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Source: *Journal of Biogeography*, Vol. 18, No. 3 (May, 1991), pp. 321-331

Published by: Wiley

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Geographic distribution of flower morphological traits in subspecies of *Lotus scoparius*

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Abstract. *Lotus scoparius* (Nutt. in T. and G.) Ottley, a shrubby legume and early colonizer of disturbed sites, occurs in coastal and cismontane California and Baja California. The two principle subspecies are parapatrically distributed from Los Angeles, California, to El Rosario, Baja California. Within San Diego County, ssp. *scoparius* occurs within 15–30 km from the coast, while ssp. *brevialatus* (Ottley) Munz occurs further inland in the western edge of the Colorado Desert. The two subspecies meet in a complex transition zone, from 1 to 10 km wide, trending parallel to the coastline. Flower morphology is the only known characteristic distinguishing the two subspecies and their putative hybrid.

Discriminant analysis of the three morphs, using nine morphologic variables, provided a univariate measure along a *scoparius*-to-*brevialatus* continuum that explained 94% of the interpopulation variance. Discriminant function scores

were regressed against spatial coordinates and distance to the Midpoint of the Transition Zone. Both analyses showed a weak normal cline among ssp. *scoparius* populations with the axis of variation perpendicular to the transition zone. In contrast, among ssp. *brevialatus* the most *scoparius*-like populations were furthest from the transition zone. No cline was detected within the transition zone. Canonical correlation analysis showed that elevation, annual rainfall, and growing season evapotranspiration were moderately correlated with the distinguishing flower traits. However, among transition zone sites no partitioning of the environment was evident. An evolutionary and biogeographic scenario is proposed by the author.

Key words. *Lotus scoparius*, subspecies, geographic variation, cline, multivariate analysis, California.

INTRODUCTION

Lotus scoparius (Nutt. in T. and G.) Ottley, is a shrubby legume found in scrub and chaparral communities of coastal and cismontane California and Baja California. The two subspecies in San Diego County, California, exhibit a parapatric distribution with ssp. *scoparius* coastal and ssp. *brevialatus* (Ottley) Munz inland. They are distinguished only by a series of quantifiable flower traits. This study analysed the distribution of those flower traits in San Diego County to illuminate geographic differentiation processes. Aspects of the problem investigated herein include the spatial distribution of the distinguishing traits, location and nature of the boundary separating the two subspecies, and possible impact of environmental factors in determining the distribution of those traits. Because vegetative characteristics for the species appear to be quite variable and not diagnostic (Ottley, 1923), only flower traits were investigated.

Intraspecific variation and the boundary between subspecies has been the specific concern of both empirical and theoretical studies of plants (Benson *et al.*, 1967; Doyle, 1984; Prentice, 1979) and animals (Lidicker, 1962; Thorpe, 1979). Ordination of *Yucca whipplei* Torrey leaf character-

istics in southern California resulted in an evolutionary series of geographic races showing clinal transitions (Hoover, 1983). Other studies have amply demonstrated that marked differentiation in plants can occur over short distances (Endler, 1977; Liu & Godt, 1983; Jain & Bradshaw, 1966; Snaydon & Davies, 1982) as it can in animals (Doyen & Slobodchikoff, 1984). Several studies in animals show that narrow boundaries may not be associated with any present-day geographic barriers or the distribution of known parasites (Creed *et al.*, 1970; Thorpe, 1979).

These field observations are supplemented by simulation studies showing that clines may develop at locations not coincident with the environmental factors selecting for each morph (Endler, 1973, 1977; Rohlf & Schnell, 1971). Endler (1973, p. 249) points out that in some cases 'even a gentle environmental gradient can give rise to marked spatial differentiation' and that these environmental differences 'may be below the practical limits of resolution in field studies'.

New World species of *Lotus* have been subject to much taxonomic revision (Gray, 1863; Greene, 1890; Ottley, 1923; Munz, 1974; Isely, 1981). Ottley recognized five varieties of *Lotus scoparius*. In addition to vars. *scoparius* and *brevialatus*, these included three, largely allopatric insular varieties of restricted distribution: the erect, woody *dendroideus* (Greene), *traskiae* (Ottley) and *veatchii*

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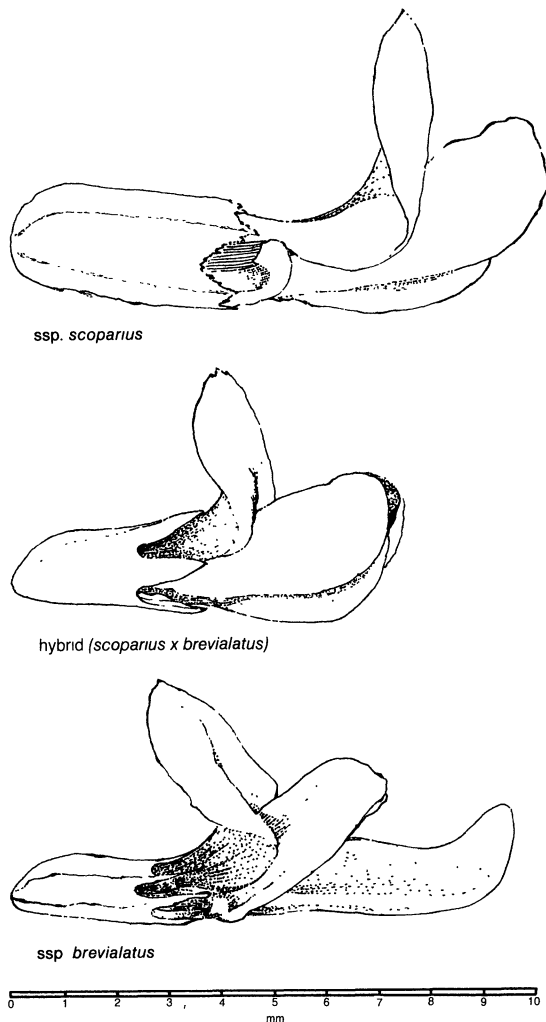


FIG. 1. Side views of all three morphs of *Lotus scoparius* (Nutt. in T. and G.) Ottley.

(Greene). Munz (1974) regarded the same five taxa as subspecies while Isely (1978) regarded them as varieties and removed the predominantly insular taxa to form *L. dendroideus*. The nomenclature of Munz will be followed for the remainder of this paper. When putative hybrids of ssp. *scoparius* and ssp. *brevialatus* are discussed, all three will be referred to as morphs (Fig. 1).

Few identifying characters beyond keel length have been cited in taxonomic treatments or keys that distinguish *brevialatus* from *scoparius*. Published localities (Ottley, 1923; Beauchamp, 1986) indicate that *scoparius* is found throughout the coastal ranges of California while *brevialatus* grows in interior southern California. Both subspecies have been reported from Baja California, although the extent of the ranges was not detailed. Little was known about the precise location of the boundary in San Diego County or the nature of the transition zone between these two subspecies (M. Beauchamp, personal communication).

Lotus scoparius establishes itself after mechanical disturbance or fire by seedling recruitment. The seeds require some heating or scarification of the seed coat for germina-

tion (Christensen & Muller, 1975; Nilsen & Muller, 1981). This can be provided by fire or heating of cleared soil. *Lotus scoparius* frequents disturbed sites such as burns, roadcuts and landslides. It is often a major component in the first few years after a fire (Hanes, 1971). Plants reach maximum relative foliar cover after 3–4 years (Keeley *et al.*, 1981; Westman, 1981; Westman & O'Leary, 1986), but average foliar cover decreases by 95% among stands older than 9 years (Hanes, 1971). In addition, *L. scoparius* sometimes grows within mature stands of *Adenostema fasciculatum* (chamise) (Christensen & Muller, 1975).

Selection of flower traits by environmental factors is difficult to assess. It is assumed for the environmental analyses in this study that the suite of characters identifying the subspecies is geographically congruent with some physiological adaptation to environmental factors. That is, the evolution of flower morphology has not been independent from the evolution of plant morphology and physiology, but is linked to it by phylogenetic history or the restrictions of population structure and gene flow.

Study area

Field studies were confined to San Diego County and the periphery of adjacent counties in southern California. The study area can be divided into three major physiographic sections, each trending northwest–southeast: (1) a central mountain corridor consisting of members of the Peninsular Ranges whose crests generally lie above 1500 m; (2) a band of foothills, coastal mesas, and stream valleys to the west; and (3) dropping sharply to the east, the low-lying basins and scattered mountains of the Colorado Desert, a component of the Sonoran Desert.

Climatic patterns are strongly influenced by physiography and proximity to the moderating ocean. Annual precipitation is low along the coast at 20–30 cm with virtually all rain falling during October–May. Summer advection fog along the coast significantly increases humidity and reduces high temperatures. Further inland, precipitation increases with elevation. The foothill zone averages near 38 cm and in the mountains precipitation can reach 100 cm (Close, 1970), with occasional snow. The proportion of rain falling in summer also increases towards the interior. Summer thundershowers are common in the mountains and account for most of the precipitation that falls in the desert – less than 15 cm total. Temperature patterns follow a similar geographic progression with diurnal and annual variation lowest near the moderating influence of the Pacific Ocean.

METHODOLOGY

Data acquisition

The historical distribution of the species was mapped from the 330 localities represented by 450 specimens found in several herbaria including San Diego Natural History Museum (SD), the Jepson (JEPS) and University Herbarium (UC) at the University of California, Berkeley, California Academy of Sciences (CAS), the Rancho Santa Ana Botanical Gardens (RSA), and San Diego State University (SDSU).

Only those 450 specimens with sufficiently preserved flowers to permit positive identification by the investigator were recorded. Some specimens, including all hybrids, had been misidentified, obscuring the boundary location.

Samples were collected and flower measurements obtained for 110 sample sites and visual identification was made of the morphs present at an additional forty-four localities during the time period of March through July 1988. Use of wild study material helps avoid the potential morphologic biases associated with the use of herbarium material common in conventional taxonomic studies (Prentice, 1979). Also the large number of sites in this study results in much finer resolution than many other studies. Most sites were located by surveying along roads, concentrating efforts in the general boundary area, and by revisiting areas where herbarium specimens had previously been collected. Additional sites were preselected by using unpublished maps of post-1981 fires larger than 40 acres acquired from the California Division of Forestry office in San Diego County. Postfire populations were considered less likely to have become established through human agency than would roadside populations.

Ten to fifteen mature flowers were sampled per site from ten randomly selected plants. A preliminary study of 500 flowers from both subspecies identified the discriminating traits and minimum sample size. In all, 1317 flowers were dissected. Measurements were made of calyx tube length, total calyx length, wing spread (measured at the widest point beyond the separation from the banner), wing length, keel length, and length of the keel's claw using a millimetre scale. Accuracy was estimated at ± 0.2 mm. Three ratios were calculated: calyx teeth to total calyx length (TERATIO), wing to keel length (KERATIO), and claw to total keel length (CLRATIO). The three ratios are largely independent of overall flower size and developmental stage.

The environmental characteristics of average slope, predominant aspect, soil pH, mean annual rainfall, growing season potential evapotranspiration (PET), elevation, and geographic coordinates were determined for each study site. Aspect, measured from 0–359 degrees, was later transformed into a 0–180, north-facing to south-facing scale. This transformation simplified a physical interpretation of the results. Soil pH data were obtained from published soil

series maps (U.S. Dept. of Agriculture, 1973). Maps of mean annual precipitation and growing season PET were used to interpolate site values (Close, 1970). Growing season PET was chosen because annual PET exhibited insufficient spatial variation.

Analytic procedures

Morphs present at the sites were mapped to locate and define the nature of the boundary and compared to the historical distributions. Discriminant analysis was performed using SPSS (Nie *et al.*, 1975) on ninety-four sites with mean values for all nine characters to maximally distinguish the two subspecies and apparent hybrid. Site mean scores and standard deviations for the First Discriminant Function were spatially analysed using SYMAP (Dougenik & Sheehan, 1975). Contour and trend surface maps of orders 1–6 were produced for each subspecies to describe any regional trends in the population means and variance. Trend surface mapping has been shown to be useful in eliciting regional patterns of quantitative morphological traits (Vandermeer, 1966; Pielou, 1979).

A transition zone between the ranges of the two subspecies was identified and drawn to encompass all areas of overlap between the subspecies. An approximate midpoint of that zone was then mapped to satisfy the following criteria: maximum separation of the subspecies onto either side, passing through as many hybrid populations as possible, while maintaining a minimum radius of curvature of the midpoint line at 1–2 km.

Canonical correlation analysis on SPSS determined the degree of correlation for the suite of flower measurements with environmental characteristics. Canonical correlation analysis is superior to multiple regression for this study because it allows multiple dependent variables (Clark & Hoskings, 1986).

RESULTS

Flower Morphology

Table 1 lists the means of the nine flower traits for the three morphs. The putative hybrid is intermediate for most

TABLE 1. Mean flower measurement by morph. All lengths in millimetres, with standard deviations in parentheses. TERATIO represents length of calyx teeth/total calyx length, KERATIO represents wing length/keel length, and CLRATIO represents claw length/keel length. All means significantly different ($P < 0.05$) from the others, except claw length of hybrid against ssp. *brevialatus* (Ottley) Munz.

Trait	<i>scoparius</i> ($n = 374$)	Hybrid ($n = 204$)	<i>brevialatus</i> ($n = 525$)
Calyx tube length (mm)	3.51 (0.36)	2.44 (0.32)	2.35 (0.23)
Total calyx length (mm)	4.24 (0.44)	3.72 (0.45)	3.49 (0.38)
TERATIO	0.162 (0.042)	0.335 (0.058)	0.326 (0.048)
Wing spread (mm)	2.65 (1.35)	2.19 (0.44)	1.76 (0.20)
Wing length (mm)	8.27 (0.70)	6.27 (0.78)	5.52 (0.50)
Keel length (mm)	7.54 (0.63)	6.32 (0.76)	7.63 (0.64)
KERATIO	1.099 (0.055)	0.993 (0.071)	0.725 (0.051)
Claw length (mm)	3.63 (0.40)	2.11 (0.49)	2.10 (0.25)
CLRATIO	0.482 (0.038)	0.331 (0.041)	0.276 (0.026)

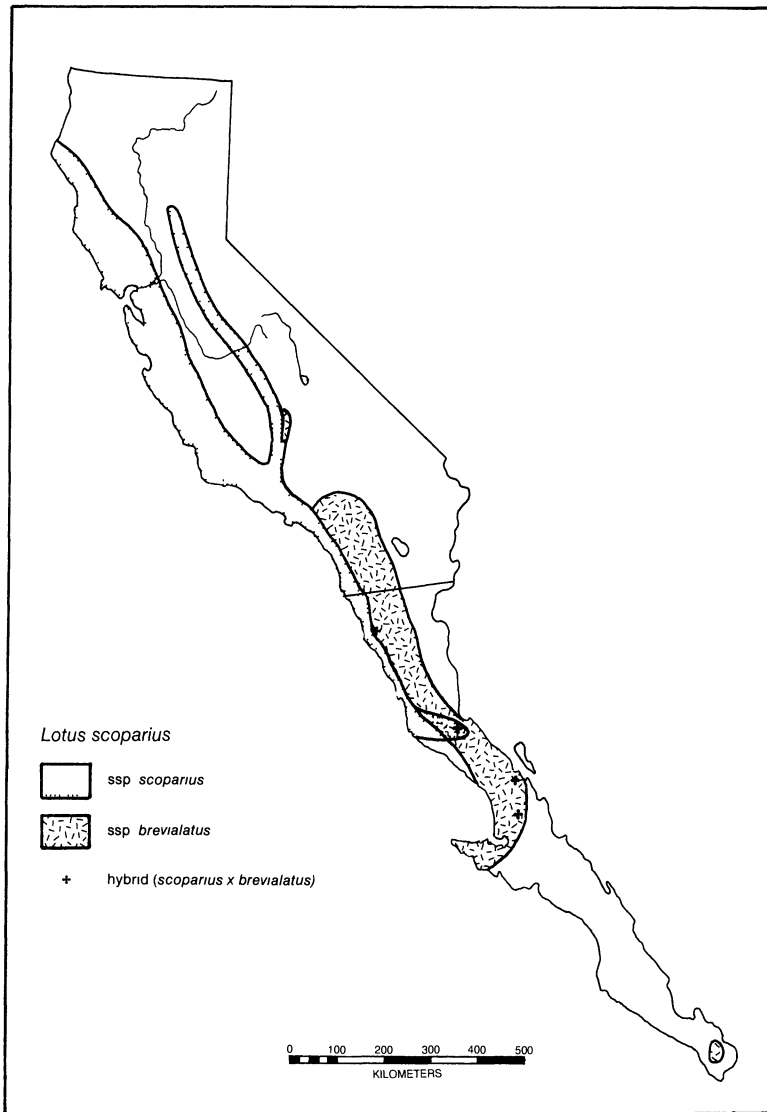


FIG. 2. Distribution of *Lotus scoparius* (Nutt. in T. and G.) Otley derived from 330 localities represented by 450 herbarium specimens.

traits except for generally being more diminutive than either subspecies. However, in only one trait (wing spread) is the hybrid truly close to the average for the parents, and in three traits (TERATIO, keel length, and claw length) the hybrid is more extreme than either parent. The identity of the hybrids was also indicated by most hybrid populations being found in the transition zone, usually between two parental populations or close to the expected boundary.

Discriminant analysis was employed to reduce the number of dimensions (i.e. characters) and derive a measure that maximally discriminates the morphs. Principle components analyses were also performed, but resulting components were neither as interpretable nor as parsimonious as the discriminant functions.

Discriminant Function 1 (DisFunc 1), accounting for 94% of the interpopulation variance (canonical correlation 0.989), provided 100% accuracy in classifying site means by morphs. DisFunc 1 appears to represent a *brevialatus* to

scoparius continuum while DisFunc 2 (canonical correlation 0.865) resolves the hybrid from the parentals, as shown in Fig. 3. A discriminant analysis employed for the 1317 flowers yields nearly identical correlations with the variables and DisFunc 1 (canonical correlation 0.968) explained 90.9% of the variance.

Hybrids exhibit the greatest discriminant function variability ($s^2 = 1.74, 2.46$), as expected for hybrid populations (Endler, 1977), while *brevialatus* exhibits roughly one-third as much ($s^2 = 0.74, 0.46$) and *scoparius* intermediate ($s^2 = 1.02, 0.92$).

Sub-species distribution

Localities from the 450 herbarium specimens of *Lotus scoparius* were mapped to display the species distribution (Fig. 2). Insular subspecies are not shown. Subspecies *scoparius* occurs throughout the coastal ranges from Humbolt

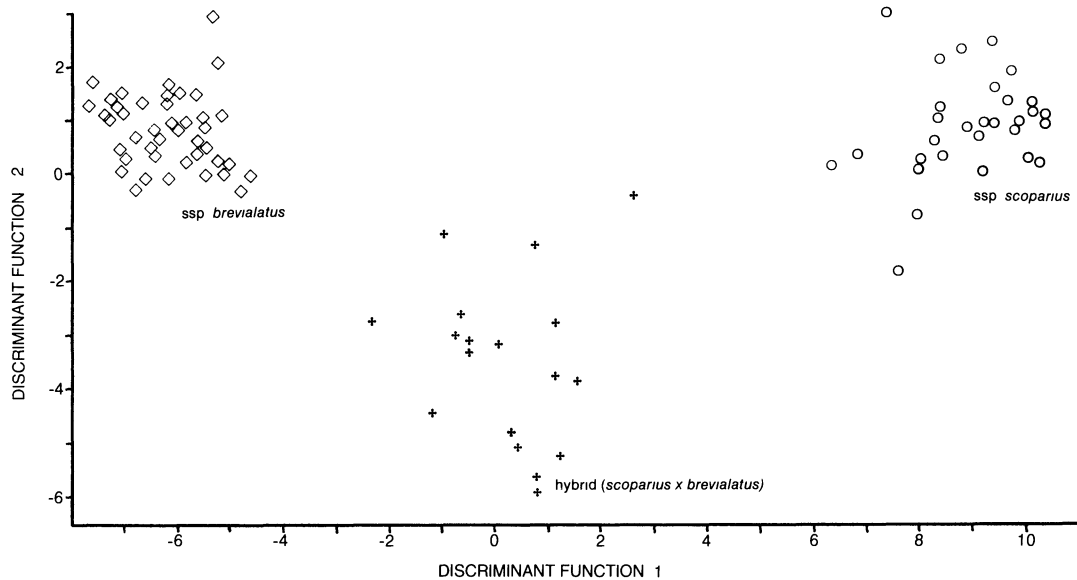


FIG. 3. Site mean scores for Discriminant Function 1 and Discriminant Function 2.

County into northern Baja California, and in a thin belt along the foothills of the Sierra Nevada. In areas where it is parapatric to *brevialatus*, from Los Angeles County to San Quintin, Baja California, *scoparius* is limited to a narrower coastal strip. From the San Bernardino Mountains in the north to the Vizcaino Peninsula in the south, *brevialatus* occupies the region stretching from the coastal foothills into the western edge of the Colorado desert or the Gulf of California. Two small disjunct clusters have also been found in the Sierra de la Laguna of southern Baja California and along the Kern River in California.

Lotus salsuginosus Greene (subgenus *Acmispon*) is the only other California *Lotus* to share the condition with *L. scoparius* of having a coastal subspecies parapatric to an inland subspecies, with the inland subspecies characterized by a keel longer than the wings. The boundary between and latitudinal extent of the corresponding subspecies are similar (Steppan, 1988). The coincidence of the distributions for the two short-winged subspecies suggests a possible convergent adaptation to a desert/interior environment or pollinators. Notably, however, the boundary between the subspecies of *L. salsuginosus* is near the eastern edge of *brevialatus*'s range: *ssp. brevivexillus* inhabits the deserts while *ssp. brevialetatus* generally does not.

One hundred and fifty-four sites were visited for which the morphs present were visually determined (Fig. 4). The boundary between *scoparius* and *brevialatus* generally parallels the coastline and is displaced 20–25 km eastward. Of the twenty-four sites with hybrid populations, sixteen are found within the transition zone. The remaining eight sites comprise two disjunct clusters. Two outlying *scoparius* populations occur along road cuts and fills of Interstate 8. Notably, the eastern cluster (Buckman Springs) is found only immediately adjacent to Interstate 8; surrounding populations are exclusively *brevialatus*. Although not planted intentionally as part of landscaping programmes nor

brought in with fill (J. Rieger, personal communication), the fact that the only outlying populations of *scoparius* were found along this heavily travelled east–west thoroughfare suggests that they were dispersed by human agency. Therefore, the two clusters were excluded from further analysis.

Comparing the distributions obtained by field surveys with the seventy-six San Diego County specimens from herbarium collections does not demonstrate any movement of the transition zone in the last 80 years. Significantly, the two most prominent hybrid clusters, around Witch Creek/Santa Ysabel and along Wildcat Canyon, possess long histories. Hybrid specimens were collected from Witch Creek in 1893 and 1894, and also in Barona Valley (2 km north Wildcat Canyon) in 1937 and 1962. No herbarium collections included *scoparius* or *brevialatus* specimens from these areas. Additional hybrids in herbarium collections were collected near Pala (10–15 km east of the present transition zone) in 1937 and from Banner (near the eastern base of the Cuyamaca Mountains) in 1936.

The Midpoint of the Transition Zone sharply delineates the boundary between subspecies in some sections (e.g. La Mesa to Mexico), but the subspecies overlap in others (e.g. northern San Diego County). At only ten sites were more than one morph present. DisFunc 1 scores were regressed against minimum distance to the MTZ to adjust for meandering by the MTZ (Fig. 5). This distance represents the nearest that one would expect to find members of the other morph available for cross fertilization. No cline is apparent across the transition zone; morph classes remain distinct. However, *scoparius* populations exhibit a shallow cline ($r^2 = 0.404$, $P < 0.001$) with a slope of 0.93 DisFunc 1 per 10 km and *brevialatus* populations exhibit a still shallower reverse cline ($r^2 = 0.231$, $P < 0.002$) with a slope of 0.19 DisFunc 1 per 10 km. Hybrid populations show no clinal pattern.

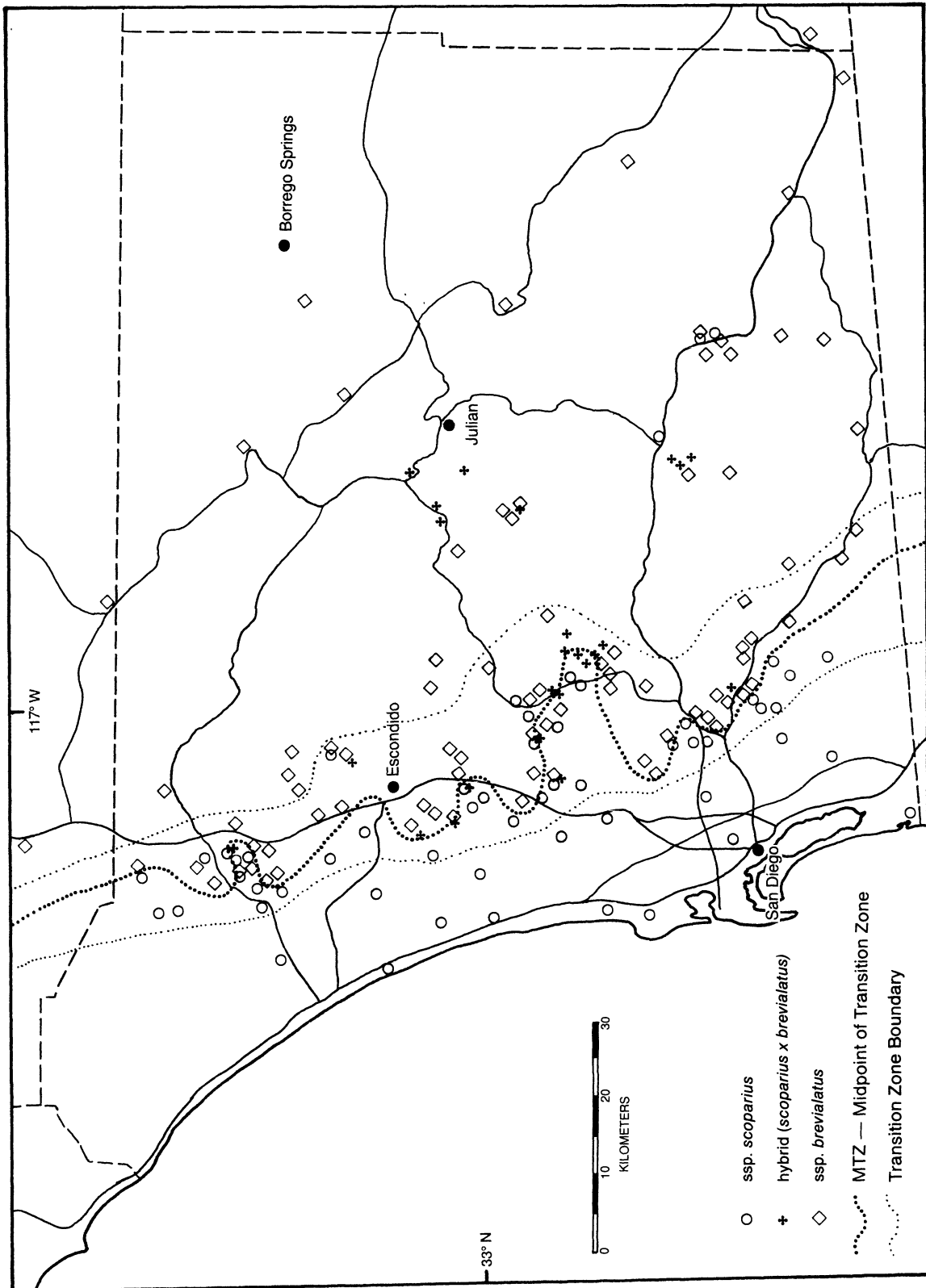


FIG. 4. Distribution of *Lotus scoparius* (Nutt. in T. and G.) Ottley in San Diego County as determined by field observation. The boundaries of the transition zone and the Midpoint of the Transition Zone are drawn to satisfy criteria outlined in the text.

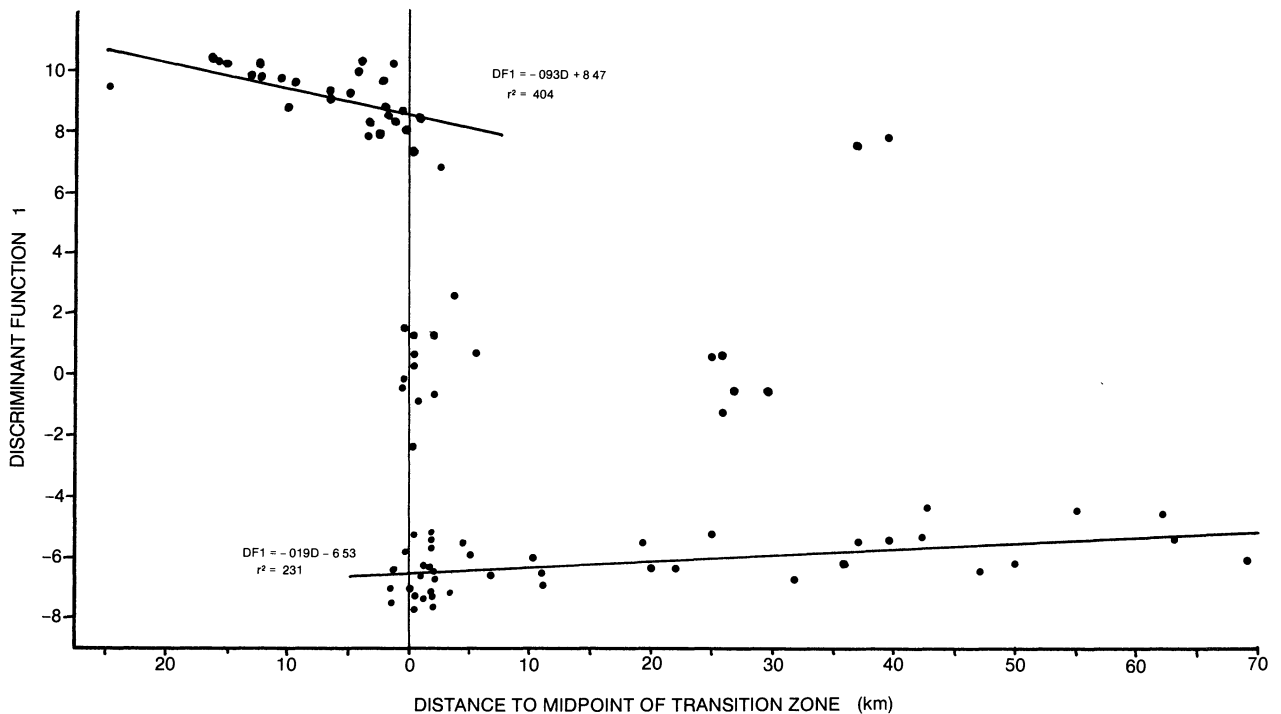


FIG. 5. DisFunc 1 scores versus distance to the Midpoint of the Transition Zone. The regression line defining the ssp. *scoparius* cline has an r^2 of 0.404 ($P < 0.001$).

Trend surface analysis

Trend surface maps for each subspecies generalize the spatial variation in morphology. In trend surface mapping, a polynomial equation is fit to any spatially distributed data using least squares. The measured character is assumed to be dependent upon its location. Lower order solutions describe the simplest spatial trends, while higher orders show greater complexity with correspondingly better fits. Sokal & Rinkel (1963) plotted linear combinations of characters after running a factor analysis. Discriminant function scores, being weighted linear combinations, are also appropriate inputs to trend surface analysis (Marcus & Vandermeer, 1966).

An analysis of variance showed that both *scoparius* and *brevialatus* exhibited significant variation among site means for DisFunc 1 ($P < 0.001$).

The first order surface for *scoparius* (Fig. 6) clearly shows a weak west-south-west to east-north-east cline ($r^2 = 0.278$, $P < 0.025$) perpendicular to the transition zone. The higher r^2 derived from Fig. 5 (0.404) indicate localized effects from proximity to *brevialatus*. The fourth order surface ($r^2 = 0.530$, $P < 0.05$) shows the cline to be steeper in the northern and southern portions of the county with a saddle in the central portion (Steppan, 1988). Marcus & Vandermeer (1966) have described r^2 s in the 0.4–0.6 range as a weak to moderate regional trend.

The first order surface map for *brevialatus* also describes a cline; though very weak ($r^2 = 0.253$, $P < 0.01$), it trends virtually parallel the the *scoparius* cline. However, the

brevialatus cline is both shallower and reversed. The most *scoparius*-like populations were found furthest inland, specifically those in the eastern-central portion of the county. The fifth order surface ($r^2 = 0.646$, $P < 0.05$) delineates this eastern 'plateau' of more-*scoparius*-like populations ringed by a series of more-*brevialatus*-like 'valleys' (Steppan, 1988). The spatial and statistical patterns indicate that local variation predominates in *brevialatus*.

Spatial patterns of variation within subspecies were investigated using trend surface maps of DisFunc 1 standard deviations. No regional trend in variability seems to be present.

Environmental variables

All environmental variable means for *scoparius* and *brevialatus* were found to be significantly different ($P < 0.02$) except for slope angle and slope aspect (Table 2). Canonical correlation analysis was performed for the eighty sites possessing data for all fifteen required variables. Multivariate tests of significance (Pillais, Hotellings, Wilks) showed the environmental variables to have a significant effect on the dependent flower traits ($P < 0.02$). Six dimensions (canonical variables) were extracted, but only the first was statistically significant. Two of the others indicated possible across-taxa associations with environmental factors (Steppan, 1988).

Correlations between both the dependent and the independent variables with the first canonical variable (CV1) are shown in Table 3. Although the correlation between

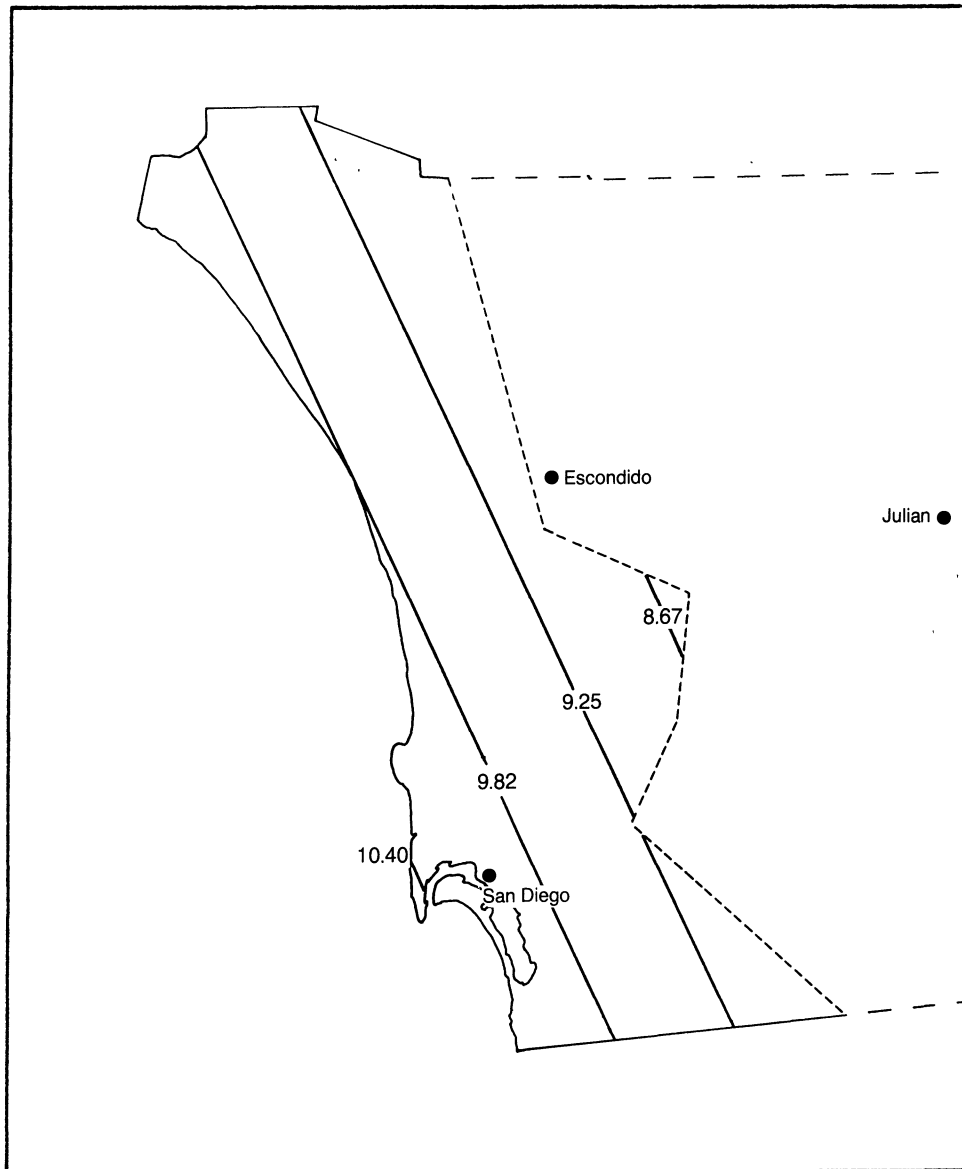


FIG. 6. First order trend surface for *ssp. scoparius* DisFunc 1 scores ($r^2 = 0.278$, $P < 0.025$). Higher values are more *scoparius*-like. The orientation of the first order surface for *ssp. brevialetatus* is parallel, though reversed.

KERATIO and CV1 is relatively small (0.337), an examination of the other correlations leads to the interpretation of CV1 as being comparable to DisFunc 1; i.e. resolves the three morphs. Canonical Variable 1 is most highly correlated with the environmental variables of elevation (-0.870), mean annual rainfall (-0.860), and growing season potential evapotranspiration (0.675). Elevation and rainfall are themselves only mildly correlated with each other ($r^2 = 0.359$, $n = 102$), as are elevation and PET ($r^2 = 0.433$, $n = 102$). The remaining environmental variables, soil pH (-0.369), slope aspect (-0.160), and slope angle (-0.034) were not important in explaining the distribution of flower traits.

While correlations with elevation, rainfall, and PET may be high, indicating a strong association between them and *L. scoparius* morphs, the variance explained by CV1 of the

dependent variables is only 27.7%. Thus, most of the variation in flower morphology as represented by the canonical variables is left unexplained by environmental factors.

If the subspecies are indeed adapted to different environmental conditions, then they should partition the environment when they are in close proximity. Sites falling within the transition zone were tested for evidence of any partitioning. In contrast to the situation for all sites (Table 2), none of the environmental variable means were significantly different between *scoparius* and *brevialatus*. Additionally, canonical correlation analysis was performed on transition zone sites. The only resulting canonical variable that was roughly comparable to CV1 (all sites) and DisFunc 1 was not significant ($P > 0.3$). There was, therefore, no significant partitioning for these six selected environmental factors within the transition zone.

TABLE 2. Mean environmental variables by morph. Standard deviations are in parentheses. *T*-values calculated for difference of means between *Lotus scoparius* (Nutt. in T. and G.) *Ottley ssp. scoparius* and *ssp. brevialetus* (Ottley) Munz.

Variable	<i>scoparius</i>	Hybrid	<i>brevialatus</i>	<i>T</i> -value
Elevation (ft)	500 (343) (<i>n</i> = 37)	1615 (1098) (<i>n</i> = 18)	1342 (1015) (<i>n</i> = 52)	4.83*
Precipitation (in.)	11.78 (1.94) (<i>n</i> = 37)	16.72 (4.86) (<i>n</i> = 18)	14.19 (3.78) (<i>n</i> = 52)	3.56*
Soil pH	6.16 (0.54) (<i>n</i> = 30)	6.19 (0.25) (<i>n</i> = 17)	6.45 (0.44) (<i>n</i> = 44)	2.51*
Growing season PET	31.0 (2.46) (<i>n</i> = 37)	27.8 (5.72) (<i>n</i> = 18)	27.7 (4.52) (<i>n</i> = 52)	4.03*
Slope angle (°)	12.87 (11.68) (<i>n</i> = 33)	12.26 (9.32) (<i>n</i> = 17)	13.65 (11.74) (<i>n</i> = 48)	0.28
Slope aspect (°)	86.0 (52.0) (<i>n</i> = 25)	101.2 (51.0) (<i>n</i> = 13)	107.7 (56.5) (<i>n</i> = 35)	1.52

**P* < 0.05.

DISCUSSION

Evolutionary and geographic history

It is clear that *ssp. brevialetus* is derived from *ssp. scoparius* because the flower morphology of *scoparius* is the dominant one in the genus, while the suite of flower traits that distinguish *brevialatus* are unique within western *Lotus* (Steppan, 1988). The smaller variance of *brevialatus* discriminant function scores might suggest that it had a shorter evolutionary history within San Diego County in which to accumulate genetic variability (Endler, 1977). Variances for *scoparius* are 38% greater than *brevialatus* for DisFunc 1 and 100% greater for DisFunc 2.

Morphological differences between the three morphs include nearly every flower part in both form and size, indicating the effects of multiple genes. Also it is difficult to explain the differences simply in terms of timing or termination of development. The dominance pattern of the relevant alleles is unclear, but the morphological discontinuity in the transition zone is consistent with significant

linkage disequilibrium (Barton & Hewitt, 1985). Such a condition along with low gene flow may reflect incipient speciation. Although the hybrid populations are more variable, no populations appear to be back-crossed with the parental subspecies. Experiments in controlled breeding are needed to better define inheritance patterns and hybrid fertility.

The differences between *brevialatus* and *scoparius* are so distinctive and numerous that they are unlikely to have evolved principally by random processes. Instead, *brevialatus* flower morphology more likely improved its fitness over *scoparius*. Insufficient evidence was obtained to determine if differential pollinator success or pollinator specificity would account for this postulated improvement in fitness.

Wherever *brevialatus* originated, it dispersed latitudinally to its present distribution stretching from the southern Sierra Nevada in the north to the Sierra de la Laguna in the south, spanning 13° of latitude. The extent to which *brevialatus* invaded new territory or displaced *scoparius* is unclear. All hybrid populations are either within the transition zone or within the interior range of *brevialatus*. It is possible that the interior populations (historical and current) are remnants of a once more extensive *scoparius* distribution. If this is also true for the hybrids collected from Banner in 1936, then an antecedent distribution for *scoparius* extending to the edge of the desert is indicated. There is no evidence of a shift in transition zone location over the last 80 years. However, the long-term stability of the boundary has not been established.

The geometry of the two subspecies ranges supports the importance of environmental factors in determining their distribution. Both ranges are very latitudinally elongate and remain parapatric for over 400 km. Without differential selection, *brevialatus* surely has had sufficient time to disperse to the Pacific coast. It has not. Thus *brevialatus* has clearly been excluded from the coastal strip. The distinct reduction in the east-west range of *scoparius* to a uniformly narrow coastal strip may indicate a competitive advantage belonging to *brevialatus* for southern foothill and mountain interior environments.

TABLE 3. Correlations between flower traits (dependent variables) and environmental variables (independent variables) with the First Canonical Variable. Correlations with absolute values greater than 0.5 are in italics.

Variable	Canonical variable 1
Claw length	<i>0.750</i>
TERATIO	<i>-0.698</i>
CLRATIO	<i>0.686</i>
Wing length	<i>0.549</i>
Calyx tube length	<i>0.523</i>
Keel length	0.361
KERATIO	0.337
Wing spread	0.319
Total calyx length	0.233
Elevation	<i>-0.870</i>
Rain	<i>-0.860</i>
Growing season PET	<i>0.675</i>
Soil pH	<i>-0.369</i>
Slope aspect	<i>-0.160</i>
Slope angle	<i>-0.034</i>

The boundary between the subspecies corresponds fairly closely with both Axelrod's (1978) and Westman's (1983) boundaries between the Diegan and Riversidian divisions/associations of coastal sage scrub. Axelrod characterizes the Riversidian division as being less equable due to greater mean annual range of temperature (about 14.5°C versus 8.5°C) but with greater mean annual rainfall (13 versus 9 inches); while Westman attributes greater water stress to the Riversidian due to greater evapotranspiration in summer.

Environmental variables of elevation, rainfall, and growing season PET significantly predicted DisFunc 1 scores (i.e. morphs). However, the association was weak and environmental partitioning in the transition zone was not evident, in contrast to some oak hybrids (Benson *et al.*, 1967). Determination of adaptive differences in *L. scoparius* must wait until controlled experiments have been conducted. Subspecies *brevialatus* is possibly more responsive to summer rains (E. Nilsen, personal communication). This and related aspects of water relations are now being tested on plants grown from seeds collected from sites throughout San Diego County.

Significantly, the two subspecies exhibit opposite trending clines, suggesting that they may not be controlled by the same factor. For example, the pattern provides little evidence for character displacement. Subspecies *scoparius* possesses the steeper cline. This weak coast-to-inland cline could result from selection pressure – possibly the same pressure that drove the evolution of *brevialatus* – or the effects of gene flow from *brevialatus*. If the cline is due to environmental effects on phenotype, then proximity to *brevialatus* should not influence *scoparius* morphology. However, when proximity to *brevialatus* is accounted for by regressing DisFunc 1 scores against distance to the MTZ, then the cline appears stronger with a higher r^2 (0.404 versus 0.278). This may suggest a genetic basis through minor variants of *scoparius*-condition alleles or limited introduction of *brevialatus* alleles after recombination had reduced linkage disequilibrium.

Transition zone width and the attendant slope of a cline is a function of the strength of selection and rate of gene flow (Endler, 1977; Pielou, 1979; Slatkin, 1973). Given the steep (and discontinuous) cline for *L. scoparius*, and the evidence pointing towards weak selection, gene flow across the zone should likewise be small.

Extension of this study to the entire species range could explore the questions untouched by this study. Principally, do the spatial patterns observed for San Diego County continue throughout the range? If the clines occur only within the parapatric latitudes, then the conclusions of this study would be significantly strengthened. Samples of ssp. *scoparius* from the San Francisco Bay Area are among the most *brevialatus*-like populations measured (Steppan, unpublished data). The large disjunction for *brevialatus* in Baja California could prove informative as it resembles a tectonically produced vicariance pattern commonly found in Baja California herpetofauna (Grismer, 1987). If the disjunction in *brevialatus* was produced vicariantly, possible times were 6 MYBP when the Cape region again became isolated from the north

(Murphy, 1983; and references therein), or stemming from Pleistocene glaciations when shrub communities extended 750 m below present elevational limits (Axelrod, 1966; Murphy, 1983).

ACKNOWLEDGMENTS

I wish to thank my committee members J. F. O'Leary, B. E. Fredrich and M. G. Simpson. Additional helpful input was provided by M. R. Beauchamp, T. Cohn, L. McClenaghan and S. C. Aitken. A. M. Kawamoto produced the botanical illustrations. W. Westman and an anonymous reviewer provided cogent and beneficial comments. This research was supported by a grant from the California Native Plant Society.

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