Demographic Performance of a Rare California Endemic, Chorizanthe pungens var. hartwegiana (Polygonaceae)

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ABSTRACT.—Managing and understanding the ecology of endemic plants depends upon understanding the habitat limitations of these highly restricted species. Using transplant experiments we quantified the demographic performance of an endangered annual plant of coastal California, *Chorizanthe pungens* var. *hartwegiana* (the Ben Lomond spineflower), in habitats with established populations and in nearby habitats where the plant is never or rarely found. Habitats used for transplants occur on the sandhills soil outcrops to which this species is endemic, including open pine forest, manzanita-dominated chaparral and open erosive sand habitat. We monitored effects of transplant habitat, site from which the transplants originated and intraspecific density on the mortality, final biomass and reproductive effort of individual spineflowers. Habitat largely influenced biomass and reproductive effort and had little effect on mortality. Although spineflowers are currently absent from both pine and chaparral habitats, transplants grew and reproduced best under pines, and worst under chaparral, with intermediate performance in the open areas to which spineflowers are currently restricted. While the habitat needs of spineflowers impose severe restrictions on their population size, management could enhance establishment in pine-dominated areas adjacent to current populations. Patterns of spineflower performance suggest that endemic plants may be excluded from potential habitats by a multiplicity of factors, complicating management for the viability of such species.

INTRODUCTION

High rates of plant endemism are characteristic of many floras of Western North America, as well as many other areas. Of the approximately 6300 native plant species, subspecies and varieties in California, 36% are endemic to the state; furthermore, the majority of these taxa are restricted to far smaller spatial scales (Skinner and Pavlik, 1994). Of the 1701 plant taxa listed in the California Native Plant Society's Inventory of Rare and Endangered Plants of California, more than 35% occur in only a single county, and more than 60% occur in either one or two counties (Skinner and Pavlik, 1994; Press *et al.,* 1996). Many endemic distributions can be defined further as relationships with particular habitat types, including localized edaphic conditions such as serpentine, unusual hydrological conditions such as vernal pools or unique disturbance regimes such as periodic flooding (Kruckeberg, 1984; Kruckeberg and Rabinowitz, 1985; Baskin and Baskin, 1988; Menges, 1990; Hickman, 1993; Jensen *et al.,* 1993). Although the highly endemic distributions and habitat affinities of many plants are well known, the proximal factors that maintain plant endemism have not been investigated for most species. However, knowledge of the ecological factors limiting rare species is important for a clear understanding of both the forces leading to current distributions and the management regimes needed to preserve these species in the future.

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We used an experimental approach to investigate the factors limiting the geographic and habitat distributions of *Chorizanthe pungens* var. *hartwegiana* Rev. and Hardham (Polygonaceae), the Ben Lomond spineflower, an annual plant limited to open areas of sandhills habitat in the southern Santa Cruz Mountains and listed as endangered under the Endangered Species Act (Morangio and Morgan, 1987; U.S. Fish and Wildlife, 1991, 1994).

As with many endemics, it is not apparent what restricts the Ben Lomond spineflower (referred to as 'spineflower') to its current narrow habitat range. Possible explanations for such localized distributions include herbivory, soil pathogens, shade intolerance or lack of seed dispersal (Baskin and Baskin, 1988; Kunin and Gaston, 1993). Whereas current distribution and abundance patterns are used to infer habitat suitability for plant species, the correspondence between distribution and habitat quality may not always be straightforward and can require estimates of demographic performance in different habitats (Van Horne, 1983; Pulliam, 1988). Similarly, studies of individual demography are often needed to determine which demographic rates limit a species to its current habitat and how management can best be used to increase population viability (Schemske *et al.*, 1994). To test the spineflower's demographic responses to different habitat types we performed transplant experiments at the Bonny Doon Ecological Reserve, Santa Cruz County, California, among the spineflower's typical habitat and three other common and nearby habitats where spineflowers are rarely or never found. The resulting data on survival, growth and reproduction of individual plants growing in each habitat allow us to address three specific questions regarding this endemic taxon's habitat needs and restrictions: (1) Does demographic performance correspond to current distribution patterns?; (2) Which life history traits are most affected by habitat, and thus most likely responsible for the habitat limitation of this species? and (3) Are the same changes in demographic performance responsible for absence from several different, potentially available habitats?

Natural history and site description.—The sandhills communities of the Santa Cruz Mountains, California, are a classic set of edaphically restricted plant communities. Sandhills areas occur on scattered pockets of pure sandy Zayante series soils derived from a loose consolidation of Miocene sand deposits, known as the Santa Margarita formation (Morangio, 1985; Morangio and Morgan, 1987). These well-drained, nutrient-poor sand deposits form microhabitats for sandhills communities, separating them from the surrounding mesic habitats of the Santa Cruz Mountains. The sandhills communities have been further fragmented and reduced by various human impacts, particularly residential development and mining (Morangio, 1985; Morangio and Morgan, 1987). While there are 2025 ha of Zayante soils, only about 200 ha are able to support the most floristically rich sandhills communities, and of this, only 81 ha are suitable for spineflower populations (Press *et al.*, 1996).

Three intergrading plant communities commonly occur in Sandhills areas: ponderosa pine (*Pinus ponderosa*) forest, ponderosa pine-sand parkland and silverleaf manzanita (*Arctostaphylos silvicola*) mixed chaparral (Morangio and Morgan, 1987). Pine forests can be relatively dense and often integrate with surrounding mixed evergreen forests. Ponderosa pine-sand parkland habitat is a gradation between open pine forest, with sparse but taxonomically diverse subshrubs and annuals, to open, often highly erosive areas dominated by endemic annuals. Finally, silverleaf manzanita mixed chaparral habitat is characterized by dense silverleaf manzanita with scattered individuals of other shrubs and, in some areas, knobcone pine (*Pinus attenuata*). At some sites fire may be a natural force that maintains a balance between these communities. In particular, fires may be important in preventing chaparral from encroaching on more open sand parkland, maintaining the open understory of ponderosa pine dominated areas and allowing regeneration of pines themselves (pers. obs.).

The spineflower is a diminutive annual plant entirely restricted to sandhills areas (Morangio and Morgan, 1987; U.S. Fish and Wildlife, 1991, 1994). Within the sandhills spineflowers are further restricted to the most open habitats, such as open sand parkland and steep or eroding areas with extremely low densities of shrubs, trees or other annuals (U.S. Fish and Wildlife, 1991, 1994). Discussion of the systematics, ecology and management of the spineflower has been largely limited to a variety of sometimes conflicting government reports and unpublished senior theses (Potts, 1993; Zador, 1993; Kluse, 1994). *Chorizanthe pungens* var. *hartwegiana* is not recognized as a distinct taxon in the most recent California flora (Hickman, 1993). However, both the California Native Plant Society (Skinner and Pavlik, 1994) and the Federal Government recognize it as a distinct taxon (U.S. Fish and Wildlife, 1991, 1994; Ertter, 1996). On 31 January 1994 the United States Fish and Wildlife Service determined that *C. pungens* var. *hartwegiana* and two closely related *Chorizanthe* taxa were endangered and that *C. pungens* var. *pungens,* which is restricted to coastal dune sites within the Monterey Bay area, was threatened under the Endangered Species Act (U.S. Fish and Wildlife, 1994).

The spineflower is a winter annual with seed germination occurring after the first significant autumn rains (Hickman, 1993; Zador, 1993; U.S. Fish and Wildlife, 1994). Plants grow slowly through the winter and flower in the spring (approximately late April to late June at our study site; pers. obs.). Termination of vegetative growth and onset of flowering appear to be highly opportunistic, and can be substantially delayed by late spring rains (pers. obs.). In open habitat spineflowers can reach seedling densities of hundreds to thousands per m^2 (Zador, 1993; Levin and McGraw, 1998). Final plant size and seed output is highly variable, with plants producing from 1 to 70 involucres, each containing a single flower that can produce a single achene (Levin and McGraw, 1998). To our knowledge, no investigations have been conducted of seed viability on this or related species.

Our investigations took place at the California Department of Fish and Game's Bonny Doon Ecological Reserve, located approximately 10 km northwest of Santa Cruz, California. Spineflowers occur in the most open habitats within the Reserve: along open trails within the chaparral, where past bulldozing of roads has created open erosive environments (Potts, 1993); in open sand patches within the chaparral, where an assortment of other characteristic sandhills forbs also occur (*e.g., Navarretia atractyloides* and *Erysimum teretifolium*) and in the most open areas among ponderosa pines at much lower densities. The soil surface in most areas dominated by pines is covered with a dense layer of undecomposed needles; in these areas spineflowers do not occur.

METHODS

To explore the ecological limits of the spineflower we transplanted soil plugs containing spineflower seedlings during the winter of 1993 into the four most common sandhills habitats at the Reserve: (1) open sand patches; (2) mixed annual-grass areas near pines; (3) dense silverleaf manzanita-mixed chaparral and (4) directly under adult ponderosa pine growing in a sparse canopy. Following transplanting we monitored survival, growth rate, flowering and seed set of randomly selected individuals and *in situ* reference individuals.

Transplanted soil plugs containing spineflower seedlings were taken from three open sand habitat source sites: A, B and C, [where the spineflower occurs at its highest abundance]. At each site 12 plugs were chosen for their relative uniformity and removed. Each plug contained between 5 and 55 spineflower seedlings, differences accounted for in our analyses. Three replicate plugs from each source site were then randomly assigned for transplanting into one of the following habitat treatments: (1) sand: in which plugs were transplanted back into open sand locations; (2) grass: areas with some open sand dominated

by annual alien grasses, especially *Vulpia myuros*; (3) chaparral: the understory of *Arcto-staphylos silvicola* bushes and (4) pine: under the sparse canopy of mature *Pinus ponderosa* trees. In a final treatment that served as a transplant reference, one square meter quadrats were established in the same three source areas from which transplanted plugs were taken. Unmoved reference plants in these quadrats were monitored to determine plant performance in the absence of manipulation, thus controlling for the effects of transplanting. Each source site was matched with a separate chaparral site and sand site. However, due to limitations of available transplant sites, all plugs from all source sites assigned to the grass habitat were transplanted into one general location, as were all the plugs transplanted into the pine treatment. Because this represents a 'pseudoreplicated' experimental design for these later two habitats effects of these treatments must be interpreted cautiously (Hurlbert, 1984).

On the mornings of 31 January and 1 February 1993, when the soil was damp and less friable, soil plugs were dug with a cylindrical bulb puller 6 cm in diameter and 5 cm deep. This plug size seemed appropriate based upon observations of the densities and sizes of dried plants from the previous year, and our concern to minimize any unnecessary damage to this rare species or its habitat. While transplant source sites were selectively chosen in areas of high spineflower density, a wide range of plant densities existed within the experimental plugs. Plugs were placed directly into holes made with the same bulb puller used to take the plugs themselves. Since a 10 cm layer of pine needle duff had accumulated at the pine transplant site, pine needles were cleared before transplanting plugs into this site. After transplanting, all plugs were watered once to reduce transplant stress. Four individuals in each plug of the transplant treatments were randomly chosen for monitoring and tagged with colored toothpicks. The number of live plants in each plug was counted each week. Plugs were marked by placing 6 cm diam plastic rings on the soil surface surrounding the transplants. In the unmoved references ten individuals were randomly marked with colored toothpicks and monitored throughout the experiment. In each reference plot densities were recorded in three randomly placed 6 cm diam rings and averaged to obtain a mean density.

During the experiment plants in all treatments experienced significant rates of mortality. To maintain adequate sample sizes for final performance measures we recorded all deaths occurring before seed set and randomly marked a new live plant nearby to follow for the duration of the study. Mortality rates were calculated from data of the second week of the experiment (15 February 1993) to just before natural senescence (7 May 1993). Per capita mortality was summarized by soil plug or, in the case of the nontransplanted references, for all individuals within each 6 cm diam ring.

All tagged individuals were monitored for growth at weekly intervals. Size was measured nondestructively using the widest diameter of the rosette and the number of leaves present on the plant. Once plants produced stems size was measured by summing the lengths of all the stems. To correlate these nondestructive size measurements with aboveground biomass we randomly selected 18 individuals outside the experimental plots for sacrifice each week. Three plants were collected from each source site and an additional nine came from plots within the mixed grass community. These plants were measured as described above for the experimental individuals then dried to constant mass (air-dried for at least 4 wk and then at 30 C for 48 h before weighing) to obtain individual aboveground dry mass. Mass of experimental plants was estimated from two regressions of actual mass on nondestructive measures for harvested plants: For plants without elongated stems: mass (g) $= -0.040 + (0.059) \times$ (diameter of rosette, cm) $+ (1.040) \times$ (leaf number) $+ (0.110) \times$ (week from beginning of study); ($r^2 = 0.83$, n $= 203$). For plants with elongated stems: mass (g) $= 3.591 + (0.650) \times$ (stem length, cm); ($r^2 = 0.615$, n $= 142$).

TABLE 1.—Results from general linear models testing effects of habitat, source site and density on spineflower performance on three measures of demographic performance. Mortality was arcsin-square-root transformed and both biomass and reproductive success (involucre number) were log-transformed for normality before analysis

Performance measure	Factor	SS	df	F	P
Mortality	Site	0.834	2	8.24	0.001
	Habitat	0.537	4	2.65	0.050
	Density	1.199	1	23.70	<0.001
	Density × Habitat	0.967	4	4.777	0.004
	Error	1.670	33		
Final mass	Site	4.513	2	4.03	0.020
	Habitat	97.122	4	43.36	<0.001
	Density	2.235	1	3.99	0.048
	Site × Habitat	16.337	8	3.65	0.001
	Error	80.643	144		
Reproduction	Site	14.820	2	10.67	<0.001
	Habitat	87.768	4	31.58	<0.001
	Site × Habitat	40.025	8	7.20	<0.001
	Error	101.435	146		

Between 21 May and 27 June 1993, as each marked plant began to senesce, it was collected, dried to constant mass, and weighed to obtain a final aboveground biomass estimate. Reproductive effort was quantified by counting the number of involucres per plant. One hundred randomly selected involucres from plants outside our experimental plots were opened to check for seed set per involucre; 77 had a mature achene (77%), indicating that involucre counts provide a reasonable estimate of reproductive success.

To test for the statistical significance of factors potentially influencing spineflower performance, general linear models (GLMs) were used. As explanatory factors the GLMs included two categorical variables, habitat treatment and source site, their interaction and one continuous variable, plant density. We also tested for interactions of density with both site and habitat. Following these analyses, we conducted Tukey-Kramer pairwise comparisons to establish differences between means, without Bonferroni correction (Sokalt and Rohlf, 1995). Normalized measures of plant performance included: arcsin-square root transformed mortality, log-transformed final biomass and log-transformed involucres per plant. We report the results of final analyses including significant effects only.

<div align="center">RESULTS</div>

Mortality.—Mortality rates were significantly influenced by habitat treatment, plant density, source site and the interaction of treatment and density (Table 1; Fig. 1A). Although habitat had a significant effect, it was the weakest influence on mortality. Plants in all habitat treatments showed relatively similar mortalities, except the grass habitat, which had very low mortality (Fig. 2A). In post-hoc pairwise comparisons there were no significant differences in mortality among habitats (Tukey-Kramer tests, $P > 0.05$). In contrast to habitat, density strongly affected mortality, accounting for almost one fourth of all variation between samples. The strongest effect of habitat was through interaction with density (Fig. 1A); density significantly affected mortality rates in the grass and chaparral habitats (for simple

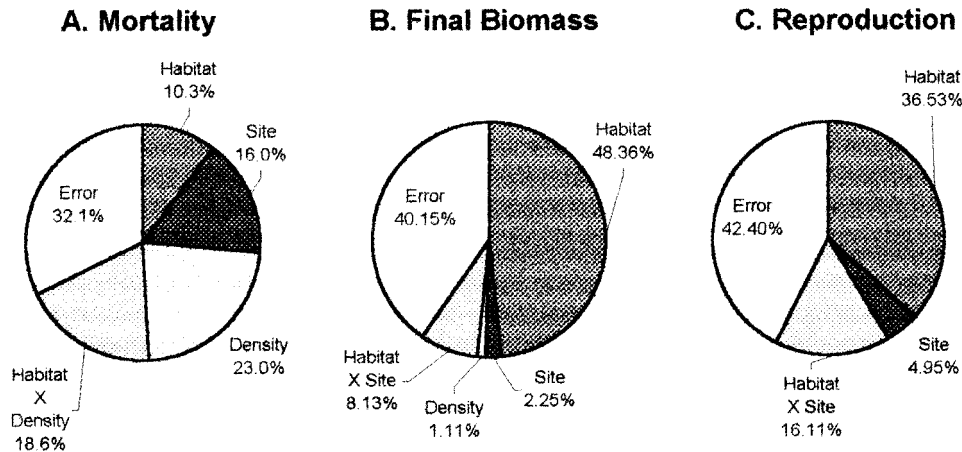**A. Mortality** **B. Final Biomass** **C. Reproduction**

FIG. 1.—Relative importance of factors influencing spineflower performance. Pie diagrams show the results of GLMs testing the influence of density, habitat treatment, source site and interaction terms on measures of individual spineflower performance. Areas attributed to each main effect and interaction in the diagrams equal the percentage of total variance (total Sum of Squares) explained by that effect in the analysis. Reference plants were nontransplanted individuals in open sand areas. Sand plants are those that were transplanted back into open sand areas. Performance measures tested are (A) Mortality, (B) Final aboveground biomass and (C) Estimated seed production (number of involucres produced per plant)

regressions on density in the two habitats, $r^2 = 0.860$ and $r^2 = 0.357$, respectively), but explained less variance within other habitats.

Growth and biomass.—Because the pattern of effects on spineflower growth rates largely matched those for the directly measured final biomasses, we report results only for these final sizes. Potentially complimenting our results, estimated mean seedling biomass differed significantly between sites, with seedlings from Site B the largest, and those from Site A the smallest (one-way ANOVA, $P < 0.005$). However, including seedling size rather than source site in GLM analyses does not change the significance of any other explanatory variable considered.

Final biomass was significantly influenced by habitat treatment, source site, spineflower density and the interaction of habitat and site (Table 1). However, these effects differed greatly in importance, with habitat treatment and the interaction of habitat and site accounting for virtually all of the explained variance (Fig. 1B). The final biomass of plants transplanted back into open sandy sites was consistently smaller than the nontransplanted reference plants (Fig. 2B). Spineflowers transplanted beneath the pine canopy grew significantly larger than plants in any other transplant treatments (sand, chaparral or grass). Spineflowers transplanted under silverleaf manzanita in chaparral were significantly smaller than plants placed in any other habitat (Tukey-Kramer pair-wise comparisons), resulting in a clear ranking of growth performance across habitats: pine > grass = sand > chaparral.

Reproduction.—The number of involucres produced per plant was strongly correlated with final biomass ($r^2 = 0.799$, $n = 160$; Fig. 3). Nonetheless, responses of reproductive effort and final biomass to the experimental variables were not identical. Involucre number was significantly affected only by habitat treatment, source site and their interaction (Table 1; Fig. 1C). As with final biomass, habitat had the largest effect on involucre production.
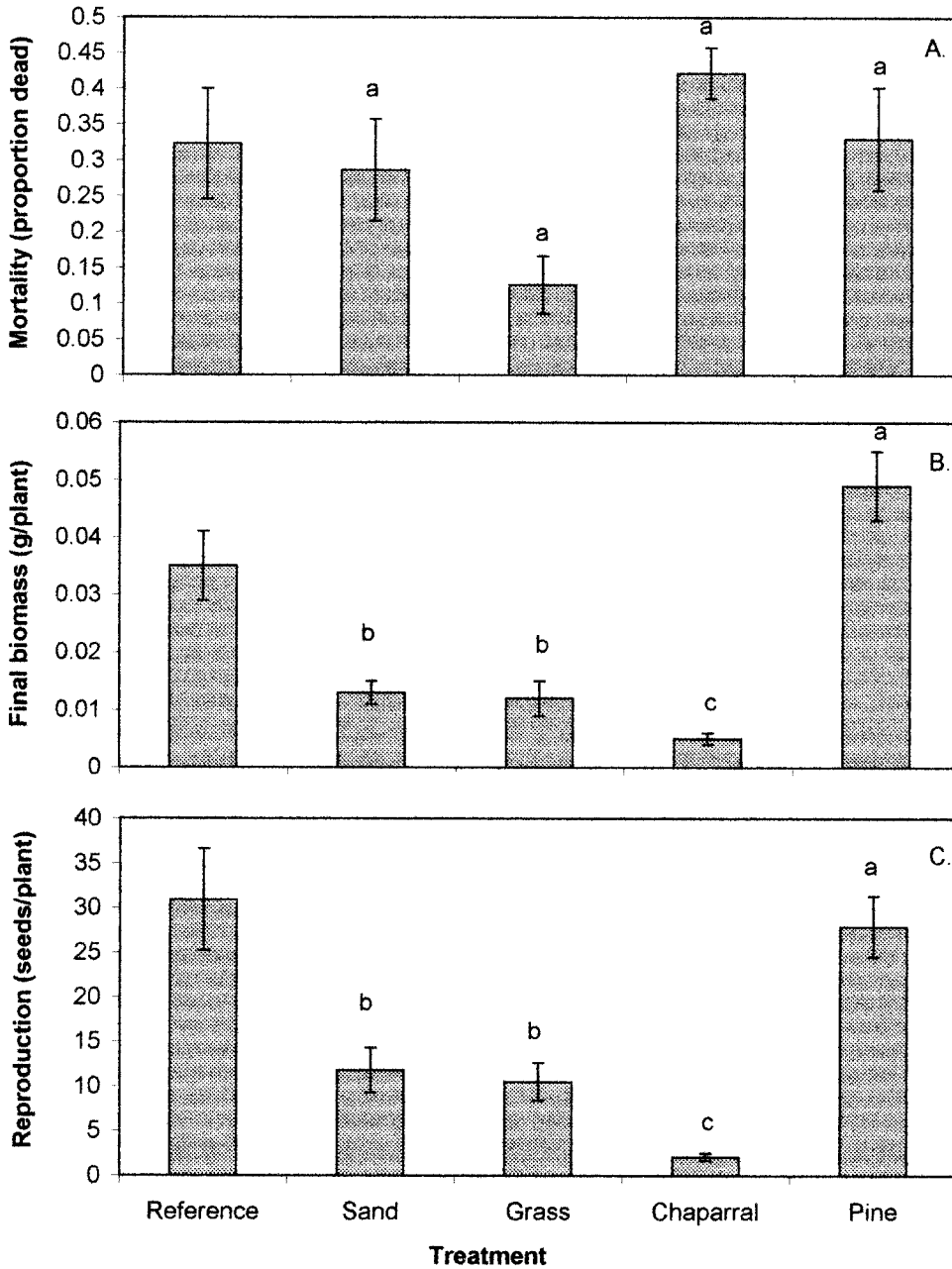
FIG. 2.—Measures of spineflower performance by transplant habitat. Bars are means $\pm$ 1 SE. Performance measures shown are (A) Mortality, (B) Final aboveground biomass and (C) estimated reproductive success (number of involucres produced per plant). Letters above bars denote results of post-hoc pairwise comparisons (Tukey-Kramer tests), with different letters indicating significant differences ($P > 0.05$)
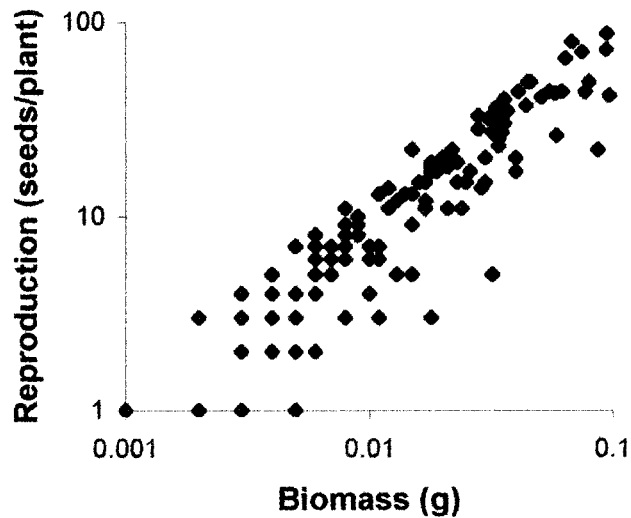
FIG. 3.—Relationship between final aboveground biomass and estimated seed production (number of involucres produced per plant). Note the data are plotted on log-log scales

However, the main effect of source site and the interaction of source site and habitat had approximately twice as much effect on reproduction as biomass (Figs. 1B, C). Patterns of reproduction across habitat treatments were similar to those for final mass. However, the larger size of plants in the pine habitat did not translate into more involucres than in the sand reference plants, and the chaparral habitat was even less conducive to reproduction than to growth. Still, the overall ranking of mean reproductive values between habitats reinforces the general pattern of demographic response seen in biomass, reflecting the high correlation between these two performance measures (Fig. 3).

DISCUSSION

Of the factors considered, the main effect and interactions of habitat type was most important in determining spineflower performance. All three measures of individual spineflower performance varied significantly with habitat type, although biomass and reproduction were more plastic than mortality. In the transplant experiments, spineflowers were only moved into microhabitats in which this taxon currently exists or are directly adjacent to areas harboring spineflower plants. Furthermore, all the transplant habitats occurred on highly similar soils, and plants were moved in soil plugs of identical sand soil. Given these features of our study, all of which should mitigate against dramatic differences in plant performance between transplant habitats, the large habitat effects we find probably underestimate the influence of habitat on demography for this species.

However, these habitat differences do not directly correlate with the current distribution and abundance of spineflowers. Plants transplanted within the taxon's current natural habitat (sand and grass areas) showed intermediate performance in all measures except survivorship, for which grass habitat appeared extremely favorable (Fig. 2). Transplants that were moved into the chaparral habitat showed uniformly poor performance; they resulted in smaller plants that produced few flowers and often died before maturity. Conversely, when moved to the other major habitat type where they do not now occur, to areas cleared
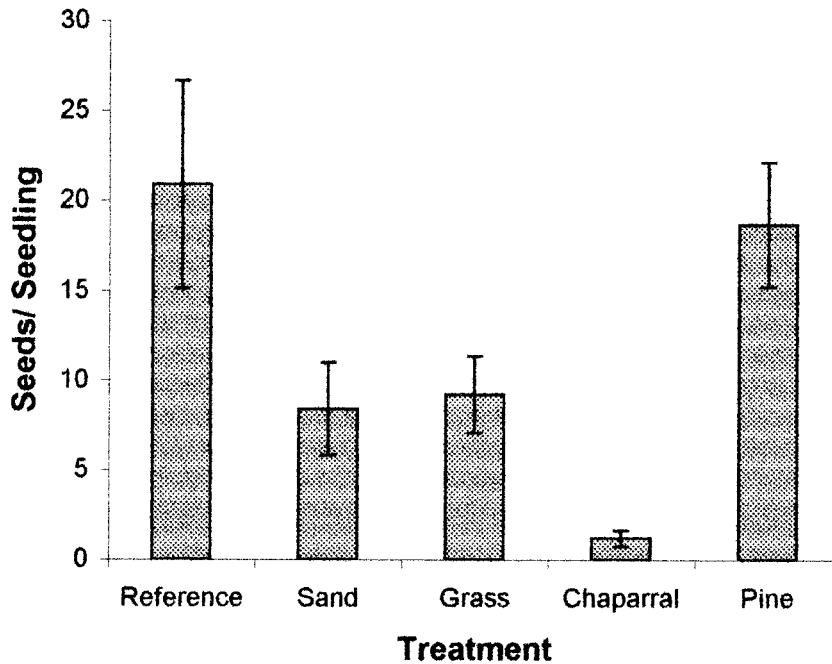
FIG. 4.—Mean number of per capita seeds per seedling in different habitats. Mean survival to flowering in a habitat was multiplied by the average involucre number (estimated minimum seed production) produced per surviving plant (mean ± 1 SE)

of duff underneath the sparse pine canopy, seedlings performed extremely well; plants showed intermediate survivorship, grew larger and produced more flowers. Whereas some of these habitat effects may be due to direct differences in soils, the results of a pot experiment, growing spineflowers in different soil and light regimes, suggest that shading is likely to be the most important factor explaining the poor performance of spineflowers growing under silverleaf manzanita bushes (Levin and McGraw, 1998).

While transplanted spineflowers grow well in the open pine forest, no natural spineflower recruitment in areas with substantial needle accumulation was observed. Because our experiments did not include manipulation or monitoring of seedling establishment, the limitation of seed germination or seedling establishment by needle accumulation was not directly tested. However, we speculate that the primary factor excluding spineflower populations in the pine habitat is limited establishment due to duff, as has been demonstrated in other systems (*e.g.*, Bergulsen, 1990; Nuzzo *et al.*, 1996). It is also possible that allelopathy excludes it from this or the chaparral habitats (*e.g.,* Rice, 1984; Tinnin and Kirkpatrick, 1985). Thus, while chaparral inhibits all stages of spineflower growth and reproduction, pines seem to limit spineflowers only during the establishment of young plants.

Currently, both pine and chaparral habitats are more extensive at the Bonny Doon Ecological Reserve than the open sand sites inhabited by the spineflower. To accurately assess the overall quality of these potential habitats for spineflowers, it is necessary to multiply our measures of spineflower survivorship and average reproduction of surviving plants (mean involucre number produced per surviving plant) to provide a minimum estimate of per capita seed production per seedling (Fig. 4). Of the transplanted spineflowers, overall seeds

per seedling is far higher in the pine areas than in any other habitat and population maintenance appeared possible in all but the chaparral habitats. This conclusion is tentative since no measurement of seed dormancy or mortality was made, which would be necessary for a complete demographic analysis.

While the mechanisms of habitat limitation differ between pine and chaparral areas, the common management implication is the need for disturbance to remove chaparral plants and/or accumulated pine duff. Aerial photos show that much of the reserve currently dominated by chaparral was once open sand that probably supported viable spineflower populations (Potts, 1993). Similarly, in other sandhills sites, open pine-sand parkland with patches of bare sand is an ideal habitat for spineflowers (Morangio and Morgan, 1987; U.S. Fish and Wildlife, 1991, 1994). Thus, either brush and duff removal, or, ideally, prescribed burning, seems necessary to maintain suitable habitat for both the spineflower and, most likely, other diminutive endemics of sandhills flora as well. However, no studies have been done to determine tolerance to heat and fire of spineflower seeds. Thus, any burning program must be planned to create a mosaic of burned and unburned areas, allowing recruitment of seeds from undisturbed areas into newly burned sites.

Furthermore, factors other than habitat could have strongly affected our measures of demographic performance. Perhaps most significant is environmental variation; the 1992–1993 winter-spring growing season had high rainfall which appears to favor spineflower growth and survival (pers. obs.). The effects of invasive introduced species may also be significant. In particular, although other work has shown a strong competitive effect of the Mediterranean grass *Vulpia myuros* on spineflowers (Zador, 1993), in our experiments spineflowers showed relatively good performance in the grass habitat. However, in addition to high rainfall during our study, the method of transplanting plugs of soil prevented grasses and the experimental spineflower individuals from being in close proximity, thereby biasing against detection of interspecific interactions. Further work to quantify the competitive effects of this and other exotics, as well as their responses to clearing or burning, is needed to better understand this threat to spineflower viability.

Studies of rare plant ecology and conservation have increasingly emphasized demographic approaches (Steenbergh and Lowe, 1983; Fiedler, 1987; Menges, 1990, 1992; Charron and Gagnon, 1991; Pavlik *et al.*, 1993; Schemske *et al.*, 1994; Schmalzel *et al.*, 1995). The use of demographic methods allows general population characteristics to be tied to specific aspects of species biology in order to clarify the factors driving current and future population status. However, many demographic studies on rare plants are entirely observational, quantifying demographic patterns under existing environmental conditions (Steenbergh and Lowe, 1983; Menges, 1990; Schmalzel *et al.*, 1995). Many other studies quantify the demographic consequences of individuals living in areas subjected to different experimental manipulations (Oostermeijer *et al.*, 1996; Mashinski *et al.*, 1997; Quinta-Ascencio and Morales-Hernandez, 1997). A third approach, the one taken here, is to transplant individuals into differing habitats in order to assess demographic responses (*see* also Pavlik *et al.*, 1993; Pavlik and Manning, 1993). This strategy has the advantages of allowing researchers to directly address the factor(s) restricting species to their current or natural habitats, as well as predict the consequences of possible management initiatives with moderately little disturbance or expense. As both our work and the aforementioned works of Pavlik have shown, this combined approach to rare plant ecology can provide information on the limitations of rare plants that cannot be inferred from simple mapping or habitat affinity studies.

Casual observation usually shows that endemic species are geographically restricted by a narrow range of characteristic habitats, but the demographic and ecological factors responsible for these limitations are often less clear (Baskin and Baskin, 1988). While it is often

assumed that a single factor is primarily responsible for endemic distributions, we found different demographic responses to two common habitats from which spineflower is excluded suggesting multiple effects at work in limiting the habitat range of this species. In particular, the patterns of demographic response we documented illustrate that simple data on current distribution may not be adequate to infer habitat suitability. Similarly, our work supports the suggestion of Schemske *et al.* (1994) that demographic studies are needed to target management strategies for rare plants, including endemic species. In the case of spineflowers, different degrees of intervention appear necessary to allow this populations to exploit areas now dominated by pines vs. chaparral. In addition to contributing to the basic knowledge of this species, we hope that increased understanding of how, and why, habitat restriction occurs will serve to focus management efforts to conserve this and similar species.

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