both show measurable differences, and are also different from one another. Mirroring Fig. 30, the Foley Lake population appears more closely related to *P. zizyphoroides*, although the difference is slight (i.e., Foley Lake plants differ from *P. zizyphoroides* by two nucleotides while those from Dog Hollow differ by three). Of the three differences between Dog Hollow and *P. zizyphoroides*, two are shared with Foley Lake. Plants from the more geographically distant Bull Flat site are the most unique among the samples, and differ from Dog Hollow plants, Foley Lake plants, and the Jackson County *P. zizyphoroides* population by 2, 3, and 6 nucleotides respectively, indicating the Bull Flat genotype has most likely been isolated from its congeners for a longer period of time.

So to summarize, the sequences show specific genetic differences between the four populations. While these differences alone cannot determine if the Great Basin populations

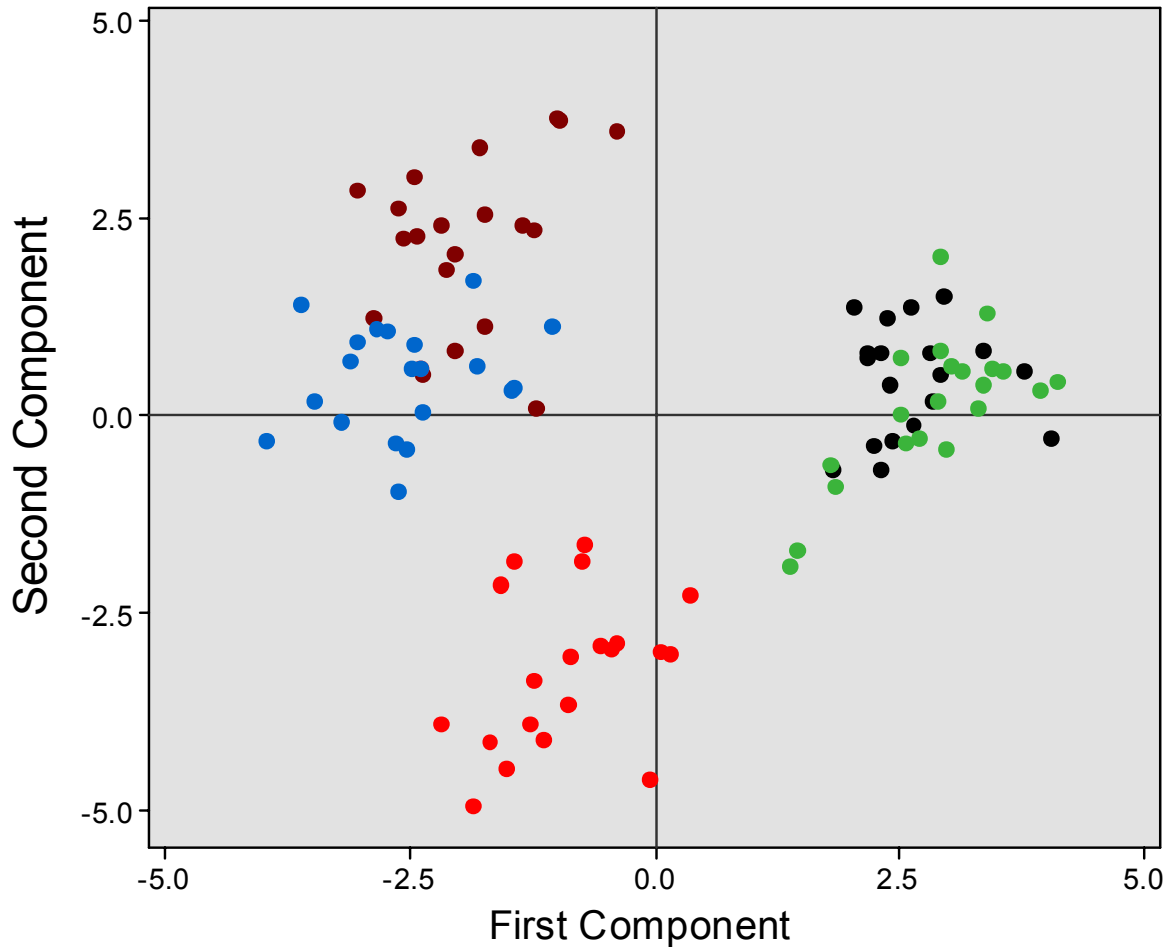


Fig. 30. Graphical results of the *Principal Components Analysis* (PCA) for *Pogogyne floribunda* and *P. zizyphoroides*. The green and black data points clustered on the right side of the graph represent plants from Dog Hollow (green) and the type locality (black). The cluster of red points (below) depict the Bull Flat population from Malheur County. In the upper left, the Foley Lake RNA plants are represented by the blue dots, while the brown data points are *Pogogyne zizyphoroides*. Dog Hollow playa plants could not be morphologically distinguished from plants collected at the type locality in California by this analysis. Bull Flat plants, the most isolated geographically, are also morphologically distinct. Based on the traits analyzed here, the pink-flowered Foley Lake RNA population is distinct from but evidently related to *P. zizyphoroides*. Traits used in the analysis were: (1) style length (mm); (2) % of the style length that is pubescent; (3) anthers exerted or not; (4) corolla limb color; (5) corolla length (mm); (6) ratio of lower corolla lobe length to upper lobe; (7) calyx length in flower (mm); (8) calyx length in fruit (mm); (9) total number of flowers produced by a plant after 16 weeks; (10) number of nutlets produced per flower; (11) stem architecture (branching at base only, or at upper nodes as well); (12) number of separate inflorescence tiers along main axis when in fruit; (13) number of inflorescence branches with multiple tiers; (14) length of terminal infructescence fruiting cluster (mm); (15) combined length of bottom three internodes; (16) % of their length the floral bracts are ciliate; (17) degree of leaf blade denticulation (none, < half blade length, > half blade length); (18) lower leaf blades persistent or not in fruit; (19) flowering stem “erectness” (lax and decumbent versus stiffly erect); (20) number of basal stem branches; (21) leaf base morphology (petiole straight or slightly bent versus petiole decurrent with a 90 degree bend); (22) mature stems greenish or deep red; (23) width of stem base when more than 75% in fruit (mm). Quantitative measurements (floral or leaf traits) were based on per plant means (n=3 per trait).

represent new taxa, they do show a marked delineation on a molecular level that is consistent with populations that have been isolated from each other for some time. Accordingly, the sequencing results thus far are probably best viewed as exploratory in nature. Although the sequence work does reveal genetic divergence among the sampled populations, the evidence for any taxonomic decision-making would be stronger if material from additional sites could be integrated into an expanded study. First and foremost, the lone *P. floribunda* population from Idaho (Fig. 1) needs to be added to both the molecular and morphometric analyses. It would also be helpful to include DNA from at or near the type locality of the species in Modoc County in the sequencing analyses. Beyond this, sequencing any other anomalous populations that come to light (see Jokerst, 1992), as well as at least one representative population from each of the five remaining species in the genus, would help place the deviations recorded among the Great Basin populations into context. In other words, is the level of divergence observed comparable with differences among other recognized taxa in the genus, or is it insignificant by comparison? This would be useful in making taxonomic interpretations. While this might sound daunting, it really isn't. The genus is small, and sequencing the additional species would not be particularly difficult.

Taxonomic overview. The populations of *Pogogyne* in the Great Basin clearly show differences that may be consistent with separate taxa, but as alluded to above, a broader evaluation is needed prior to any final decisions. Of the three study populations, plants from the Bull Flat site are more divergent at the molecular level, while those from Foley Lake are the most unique morphologically. The overall morphological disparity among the populations is depicted by the PCA graph (Fig. 30), primarily based on several character differences that are unique or nearly unique to each study location. But were the traits considered critical by Jokerst (1992) in his identification of *Pogogyne floribunda* as important as originally thought?

While some potentially key differences between the populations are absolute, others previously believed to be taxonomically diagnostic for the species as a whole may not be. Jokerst (1992) placed emphasis on corolla color in his separation of *Pogogyne floribunda* from *P. zizyphoroides*, with the former species encompassing the only white-flowered populations known for the genus. However, corolla pigmentation as a reliable separator breaks down if we include all the Oregon Great Basin populations with those from California in circumscribing *P. floribunda* (Fig. 31). Jokerst (1992) describes *P. floribunda* as having a white corolla with three purple dots on the lower lip, a character that was apparently consistently represented across the known range of the species at that time (i.e., the Modoc Plateau of northeastern California). Plants from nearby Oregon, at the Dog Hollow playa site, have since been shown to also have white corollas with purple to red speckles (though these are often more of a small smudge as opposed to three distinct spots). But the unspotted portion of the corolla limb is clearly white and not suffused with purple, and this essentially matches the original description by Jokerst (1992).

In contrast, corollas from Bull Flat plants are pure (almost ivory) white, and did not exhibit any purple coloration whatsoever. Those from the Foley Lake RNA site, meanwhile, are distinctly pink to pale purplish-lilac throughout (this would be unique in *P. floribunda*), and are reminiscent of *Pogogyne zizyphoroides* (Fig. 31). Other aspects of this population (see Fig. 32), i.e., the more flexuous stems, the upper node branching, and the continuously open inflorescence axes (as opposed to the ultimately congested stems in the Dog Hollow playa plants and those from Modoc County, see Fig. 33), are also suggestive of *P. zizyphoroides*, though there are important differences between the latter species and the Foley Lake plants as well (Fig. 30). The Bull Flat plants share some of these habit traits, by also having much less rigid stems, open inflorescence tiering, and more branching from the base.



Fig. 31. Corolla pigmentation for *Pogogyne* populations from the Oregon Great Basin. Clockwise from upper left: Bull Flat (Malheur County); Foley Lake RNA (Lake County); Dog Hollow Reservoir playa (Klamath County); and (for comparison) *Pogogyne zizyphoroides* from the Rogue Valley in Jackson County (southwest Oregon).



Fig. 32. *Pogogyne* plants (in early flower, ca. 20% in fruit) from the Foley Lake RNA population. Plants are characterized by pink to lilac corollas, open inflorescences, flexuous, \pm basally decumbent stems, and flowering branches commonly originating above the base. (Collected in mid-July)



Fig. 33. Type collection of *Pogogyne floribunda*, collected in Modoc County, California by James Jokerst in July, 1990. (On file at the New York Botanical Garden, Bronx, New York.)

Inflorescence architecture was the other primary attribute focused on by Jokerst (1992) as being highly diagnostic for *P. floribunda*. He stated that: “The growth habit...of the new *Pogogyne* (is) unique in the genus...typically branched at the base with few to many upright stems, each densely flowered throughout (i.e., flowers conceal the stem).” While the type collection clearly shows this feature (Fig. 33), field study shows it is a relatively plastic trait. Jokerst (1992) conceded that older plants collected in late summer may have bare lower stems, potentially due to partial burial by the Vertisol playa soils, abscission of older flowers, or rooting in soil crevices. However, many plants at the Dog Hollow site, even early in the season, displayed partially naked, more open inflorescence stems (Fig. 34). The verticillate floral arrangement does tighten up as plants age and set fruit, though, and stems are eventually more uniformly packed with flowers than the populations at Foley Lake RNA and Bull Flat (and much more so than *P. zizyphoroides*, as stated by Jokerst). The point here is to caution surveyors that traits that may seem critical in determining the identity of a species, based on an original description, are always subject to modified interpretation as more data are obtained. The Dog Hollow playa plants may differ a bit from the species account provided by Jokerst (1992), yet they are still clearly recognizable as typical *P. floribunda*.



Fig. 34. *Pogogyne floribunda* plant from the Dog Hollow Reservoir playa site, with the discontinuous inflorescence commonly seen on younger plants. Contrast this with the fully cloaked flowering stem (see Figs. 12 and 33) that characterizes fruiting plants, a trait shown to be taxonomically important by Jokerst (1992).

But does the evidence warrant taxonomic segregation for any of the other Great Basin *Pogogyne* populations examined? Very possibly, once additional sequencing information is available. The morphological, geographic, and ecological data tentatively support separation of the Foley Lake RNA population as a *unique endemic*, possibly as a new species or subspecies. Interestingly, if the designation is at the subspecific level, the question then becomes what *species* does the population represent, *P. floribunda* or *P. zizyphoroides*? Geographic distribution and ecological tolerance suggest the former, while morphology implicates the latter. The molecular data likewise support an affiliation with *P. zizyphoroides*. The white-flowered Bull Flat population is even more isolated genetically (not to mention geographically), and also has a unique suite of morphological traits – but is this level of differentiation for any of the populations (particularly the genetic aspect) taxonomically significant in the genus? That remains to be seen as we evaluate other populations (e.g., the Idaho site) and taxa. So as attractive as it may be to formerly describe one of more of these variants as a new species or subspecies, it is most

prudent to wait until a broader molecular evaluation of the genus can be completed, hopefully in the near future.

Conservation issues. Although the recommendation here is to wait on any formal taxonomic recognition, this does not invalidate the conclusion that the populations studied during this project are unique and worthy of strict conservation. The Dog Hollow playa population is biologically most comparable to the plants in California, and with them comprise a geographically and ecologically related cluster of several sites with potentially millions of plants overall in favorable years. Now millions may sound like a lot, but when you are considering these are all tightly bunched in a handful of potentially at-risk playas (see Haukos and Smith, 2003 for an overview of the problems facing these unusual habitats), management of the sites as a sensitive resource is clearly required. So even though the Dog Hollow playa plants do not appear to be taxonomically or evolutionarily unique, they nonetheless represent an important population of a rare and vulnerable species.

From a biodiversity standpoint, the sites at Bull Flat and Foley Lake RNA are even more critical. These populations are considerably smaller and less fecund than the one at Dog Hollow, and are arguably much more distinctive within the genus. Beyond flower color and other phenotypic traits, the molecular data indicate these plants have been isolated from other *Pogogyne* populations for a substantial length of time. This negates any potential argument that they are merely the result of recent immigration on, say, the feet of waterfowl who happened to be passing through, and are therefore no different than *Pogogyne* populations elsewhere. But how “old” are the particular genotypes that make up the Foley Lake RNA and Bull Flat populations? Of course, no molecular clock exists for *Pogogyne* evolution (this study represents the first attempt at examining DNA for the genus). And while estimating the time of divergence for a genetic line based on an assumption of substitution rate constancy is not wholly embraced (Muse, 2000), the availability of chloroplast gene sequences has been considered by others an “unprecedented opportunity” to evaluate the evolutionary history of seed plants (Clegg, 1993). Although it’s a rough guess, by using a nuclear molecular clock for dicots in general (Wolf et al., 1987), we can estimate that the Foley Lake line split from *P. zizyphoroides* between 600,000 and 1.3 million years ago, during the so-called ice ages of the Pleistocene. While even this broad timeframe is pretty speculative, we *can* say with confidence that the divergence of the Foley Lake plants certainly did not take place recently (i.e., within modern human history, for example). This argument is even more applicable to the Bull Flat plants, which have accumulated more nucleotide substitutions in their chloroplast gene sequences. Both Bull Flat and Foley Lake plants have proven to be unexpectedly divergent.

Taxonomic recognition of the Bull Flat or Foley Lake plants, followed by formal listing under the Endangered Species Act, would place immediate pressure on BLM with respect to managing and protecting the two sites. Rather than simply waiting, BLM has the chance to act now to improve local conditions for these populations, thereby potentially influencing the efficacy of future recovery planning. According to the BLM (see BLM Manual 1613), Research Natural Areas are places that contain important ecological and scientific values and are *managed for minimum human disturbance*. Unfortunately, *Pogogyne* habitat in the Foley Lake RNA has been subject to intense grazing, despite the status of the site as an RNA. The official web site for Foley Lake RNA (<http://www.fsl.orst.edu/rna/sites/foleylake.htm>) states that “*Livestock grazing in the RNA is being monitored to determine its effect on RNA values.*” Yet the main RNA web page for Oregon has the following statement: “*RNAs are managed to maintain the natural features for which they were established, and to maintain natural processes.*” The two actions are completely incongruous. You can’t allow heavy grazing (Fig. 28) in seasonal riparian areas and playas and expect to maintain natural ecological processes.

The effect on “RNA values” is clearly detrimental. Remedial action is called for, and can easily be implemented by BLM if it chooses to do so. By simply following existing Bureau guidelines for RNA and ACEC management protocol (under BLM policy, RNAs are concurrently designated as Areas of Critical Environmental Concern; Lou Whiteaker, pers. comm.), BLM can immediately protect this site without having to implement any land-use designation specific to *Pogogyne*.

The Bull Flat population exists in an area (the Owyhee Uplands) where pluvial lakes and playas are less common than elsewhere in the northern Great Basin (Vander Schaaf, 1996). There are two larger playa lakes situated on the plateau in the extreme southeast corner of Oregon: Lookout Lake and Bull Flat Lake, both of which are dominated by silver sagebrush. Neither has been rigorously inventoried for *Pogogyne*. There are also several smaller playas in the area that have not been surveyed with regards to plant communities or sensitive species, so there could potentially be additional *Pogogyne* populations existing in the area (and perhaps we should expect there are, if indeed the Bull Flat plants have been isolated for many thousands of years – it’s hard to imagine this one site is the only one out there, and botanists just happened to stumble on it). But even so, the limitation of playa habitat and the ubiquitous nature of grazing in this part of the state underscore the threats faced by sensitive wetland plant species in the *Artemisia* zone of southeast Oregon. Not enough is being done to further their conservation.

CONCLUSIONS AND RECOMMENDATIONS

This study was originally conceived as a two year monitoring project on BLM’s Klamath Falls Resource Area, focusing on the status of a single *Pogogyne floribunda* population. It eventually evolved into considerably more, and as a result we now have a much better understanding of the biology of the species, the genetic diversity (and potential taxonomic differences) among its Great Basin populations, and the conservation status of the genus in Oregon.

The plants studied have a more variable reproductive strategy than might have been assumed, based on floral morphology, with self-pollination not necessarily the exclusive means of reproducing. While outcrossing is probably infrequent, it is potentially important in maintaining and enhancing local genetic diversity, and may have played a role in the evolutionary diversification of populations. In good years, plants are abundant seed producers, replenishing the seed banks that are essential to the long-term survival of populations. Seed germination is curiously variable, and the species appears to “bet hedge” in the sense that some seeds are germinable when dispersed, while others are dormant. In dry years, the species may not appear at all, though it is important to recognize and protect the boundaries of populations and habitat even in poor years, to conserve the cryptic but critical seed banks. The species appears potentially susceptible to foliar and flower predation, though little evidence of this was actually recorded in the field over the course of the study. Predators that infest cultivated mint fields may be the greatest threat along these lines, though the likelihood of a shift by insect pests from *Mentha* to *Pogogyne* in nature appears remote, since mint farms and *Pogogyne* populations are not currently in close proximity. Plants proved easy to cultivate, and will grow and produce seed just as readily in a greenhouse potting mix as in native soil collected from the field. Ease of cultivation has important implications for long-term conservation planning.

Monitoring plot data showed that the populations are probably fairly consistent in terms of their distribution from year to year. This is not terribly surprising, considering they reappear from seed banks and have very defined habitat limits based on playa and channel margins. Cattle are common components of the ecosystems inhabited by the *Pogogyne* populations. The

evidence suggests that the dense population occurring on the Klamath Resource Area (Dog Hollow) is probably capable of withstanding modest grazing impacts, though specific and broader studies are needed to truly determine the effects of repeated grazing and trampling. The other two study sites on the Vale and Lakeview Districts (Bull Flat and Foley Lake RNA) also need explicit study regarding grazing effects, but their smaller size, much looser population structure, and exposure to heavier livestock concentrations imply that *Pogogyne* plants here likely face more serious threats from cattle than at Dog Hollow. The plants are probably not negatively impacted by competition with native annuals, and so far, exotic species are not a significant threat either, though continued trampling of the sites may change this dynamic if weeds are able to invade the playas as a result of the disturbance. Soil moisture is a critical factor governing the distribution and recruitment of *Pogogyne* plants – too much or too little can be a problem. Changes in hydrology that too quickly dry out *or* prolong the flooding of a playa can potentially be equally destructive.

A primary initial goal of the study was to determine if the Dog Hollow playa *Pogogyne floribunda* population was taxonomically comparable to the populations growing in nearby California, and it is. Ultimately of greater interest were the phenotypic and genetic differences exhibited by the more disjunct Bull Flat and Foley Lake RNA populations. Morphometric and chloroplast DNA data indicated that these populations are divergent from typical *P. floribunda*, and have been potentially separate from the Modoc Plateau *Pogogyne* group (including Dog Hollow) and the related species *P. zizyphoroides* for perhaps tens of thousands of years. While these populations may very well be worthy of formal taxonomic recognition, any decision along these lines awaits additional molecular surveys, to place the measured divergence into context within the genus. In the meantime, it is highly recommended that these vulnerable populations be rigorously protected by BLM on public lands, considering their emerging status as *unique genetic resources*.

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Photo credits: Fig. 6 (*Pogogyne clareana*), Dieter Wilken, Santa Barbara Botanic Garden (http://www.centerforplantconservation.org/ASP/CPC_ProfileImage.asp?FN=3552b); Figs. 15-17, Richard Worth, Oregon Department of Agriculture; and Fig. 31 (lower left), Melissa Carr, OSU. Other photos were taken by the author.

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