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16. ABSTRACT

In this study, we test the hypothesis that pollination processes decline in recreated vernal pool habitats by comparing the pollination of Blennosperma nanum nanum (Asteraceae)in a recreated and natural vernal pool habitat. The recreated site we used is the CALTRANS Davis interchange, an isolated habitat fragment, and the natural site is Jepson Prairie Preserve. The results of our two-year study indicate that pollination processes are markedly diminished at the Davis Interchange relative to Jepson Prairie Preserve. At the interchange site, insect visitation rates to B. n. nanum flower heads were at least an order of magnitude lower than those at Jepson, and insect visitor species richness was reduced by three-fold compared to the visitor species richness at Jepson. The seed set of B. n. nanum plants at the recreated site was consistently lower than the seed set of plants at Jepson. In addition, the results suggest that plants at the interchange site are pollen limited, whereas plants at Jepson are resource limited. Thus, our data imply that plants at the interchange have lower reproductive success than their counterparts at Jepson. We conclude that the recreated Davis Interchange is not ecologically similar to Jepson Prairie Preserve, and contend that vernal pool creations or mitigations in highway interchanges or similarly isolated habitats are unlikely to be successful.

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Vernal pool creation, habitat fragmentation, pollination, Blennosperma nanum nanum, Andrenid bees, Empidid flies, highway interchange

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**Fragmentation and recreation of vernal pool habitats:
are pollinators too few and far between?**

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CONVERSION FACTORS

English to Metric System (SI) of Measurement

<u>Quality</u>	<u>English Unit</u>	<u>Multiply By</u>	<u>To Get Metric Equivalent</u>
Length	inches (in) or (")	25.40 .02540	millimetres (mm) metres (m)
	feet (ft) or (')	.3048	metres (m)
	miles (mi)	1.609	kilometres (km)
Area	square inches (in ²)	6.432 x 10 ⁻⁴	square metres (m ²)
	square feet (ft ²)	.09290	square metres (m ²)
	acres	.4047	hectares (ha)
Volume	gallons (gal)	3.785	litre (l)
	cubic feet (ft ³)	.02832	cubic metres (m ³)
	cubic yards (yd ³)	.7646	cubic metres (m ³)
Volume/Time (Flow)	cubic feet per second (ft ³ /s)	28.317	litres per second (l/s)
	gallons per minute (gal/min)	.06309	litres per second (l/s)
Mass	pounds (lb)	.4536	kilograms (kg)
Velocity	miles per hour (mph)	.4470	metres per second (m/s)
	feet per second (fps)	.3048	metres per second (m/s)
Acceleration	feet per second squared (ft/s ²)	.3048	metres per second squared (m/s ²)
	acceleration due to force of gravity (G)	9.807	metres per second squared (m/s ²)
Density	(lb/ft ³)	16.02	kilograms per cubic metre (kg/m ³)
Force	pounds (lb)	4.448	newtons (N)
	kips (1000 lb)	4448	newtons (N)
Thermal Energy	British thermal unit (BTU)	1055	joules (J)
Mechanical Energy	foot-pounds (ft-lb)	1.356	joules (J)
	foot-kips (ft-k)	1356	joules (J)
Bending Moment or Torque	inch-pounds (in-lb)	.1130	newton-metres (Nm)
	foot-pounds (ft-lb)	1.356	newton-metres (Nm)
Pressure	pounds per square inch (psi)	6895	pascaIs (Pa)
	pounds per square foot (psf)	47.88	pascaIs (Pa)
Plane Angle	degrees (°)	0.0175	radians (rad)
Temperature	degrees fahrenheit (°F)	$\frac{^{\circ}\text{F} - 32}{1.8} = ^{\circ}\text{C}$	degrees celsius (°C)
Concentration	parts per million (ppm)	1	milligrams per kilogram (mg/kg)

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Introduction

The ultimate goal of vernal pool habitat recreation is to restore and/or recreate vernal pool communities that are indistinguishable from natural vernal pool communities. The achievement of this goal is quite controversial: some would argue that it is not possible, while others would claim the goal has already been reached. Attempts to compare the so called “functional values” (Ferren and Gervitz 1990) of natural and recreated habitats have been clouded in uncertainties over what to measure, how to measure it, and how to interpret subsequent differences. At present, there is no conclusive evidence that restored/recreated vernal pool habitats provide the functional or ecological values that are typical of natural vernal pool habitats (Ferren and Gervitz 1990). A further impediment to the resolution of this controversy is that relatively little is known about the basic ecology of most vernal pool organisms in natural vernal pool communities.

From a scientific perspective, much can be learned from the study of basic ecological processes in restored or recreated communities, whether or not they have been deemed “successful” (Cairns 1987). Moreover, carefully planned comparative studies of ecological phenomena in natural and restored/recreated communities not only provide ecological information about each respective community, but also, and more importantly, may indicate whether restored/recreated habitats are ecologically similar to natural habitats (Alexander 1992). The increasing number of vernal pool recreation projects over the last seven years (Ferren and Gervitz 1990) provides a source of novel research opportunities that is just beginning to be utilized. Our purpose here is to take advantage of these new opportunities to compare plant-pollinator interactions in a recreated and natural vernal pool community.

A priori, there are two reasons to expect a decline in pollination processes of recreated vernal pool habitats. Typically, recreated vernal pool sites are isolated habitat fragments located within a matrix of developed areas. Previous empirical studies indicate that plant-pollinator interactions decrease with increasing fragmentation of the habitat. Studies of hummingbird (Feinsinger et al. 1982) and insect pollinator-plant interactions (Spear 1987; Jennersten 1988) found fewer visitor species and a decrease in the number of visits per flower in “island” versus “mainland” populations of the same plants. Similar reductions were also found in the fruit set and seed set per flower. A second reason, independent from the first, is simply that many pollinator species are probably missing from recreated vernal pool communities. The reason for this is that vernal pool insect species are not usually mitigated for, and natural immigration by many potential pollinators becomes less likely as the distance from natural vernal pool habitats increases.

Consequently, the lack of potential pollinators in recreated habitats may be quite severe, due to the combined effects of fragmentation and lack of mitigation.

In this study, we test the hypothesis that pollination processes do not differ in recreated and natural vernal pool habitats by comparing the pollination of Blennosperma nanum nanum (Asteraceae) in a recreated and natural vernal pool habitat. We expect, however, that pollination processes decline in recreated vernal pool habitats because of the reasons stated above. The recreated site we used is the CALTRANS Davis Interchange (Chainey 1989; Dawson 1989; Ferren and Gervitz 1990), and the natural site is Jepson Prairie Preserve, approximately 25 km away from the recreated site. Our study, in an improvement over previous studies, provides a strong experimental test of the above hypothesis and also contributes basic and applied ecological knowledge, both of which have implications for the conservation of vernal pool habitats.

Background and Objectives

To test our hypothesis, we address the following objectives or questions: 1) Does the number of insect species visiting B. nanum nanum differ at the recreated versus natural site? 2) Do visitation rates to B. nanum nanum differ at the recreated than at the natural site? 3) Does the seed production of B. nanum nanum differ in the recreated site than in the natural site? 4) Is seed production of B. nanum nanum pollen-limited (Bierzuchudek 1981) at both sites, or only at the recreated site? Jepson Prairie Preserve provides a suitable comparison for the Caltrans site because pools in the interchange were originally planted with plant material taken from vernal pool habitat directly adjacent to Jepson.

We chose B. nanum nanum as our study organism for several reasons. It is a self-incompatible annual (Ornduff 1963) and therefore requires outcrossing by pollinators in order to produce seed. Secondly, more is known about the pollinators (Thorp 1969, 1976, 1990) and pollination ecology (Leong, unpubl. data) of this plant than many other locally occurring species. Flowers heads of B. nanum nanum are visited by generalist and specialist pollinators, and one of the most common visitors is a solitary bee, Andrena (Diandrena) blennospermatis Thorp. Females of this species collect pollen exclusively from B. nanum nanum flowers. Thirdly, these plants are relatively easy to grow from seed in a greenhouse; this enabled us to test our objectives more experimentally. Lastly, we chose B. nanum nanum because it is a vernal pool plant species that can exist in a range of hydrological regimes - in standing water to drying pool edges and hogwallows. Because of these characteristics, B. nanum nanum plants stand a better chance of surviving in recreated habitats than many other vernal pool plant species that require more stringent

hydrological regimes or particular kinds of pollinators. Therefore, we think that B. nanum nanum is a good “indicator species” for many of the flowering vernal pool plants.

Several aspects of the history of the Davis Interchange site are pertinent to our experimental comparisons. In 1986, as one of the first vernal pool creation projects in California, eight separate artificial pools were created on what was formerly annual grassland. The aim of this project, sponsored by CALTRANS, was to construct viable, self-sustaining vernal pools in highway intersections for aesthetic and ecological benefits. Standard vernal pool mitigation techniques were employed to create these pools and the interstitial areas in between (see Chainey 1989 and Ferren and Gervitz 1990 for details). This site was created six years prior to our experiments and thus serves as an example of a well established recreated vernal pool habitat. It is likely then, that our experiments measured the mature, rather than initial ecological properties of this site.

Although post-construction monitoring has occurred at the interchange site, no attempts were made to compare any aspect of the artificial pools to local natural vernal pools. Ferren and Gervitz (1990) conclude that it is difficult to assess the success of this interchange project because such data are unavailable. Despite the lack of suitable evidence, Chainey (1989) concluded that there was “moderately successful creation of artificial vernal pools” at the Davis Interchange. To date, this view has not been seriously challenged. Our experiments represent the first attempt to compare any ecological aspect of the interchange habitat to local natural vernal pool habitat. The results from our experiments may provide more than just information on pollination processes; they may also provide the knowledge needed to critically evaluate the success of the Davis Interchange project.

Conclusions and Recommendations

Based upon the results of this two year study, we conclude that pollination processes are markedly diminished at the Davis Interchange relative to Jepson Prairie Preserve. At the interchange site, insect visitation rates to B. nanum nanum flower heads were at least an order of magnitude lower than those at Jepson, and insect visitor species richness was reduced by three-fold compared to the visitor species richness at Jepson. The few insect visitor species that were present are generalist pollinators that are not closely associated with vernal pool habitats or plants. The seed set of B. nanum nanum plants at the recreated site was consistently lower than the seed set of plants at Jepson - by as much as 25%. In addition, the results from the pollen augmentation tests suggest that plants at the interchange site are pollen limited, whereas plants at Jepson are not pollen, but resource limited. Therefore, our data imply that B. nanum nanum plants at the interchange have lower reproductive success than their counterparts at Jepson, and it is likely that a lack of pollination accounts for this decrease.

Data from other studies, in conjunction with ours, imply that vernal pool plant populations are not self-sustaining at the recreated site. Post-construction monitoring data indicate that the percent cover of common vernal pool species has rapidly decreased, while the percent cover of non-vernal pool weedy species has dramatically increased. Observational evidence suggests that weedy species, through competition for light and other resources, decrease the germination success of B. nanum nanum and perhaps other species as well. The available evidence suggests that the population declines of vernal pool plant species at the recreated site may be due, in large part, to reductions in reproductive and germination success.

It is evident, from the results of our study alone, that the recreated, interchange site is not ecologically similar to Jepson Prairie Preserve, a local, natural vernal pool site. From the perspective of vernal pool plants, the recreated site clearly does not provide at least one "functional value", adequate pollination, and perhaps many others that are present in similar local, natural vernal pool habitats. Our data imply that the primary reason for the lack of adequate pollination is simply that pollinators are too few and far between at the recreated Davis Interchange.

We recommend that future vernal pool recreation attempts take steps to ensure the establishment of appropriate vernal pool pollinator assemblages. While this will not guarantee that the recreated habitat provides adequate pollination, the site, at least, will have a much better chance of doing so. Many pollinator species, however, are not as amenable to intersite transplantation and establishment as vernal pool plant species are, and in many

cases, establishment of self-sustaining pollinator populations may not be feasible. Additional research should be conducted on the feasibility of pollinator transplantations and on determining the colonization distances of pollinator species. A comparative field germination study should be conducted as well to follow up the results of this study. In general, we recommend that vernal pool recreation attempts direct more efforts towards the scientific monitoring of ecological processes in appropriately paired recreated and natural vernal pool sites. A firm understanding of the ecological processes in natural and recreated vernal pool habitats is needed to replace the existing “pool” of inconclusive data. Only then will it be possible to make any substantive progress in the vernal pool creation/mitigation debate.

Implementation

This study may be utilized to understand better the long term effects of vernal pool recreations and specifically, the effects of the recreation process at the Davis Interchange. It is clear from our results that vernal pool creations or mitigations in highway interchanges or similarly isolated habitats are unlikely to be successful. At the Davis Interchange, vernal pool organisms and their ecological interactions are in double jeopardy because of the detrimental effects of habitat fragmentation and vernal pool recreation. Moreover, because the vernal pool recreation does not include active management of invasive biota, any “functional values” of this recreated ecosystem are likely to deteriorate further. Changes in the implementation of the vernal pool creation process may be to no avail if such sites are isolated habitat fragments. In general, our results may help others to assess the desirability and effectiveness of vernal pool creations as mitigation tools and may be useful to those concerned with issues of habitat fragmentation and its consequences for vernal pool ecosystems.

Methods

We compared the pollination success of B. nanum nanum at Jepson Prairie Preserve, 12 miles south of Dixon, Solano Co., California, and at the Davis Interchange, a recreated vernal pool site at the interchange of Interstate 80 and Highway 113, Davis, Solano Co., California. The former contains extensive, natural vernal pool habitat while the latter is an isolated, recreated vernal pool fragment or “island”. The interchange site was recreated for experimental purposes, rather than for a specific mitigation. For further details of the construction and history of the recreated interchange site, see Chainey (1989) and Dawson (1989). Jepson Prairie Preserve covers approximately 800 ha, while the interchange site covers only 0.4 ha. The two sites are approximately 25 km apart. Currently, no populations of B. nanum nanum occur within the interchange site, but populations may have existed there at an earlier time. In contrast, within Jepson Prairie Preserve, extensive populations of B. nanum nanum occur. At both sites, we conducted visitation and seed set experiments over two consecutive years, during March - April 1992 and 1993. Because the experimental protocols differed between years, we discuss the experiments from each year separately.

1992 Study. Throughout the natural flowering season of B. nanum nanum at Jepson, we collected visitation and seed set data at both sites. The data were collected from potted arrays of greenhouse grown B. nanum nanum placed at both sites in early March and left in the field until mid-April. At Jepson, we placed arrays in two transects (A and B) at various distances from a natural, but isolated, B. nanum nanum patch as well as in the patch itself (Figure 1). Arrays in transect A contained 26 plants and arrays in transect B contained 14 plants. For purposes of this study, we group arrays as either patch or non-patch arrays, and assume that data from the patch arrays represents estimates of typical levels of B. nanum nanum pollination at Jepson. At the recreated, interchange site, two arrays of 15-16 plants each were placed near two artificial pools approximately 20 m apart. We refer to each array as a plot in subsequent analyses.

To quantify pollinator visitation rates to B. nanum nanum, we made observations on an artificial array of 40 cut flowers placed adjacent to each plot. By using a standard flower array, we could control for differences in flower densities among plots. We observed pollinator visitation to an array during 8 - 12 minute periods, with repeated observations on plots as subsamples ($n = 14 - 17$). Observations were made throughout early March to mid-April during the morning and early afternoon of non-rainy days, when pollinators are most active. We counted only those visits in which the insect's mouthparts contacted the disk or ray florets of the flower head. Visitation rates were not correlated

with measurements of ambient air temperature or date. The species richness of B. nanum nanum visitors at both sites was obtained by identifying insect visitors in the field and from field collections. We identified B. nanum nanum insect visitors to the lowest taxonomic level that was possible during field observations.

To determine the seed production of B. nanum nanum at both sites, we compared the seed set (seed to ovule ratio) of plants in the patch plots at Jepson vs. the seed set of plants in the plots at the recreated site. We used the patch plot data in the site comparison because it is an estimate of seed set of a naturally occurring population (patch) at Jepson. In fact, the results from a similar experiment indicated that the seed set of plants in patch vs. nonpatch plots did not differ (Leong, unpubl. data); therefore, the choice of plots upon which the comparison is based does not change the seed set estimate for Jepson. We based the seed set analysis on mean seed set per plant, where the seed set of all flower heads harvested from a plant was averaged. At Jepson, the average number of flower heads per plant was 4.3 ± 2 (Transect A), and 4.6 ± 3 (Transect B). At the interchange site, the average number was 5.4 ± 5 . We included only mature, fully developed seeds in our seed counts.

We tested for pollen or pollinator-limitation of maternal reproduction in B. nanum nanum by comparing the seed set (seed to ovule ratio) per flower of two groups: flower heads that were naturally pollinated and those that were naturally pollinated and augmented with hand pollinations. Although comparing the seed set of entire plants subjected to the above treatments would be the optimal test of pollen limitation, it was not possible due to time and logistical constraints. However, comparison of seed set from individual flower heads can suggest possible pollen limitation. We hand pollinated 12-13 flower heads in each plot at both sites (Transect A only, at Jepson) during March 19-21. Recipient flower heads were hand-pollinated on two consecutive days, with two pollen donors each day. We added pollen to flower heads by rubbing the disk florets of the pollen donor against the ray and peripheral disk florets of the recipient flower head. This procedure is effective (Leong, unpubl. data) because most of the disk florets are exclusively staminate, while the ray and a few of the peripheral disk florets are pistillate only. Seeds were harvested and counted and seed set per flower was compared between augmented and naturally pollinated flowers open simultaneously.

1993 Study. We conducted experiments during March 4 - 17 at both sites, during the peak of the flowering season of B. nanum nanum. Within this period, we repeated one experiment twice, but used independent samples in each repetition. This experiment tested for site differences in visitation, seed set, and possible pollen limitation of B. nanum nanum. As before, we used potted arrays (plots) of greenhouse grown B. nanum nanum

placed at both sites, except we did not leave plants in the field over the course of the experiment. Instead, each morning, plants were moved from a common greenhouse into the field and back again in the late afternoon in order to further control for environmental site effects. This transportation did not affect the pollination regime of the plants because B. nanum nanum flowers close in the late afternoon and do not open until nine to ten in the morning. Each experiment lasted about a week: plants were placed out in the field for one or two days to acclimate, and then visitation and seed set data were collected over the next four or five days. Immediately after the end of the first experiment, we rerandomized the same plants and placed them in the field the next day to start the second experiment.

The experimental layout of the plots in each site differed from the year before. Within an approximate area of 85 m by 25 m in each site, we placed seven plots of sixteen potted plants per experiment. These areas encompass the areas used in last year's study. We used a stratified random sampling method to pick the locations of the seven plots within each site, in each experiment. Initially, we delineated areas of suitable B. nanum nanum microhabitat within the site area, and then we randomly chose locations for the plots among and within these suitable microhabitats. At Jepson, we followed a further sampling restriction in that we avoided placing plots any closer than 1 m from existing natural B. nanum nanum patches because there is some evidence that insect visitation to plots closer than 1 m from a patch shows an exponential increase (Leong, unpubl. data).

We quantified visitation rates by observing insect visitors to flowers of the potted plants within the plots. To control for a floral density effect, we recorded the number of open flowers per plot during observations, but found that insect visitation was not correlated with the number of open flowers in a plot. We observed each plot for 20 minutes, once per experiment. The species richness of B. nanum nanum visitors at both sites was obtained as before. Voucher specimens of B. nanum nanum visitors from both years are deposited in the Bohart Museum, Department of Entomology, University of California, Davis.

We determined the seed set of B. nanum nanum at both sites as before, except that due to a different sampling regime, seed set analyses were based upon a single flower head per plant. For each experiment, we chose twelve of the sixteen plants in each plot, one flower head per plant, on which to measure seed set. Plants that had flower heads at a similar stage of maturation and whose stigmata were receptive were selected. Six plants were controls where the flower heads were naturally pollinated, and six plants were the treatment group where the flower heads were naturally pollinated and augmented with pollen. Because of time constraints, we hand-pollinated flower heads on one day only, with two pollen donors. We compared the seed set of the control and treatment flower

heads to test for possible pollen limitation. Plants were continually brought out to their respective sites until the flower heads sampled matured to the point that the heads had permanently closed. After both experiments, plants were maintained in a common screenhouse while we harvested the matured seed heads from both experiments.

In the statistical analyses, we considered a plot to be the experimental unit in the comparison of visitation and seed set between sites. We used parametric analyses when the data approximated the required assumptions; otherwise, we used nonparametric analyses. To analyze seed set differences between sites, we used ANOVA (Model III) in both years. For the 1992 data, we used a nested design, with plot nested within site. For the 1993 data, we used a split plot design, with plot nested within site, site as the whole plot factor, and pollination treatment as the subplot factor. Missing data were ignored because the number of missing samples were relatively few.

Results

Insect Visitation Rates

In both years, plots of B. nanum nanum at Jepson were visited at a significantly higher rate than those at the interchange site. In 1992, the mean visitation rate to arrays at Jepson inside the B. nanum nanum patch was two orders of magnitude greater (Kruskal-Wallis H; $p < .05$; $n=13$) than the mean visitation rate to arrays at the recreated site (Figure 2A). However, although the mean visitation rate to the nonpatch arrays at Jepson was an order of magnitude greater than the mean visitation rate to arrays at the interchange site, these differences are not statistically significant (nonparametric Tukey type test, see Zar (1984)). For the 1992 statistical comparisons, the mean visitation rate of each array was entered as an independent observation. In both 1993 experiments, the mean visitation rate to plots at Jepson was an order of magnitude greater than the mean visitation rate to those at the interchange site (Figure 2B). Except in this case, the differences in mean visitation rates were statistically significant (Mann-Whitney U; $p < .01$; $n=14$; both experiments). The number of flower heads open per plot during visitation observations did not significantly differ between sites in both 1993 experiments (Mann-Whitney U; $p > .3$; $n=14$). It is likely that the nonsignificant difference between the mean visitation rate to nonpatch Jepson and interchange arrays in 1992 is a consequence of low statistical power due to small sample sizes. Therefore, this nonsignificant site difference is probably not biologically meaningful. The fact that the same comparison repeated twice in 1993 yielded significant site differences in mean visitation rate supports this view. For both sites, the mean visitation rates in the later experiment (B) were higher (Fig.2B).

Species Richness of B. nanum nanum Visitors

There was a greater number of insect species visiting B. nanum nanum at Jepson than at the recreated "island" site over both years. In 1992, we estimate from our observations that at least 16 insect species visited B. nanum nanum at Jepson whereas only 5 species visited B. nanum nanum at the recreated "island" site (Table 1). We identified insect visitors to the family or generic level and used morphological differences between individuals to discriminate species if we could not identify the individual. Although bees and flies were present at both sites, the specialist solitary bees associated with vernal pool habitats (Thorp 1969, 1976, 1990) occurred only at Jepson. The bees and flies that were present at the interchange site are generalist flower visitors that tend to occur in many

different habitats (Powell and Hogue 1979). Therefore, not only was there a three-fold reduction in the species richness of B. nanum nanum visitors at the interchange site, the kinds of floral visitors that occurred there are not closely associated with vernal pool habitats. Even though these are very conservative estimates of visitor species richness, they indicate that the potential pollinator pool at the “island” site is quite limited.

In 1993, a greater number of insect species visited B. nanum nanum at Jepson than at the recreated “island” site, but the overall estimate of species richness at both sites is lower than in 1992. We estimate that at least 6 insect species visited B. nanum nanum at Jepson whereas only 2 species visited B. nanum nanum at the recreated “island” site in experiment A (Table 2). In experiment B, at least 7 insect species visited B. nanum nanum at Jepson whereas only 1 species visited B. nanum nanum at the recreated site (Table 2). Again, specialist solitary bees were present only at Jepson.

The year-to-year differences in visitor species richness within sites are most likely due to seasonal and spatial differences in the experimental design. In 1992, the experiment lasted the entire flowering season, so it is not surprising that we observed a greater number of insect species. The spatial design of the experiments differed greatly between the two years, and in particular, the proximity of the plots to natural patches of B. nanum nanum. Data from a similar experiment indicate that plots of B. nanum nanum plants placed in or near a natural plant patch are visited by a greater number of insect species than those farther away (Leong, unpubl. data). The data indicate that specialist solitary bees, including A. blennospermatis, tend to visit flowers within natural patches almost exclusively; visitation decreased rapidly as distance from a patch increased. Thus, it is likely that the presence of plots within natural patches in 1992, and the absence of the same in 1993, accounts, in large part, for the overall decrease in visitor species richness at Jepson in 1993.

Seed Set

The B. nanum nanum plants at Jepson Prairie Preserve consistently produced significantly higher seed set than their counterparts at the recreated site. In 1992 (Table 3A), the site effect was significant, despite very low sample sizes. The nested effect of plot within site did not account for a significant portion of the overall variation in seed set. At the interchange site, B. nanum nanum seed set, on average, was 80.9% of the mean B. nanum nanum seed set at Jepson (Figure 3). Similarly, in both 1993 experiments, the seed set of plants at Jepson was significantly greater than at the interchange site (Tables 3B and 3C), even though the mean seed set at Jepson decreased in the second experiment (Figure 3). The mean seed set at the recreated site was 74.1% of the mean seed set at Jepson in

experiment A; for experiment B, the mean seed set at the recreated site was 89.0% of the mean seed set at Jepson. In addition, there was a strong effect of plot within site in experiment A (Table 3B), but no significant effect of plot within site in experiment B (Table 3C).

It is likely that the decrease in mean seed set during the second experiment at Jepson is due to a somewhat premature end to the field component of this experiment. Due to bad weather, we were not able to put the plots out in the field during the last scheduled day of the experiment. Consequently, some of the flower heads that were still open may have missed opportunities for pollination. We think that this period of missed opportunity had a proportionately greater effect on the Jepson plots because visitation to flower heads was much higher at this site.

Potential Pollen Limitation

Data from the 1992 pollen augmentation tests at both sites suggest that B. nanum nanum plants at Jepson Prairie Preserve are not pollen limited, whereas plants at the recreated site are pollen limited. The seed set per flower of open pollinated flowers was significantly less than the seed set per flower of augmented flowers at the interchange site (Mann-Whitney U; $p < .02$) (Figure 4A). In contrast, at Jepson, the seed set per flower of open pollinated flowers was not significantly different from those of augmented flowers in all plots tested (Mann-Whitney U; $p > .2$; all plots) (Figure 4B). The results from Jepson are consistent with the results of a 1991 pollen limitation test on whole plants (Leong, unpubl. data) that found that B. nanum nanum plants were resource, rather than pollen limited.

While the results suggest that B. nanum nanum plants at the recreated site were pollen limited, we caution that the test for pollen limitation that we employed was not the most definitive one (e.g. Horvitz and Schemske 1988; Zimmerman and Pyke 1988; Johnston 1991). A more rigorous test would compare whole plants subjected to the above treatments. However, results from the 1992 site comparison further support the interpretation of pollen limited seed set at the recreated site. At this site, the mean seed set of naturally pollinated plants over the entire flowering season (Figure 3) was approximately equal to the mean seed set per flower head of control heads in the pollen augmentation test (Figure 4A). This suggests that the difference found in seed set between open and augmented flower heads is representative of differences on a whole plant level.

In 1993, results from pollen augmentations suggest that there was a trend towards pollen limitation at the recreated site, but the treatment effects were not quite statistically

significant in both experiments (Tables 3B and 3C). Regardless of site, the mean seed set of augmented flower heads was higher than that of control heads (Figure 5A), and most of this difference was accounted for by differences between treatment and control heads at the interchange site (Figure 5B). In both experiments, there was very little difference between the mean seed set of open vs. augmented flower heads at Jepson. No site by treatment interaction effects were evident in either experiment (Tables 3B and 3C), because the mean response to pollen augmentations at each site was not greatly different. We think that the difference in response to the pollen augmentations between the two years is due to the slightly different method of hand pollination that we used in 1993. We added pollen to flower heads on one day only, whereas in 1992, we added pollen on two consecutive days. These results suggest that the one day method of hand pollination may not be as effective as the two day method. Because of a less effective method of hand pollination, our ability to detect a difference in seed set undoubtedly decreased. Therefore, we suspect that the nonsignificant treatment effect was due to a decrease in experimental accuracy, rather than to a true lack of response to pollen augmentations.

Discussion

The results of this study clearly indicate that the pollination success of B. nanum plants differs between the natural and recreated vernal pool sites. Plants at the fragmented and isolated, recreated vernal pool site consistently exhibited a reduction in several aspects of pollination when compared to B. nanum nanum plants at Jepson Prairie Preserve. At the Davis Interchange, insect visitation rate, visitor species richness and seed set were significantly less than at Jepson; in addition, the data suggest that plants were pollen-limited at the recreated site, but resource limited at Jepson (Leong, unpubl. data). Our findings are similar to the results of other studies that compared pollination in island- and mainland-like habitats, with one exception (Ellis and Mills 1991). Most studies found evidence of a reduction in floral visitation (Feinsinger et al. 1982; Jennersten 1988) and seed set (Linhart and Feinsinger 1980; Spears 1987; Jennersten 1988) of plants on isolated island-like habitats. Data from a few studies also suggest that plants in isolated, island-like habitats are pollen limited (Spears 1987; Jennersten 1988; Worthen and Stiles 1988), whereas their mainland counterparts are not. On a smaller scale of floral patches, Sih and Baltus (1988) also found that fruit set, and visitation by some kinds of insects, decreased in smaller patches of catnip. In contrast, Ellis and Mills (1991) found that variation in seed set and insect visitation of Pogogyne abramsii, an endangered vernal pool species, was not attributable to either habitat size or the reconstructed status of the habitat.

The above comparison with earlier studies suggests that our results may reflect a fragmentation or site effect, but perhaps not a treatment effect (natural vs. recreated status). Although we found consistent differences in several aspects of pollination between the two sites, it could be argued that such differences merely represent site rather than treatment effects because our experiments have no replication at this level. We argue, however, that site effects are an inseparable part of the recreation treatment itself. A true attempt to recreate a vernal pool habitat similar to a natural source habitat includes an obligation to recreate the local site conditions of the source habitat. Therefore, the recreation treatment is comprised of a vernal pool creation effect plus an effect of underlying site differences, in which the former attempts to ameliorate for the latter. In this view, the net recreation treatment effect is, paradoxically, both a cause and a consequence of differences between the source and recreated site. Consequently, once the recreation treatment has been effected, subsequent site differences no longer represent only differences between sites. It is likely then, that the pollination differences we found are due to the entwined and inseparable effects of treatment and site.

The consistent differences in B. nanum nanum pollination between Jepson and the interchange site indicate that these differences are not artifacts or random occurrences; on the contrary, they reflect a real ecological dissimilarity between the two sites. Several aspects of our experiments support this contention. At the recreated site, there were consistent decreases in seed set, insect visitation rate, and visitor species richness within and between flowering seasons. Even more remarkable is the fact that these differences were maintained over quite dissimilar rainfall regimes: drought conditions in 1992, and more than an average amount of rainfall in 1993. The average seed set of plants at the recreated site remained almost identical through all three experiments (Figure 3), suggesting that seed production at this site is consistently depressed relative to the natural site. Furthermore, the experimental protocols we employed make it highly unlikely that factors other than pollination differences between the sites influenced the seed set of plants. This is especially true in 1993, when plants were in a common greenhouse except when flower heads were open. In this regard, our study is more rigorous than previous studies because we experimentally controlled for pre- and post-pollination environmental differences.

Differences in floral visitation between the two sites have several important ecological implications for the pollination of B. nanum nanum plants at the recreated site. The assemblage of floral visitors at the interchange site is markedly dissimilar to those found at Jepson (Tables 1 and 2). This implies that the average quality of a floral visit (the amount of pollen removed and/or deposited per visit), also differs between the sites because insect visitors differ in their ability to remove and deposit pollen (Schemske and Horvitz 1984; Herrera 1987; Wilson and Thomson 1991). Thus, it is probable that plants at the recreated site have altered patterns of pollen flow relative to plants at Jepson. The decrease in visitation rate and visitor species richness at the recreated site suggests that seed production might be pollen limited (Bierzychudek 1981), and indeed, that is confirmed by the results of our pollen augmentation tests. In addition, reduced visitation rates in conjunction with the presence of few potential pollinators may indicate that plants are competing for pollinators at the interchange site. At this site, there is a strong potential for competition among plants for pollinators (Rathcke 1983; Waser 1983; Feinsinger 1987) because numerous weedy species co-occur and flower simultaneously with the relatively few vernal pool plant species.

The consistent and sizeable reduction in seed set (10-25%) of B. nanum nanum plants at the recreated site relative to those at Jepson indicates that plants have a lower reproductive success at the interchange than at Jepson. The lack of pollinators and thus pollination is the most probable cause of this reduction in reproductive success. Moreover, we suspect that the germination success of seeds is very low at the interchange as compared

to Jepson. In 1993, there were many more volunteers within the areas of our 1992 non-patch plots at Jepson than within the areas of our plots at the recreated site (Leong, pers. observ.). While we cannot be absolutely certain, it is highly likely that these volunteers grew from seeds produced by the plants in our plots because no other B. nanum nanum plants were nearby. The likely mechanism for lowered germination success at the interchange is the presence of a thick cover of weedy species that reduces the amount of light and resources needed for germination of B. nanum nanum seeds. A lowered reproductive output, compounded by a lower germination success, indicates that plants are clearly at a disadvantage in the recreated vernal pool habitat. It is possible that over a number of years, this trend could result in significant decreases in population size.

Three years of percent cover data of plants in the eight artificial pools within the interchange site suggest that decreases in the population size of most vernal pool species have already occurred (Dawson 1989). These data indicate that between 1987-1989, the percent cover of common vernal pool species (i.e., species of Navarretia, Eryngium, Lasthenia, Downingia, Plagiobothrys and Psilocarpus) rapidly decreased, while the percent cover of non-vernal pool, weedy species (Hordeum leporinum, Trifolium sp., Centaurea solstitialis, Avena fatua, Lolium perenne, and Vicia vilosa) dramatically increased. By 1989, these weedy species were the dominant plant species in seven of the eight pools and their percent cover within plots in the pools ranged from 20-70%. It is uncertain whether these vernal pool species also suffered a reduction in reproductive success, as we found for B. nanum nanum plants. The results of our experiments with B. nanum nanum do suggest, however, a plausible mechanism for their decline. The simultaneous and rapid invasion by weedy species further suggests that a decrease in germination success, brought about by competition, may have played a role in these population declines.

The combined results from our experiments on B. nanum nanum, plus the previous monitoring of percent cover, strongly imply that vernal pool plant populations are not self-sustaining at the recreated site. Available evidence indicates that the diminishment of pollination processes and perhaps a reduction in germination success accounts in some degree, for this lack of sustainability. From the perspective of vernal pool plants, the recreated site clearly does not provide at least one "functional value," adequate pollination, and perhaps many others that are otherwise present in similar local, natural vernal pool habitats. We suspect that the weedy species will eventually outcompete most of the vernal pool plant species at the interchange site, unless active management steps are taken.

Some may argue that we have not employed appropriate "performance criteria" (Ferren and Gervitz 1990) in our experimental comparisons. At present, there is little agreement, either in academic or regulatory circles, as to what constitutes a successful

vernal pool recreation. It may be argued that we have made an arbitrary comparison and that using only one local natural habitat as a comparison is of limited worth. We believe that Jepson Prairie Preserve is the best and only possible choice for the interchange comparison for two reasons. Besides being the best local example of relatively undisturbed vernal pool habitat, it is the closest natural habitat to one of the original vernal pool source sites (Alexander 1992). Other natural sites that are more distant would differ too much in their local properties to be of use in the interchange comparison. There can be no argument, however, in interpreting the "performance differences" indicated by our results. At the recreated site, B. nanum nanum visitation rates were one to two orders of magnitude lower, visitor species richness decreased by two thirds, and seed set was consistently lower, by as much as 25%. With differences as blatant as these, we must disagree with the previous conclusions of "moderately successful creation of artificial vernal pools" at the interchange site (Chainey 1989).

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Table 1. Insect visitors of B. nanum nanum plots in 1992. Numbers in parentheses refer to the number of species within each taxon.

Jepson Prairie Preserve	Interchange Site
Hymenoptera	Hymenoptera
Andrenidae	Halictidae
<u>A. (Diandrena) blennospermatis</u>	<u>Halictus</u> sp. (1)
<u>A. (Hersperandrena) limnanthis</u>	<u>Dialictus</u> sp. (1)
<u>Andrena</u> spp. (3)	Apidae
Unknown solitary bee (1)	<u>Apis mellifera</u>
Diptera	Diptera
Empididae	Empididae
<u>Rhamphomyia</u> spp. (2)	<u>Rhamphomyia</u> sp (1)
Syrphidae (2)	Syrphidae (1)
Calliphoridae (1)	
Anthomyiidae	
<u>Scatophaga stercoraria</u>	
Miscellaneous small flies (4)	

Table 2. Insect visitors of *B. nanum nanum* plots 1993. Numbers in parentheses refer to the number of species within each taxon.

Jepson Prairie Preserve	Interchange Site
Experiment A	Experiment A
Hymenoptera	Hymenoptera
Andrenidae	Unknown small wasp (1)
<u>Andrena</u> spp. (2)	
Unknown small wasp (1)	
Diptera	Diptera
Empididae	Syrphidae (1)
<u>Rhamphomyia</u> spp. (3)	
Experiment B	Experiment B
Hymenoptera	Diptera
Andrenidae	Syrphidae (1)
<u>Andrena</u> spp. (3)	
Diptera	
Empididae	
<u>Rhamphomyia</u> spp. (3)	
Rhagionidae (1)	

Table 3A. ANOVA summary table of the 1992 seed set comparison between sites. The dependent variable is mean % seed set per plant.

Source	d.f.	Sum of Squares	Mean Square	F
Site	1	1846.4	1846.4	17.5*
Plot(Site)	2	211.4	105.7	0.65
Residual	65	15789.0	242.9	

Table 3B. ANOVA summary table of 1993 experiment A, seed set comparison. The dependent variable is % seed set /flower head.

Source	d.f.	Sum of Squares	Mean Square	F
Site	1	8752.6	8752.6	9.7**
Plot(Site)	12	10803.6	900.3	4.3***
Treatment	1	609.4	609.4	2.9 ^a
Treatment*Site	1	81.6	81.6	.39
Residual	147	30487.0	207.4	

Table 3C. ANOVA summary table of 1993 experiment B, seed set comparison. The dependent variable is % seed set /flower head.

Source	d.f.	Sum of Squares	Mean Square	F
Site	1	1090.3	1090.3	5.5*
Plot(Site)	12	2355.1	196.3	.79
Treatment	1	743.6	743.6	3.0 ^a
Treatment*Site	1	547.1	547.1	2.2
Residual	148	36970.9	249.8	

* $p < .05$ ** $p < .01$ *** $p < .005$ ^a $.09 > p > .05$

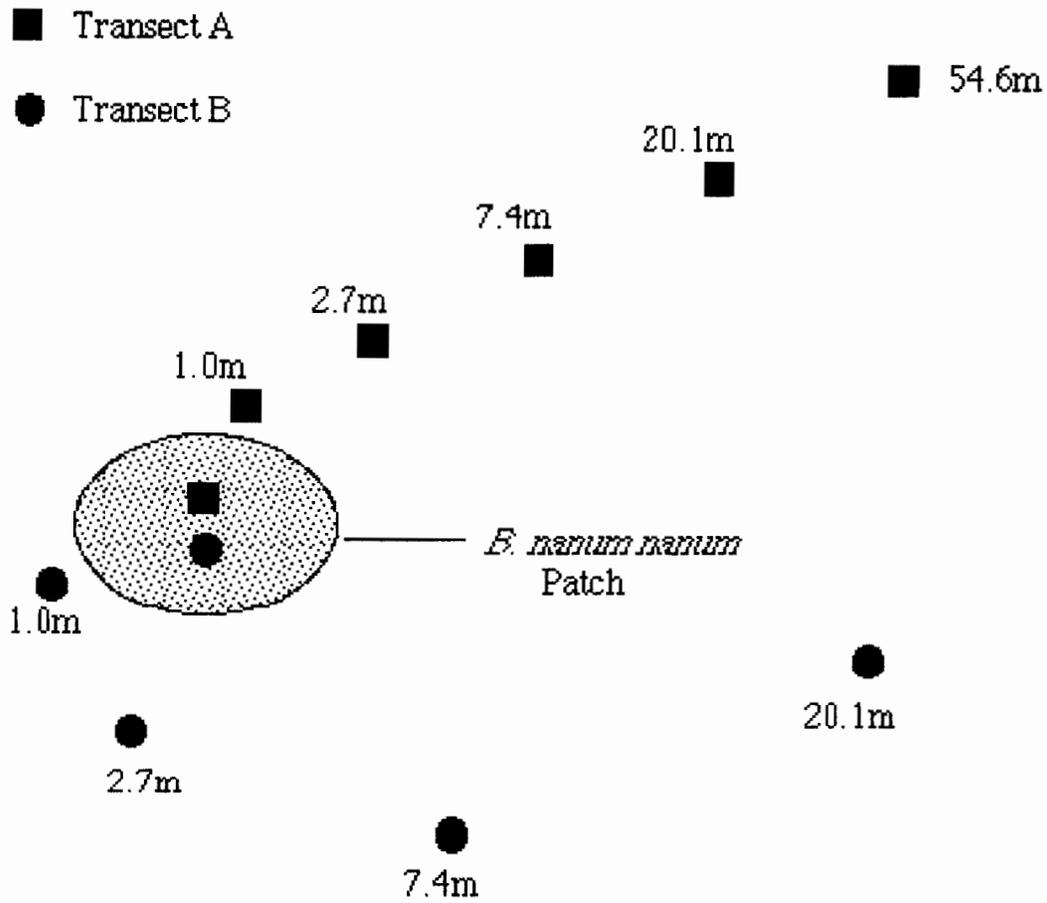


Figure1. Experimental layout of *B. nanum nanum* plants at Jepson 1992. Each square or circle represents an array of potted plants. Distances indicated are distances from the edge of the patch.

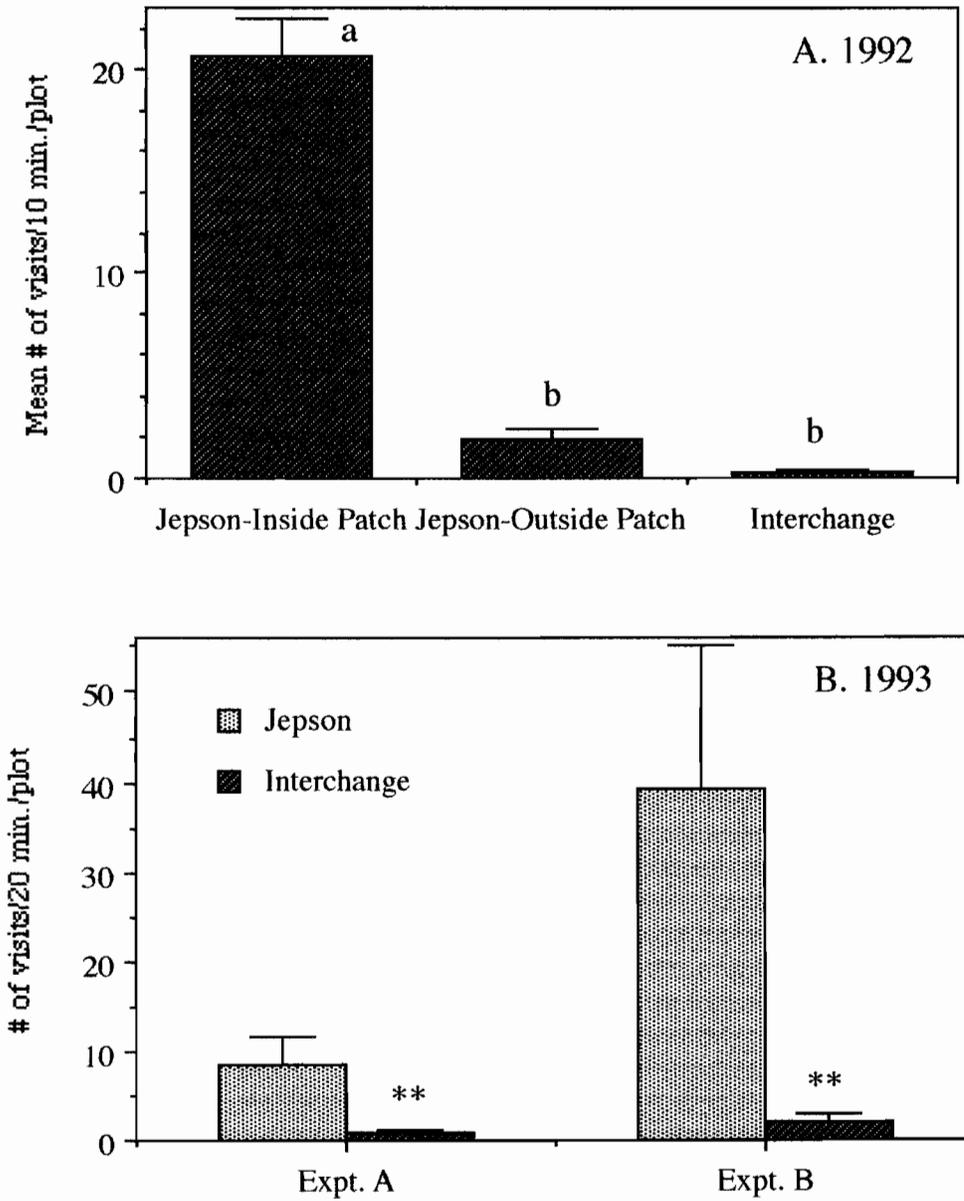


Figure 2. Mean visitation rates and standard errors of all insect visitors. A. 1992 study. Means with different letters are significantly different (see text). B. 1993 experiments.

** $p < .01$

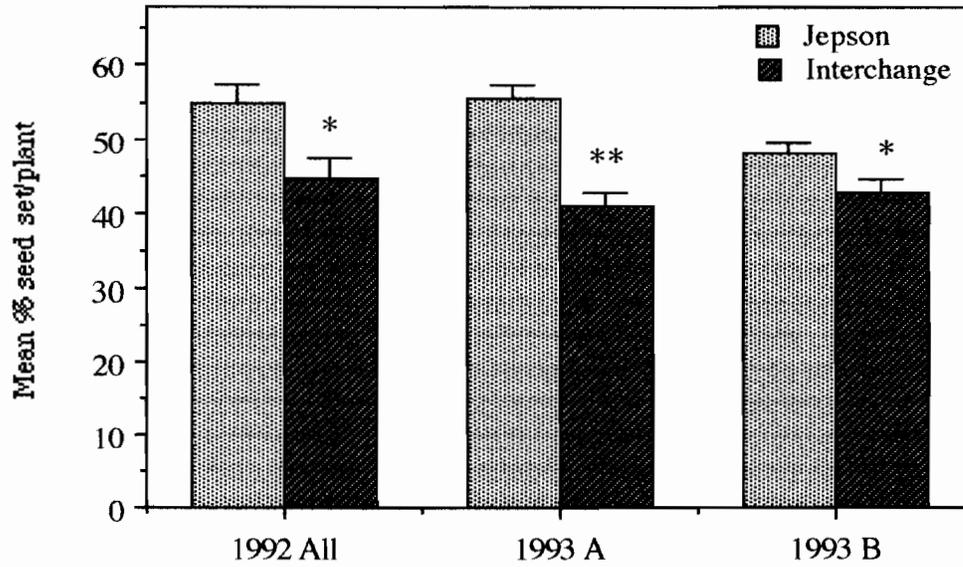


Figure 3. Mean seed set and standard errors of *B. nanum nanum* plants from both sites and years. See also Table 3. All data have been arcsine transformed.

* $p < .05$ ** $p < .01$

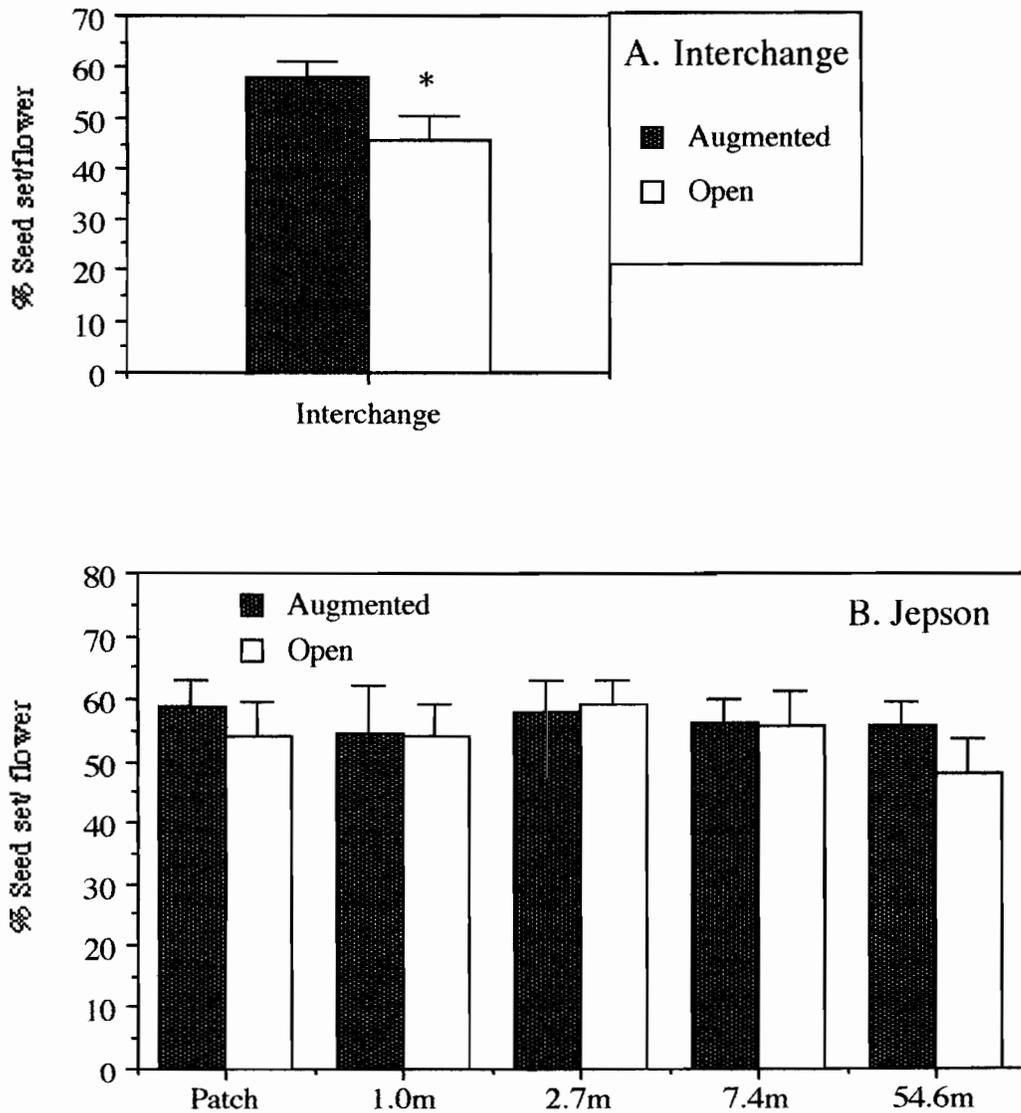


Figure 4. Mean seed set and standard errors from 1992 pollen limitation tests. All data have been arcsine transformed. A. Interchange site. B. Jepson Prairie Preserve. Data from the 20.1 m plots were omitted because plots were damaged by seed predators.

* $p < .05$

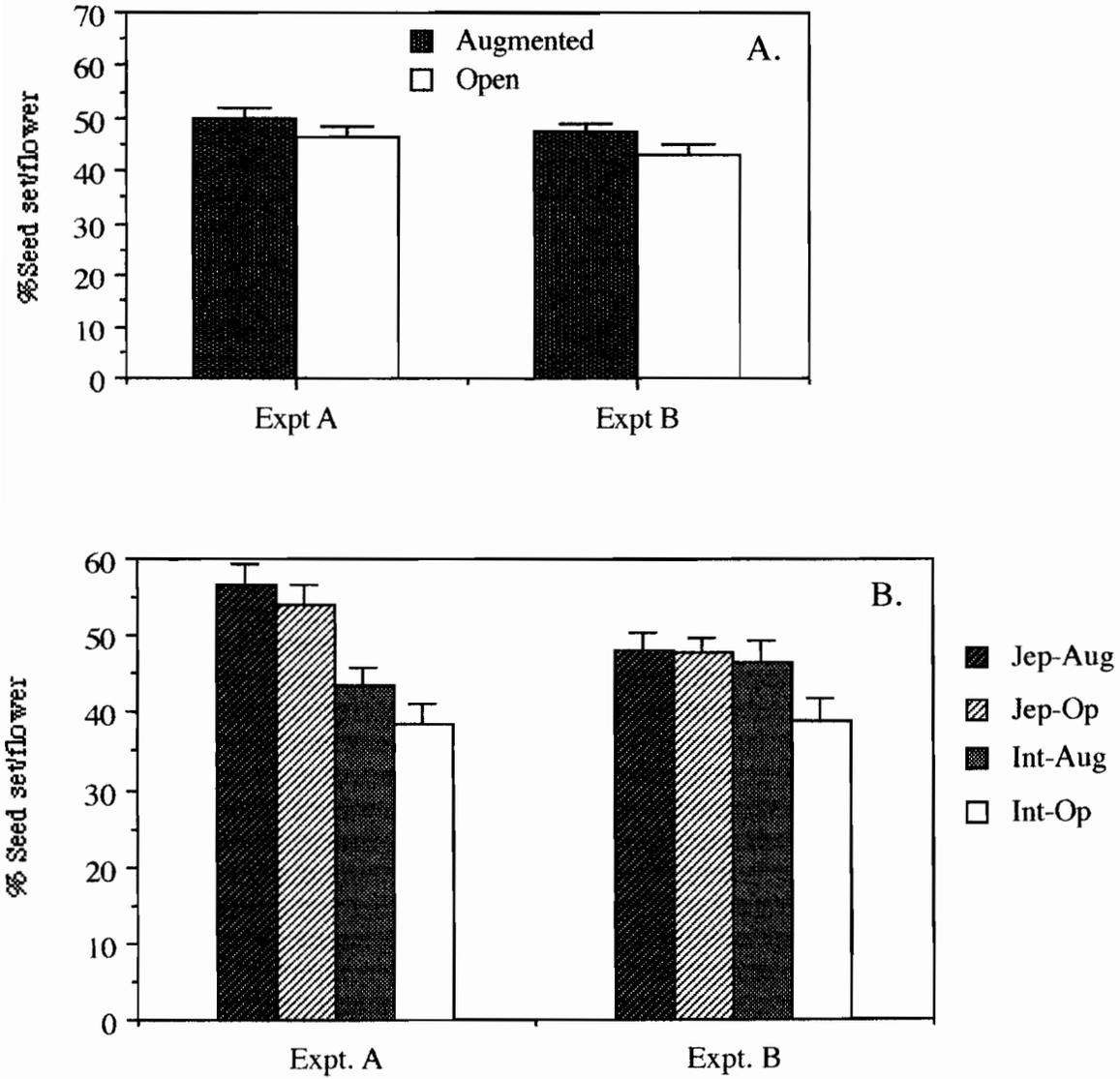


Figure 5. Treatment effects from 1993 experiments. See also Table 3. A. Treatment means and standard errors. B. Treatment by site means and standard errors. All data have been arcsine transformed.