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FLORAL VARIATION IN *DELPHINIUM VARIEGATUM* (RANUNCULACEAE)

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ABSTRACT

Delphinium variegatum is subdivided into three subspecies distinguished by three floral characters. *Delphinium v. variegatum* is found in central and northern California, while *D. v. kinkiense* (an endangered taxon) and *D. v. thornei* are endemic to San Clemente Island off the coast of southern California. Broad variation is documented in most natural populations for all three floral characters. Our results indicate that the two metric characters, lateral sepal length and lower petal blade length, provide no clear distinction between the taxa. Sepal color is the least ambiguous for differentiating the subspecies, but is problematic in distinguishing between *D. v. kinkiense* and *D. v. thornei.* Sepal color exhibits a complex pattern of variation on San Clemente Island in which northern populations generally contain primarily light-flowered individuals, southern populations generally contain primarily dark-flowered individuals, and central populations may contain substantial numbers of both light- and dark-flowered individuals as well as intermediates. However, one southern population contains primarily light-flowered individuals, and almost half of the populations contain individuals having sepal colors considered to represent the two different subspecies. Further taxonomic study including additional characters is recommended to determine whether *D. v. kinkiense* and *D. v. thornei* should be considered distinct taxa.

Delphinium variegatum Torrey & A. Gray (Ranunculaceae) is a perennial larkspur that is found in grassland and open woodlands of mainland California and San Clemente Island, the southernmost of the Channel Islands off the coast of southern California (Warnock 1990b). One subspecies, *D. v.* ssp. *variegatum* (Royal larkspur), is found exclusively on the mainland and ranges approximately from northern to central California, from the coast to the Sierra Nevada ?? foothills (Fig. 1). The other two subspecies, *D. v.* ssp. *kinkiense* (Munz) M. J. Warnock (San Clemente Island larkspur; Warnock 1990a) and *D. v.* ssp. *thornei* Munz (Thorne's larkspur; Munz 1969) are insular endemics found only on San Clemente Island. The Channel Islands are thought to provide refuge for a number of species with northern affinities, including *D. variegatum* (Raven and Axelrod 1978), that once extended farther south on the mainland during Pleistocene pluvial cycles (Raven 1963).

The island endemic subspecies of *D. variegatum* are vulnerable to extinction because of their limited distribution (Skinner and Pavlik 1994). *Delphinium v. kinkiense* is listed as endangered by the U.S. Fish & Wildlife Service (USFWS) and by the California Department of Fish and Game. However, the rarest of the subspecies, *D. v. thornei,* has no special legal status, although the USFWS considers it to be a species of concern. Both of these taxa are on the California Native Plant Society List 1B (plants rare, threatened, or endangered in California and elsewhere; Skinner and Pavlik 1994).

The subspecies of *D. variegatum* are distinguished primarily by three floral characters: sepal color, lateral sepal length and lower petal blade length (Warnock 1990b, 1993, 1997; summarized in Table 1; Fig. 2). However, there is overlap among the subspecies. The mainland subspecies, *D. v. variegatum,* is differentiated from the two island subspecies by its deep royal blue flowers, as the ranges for the two metric characters encompasses the variation observed in the entire species. The two island subspecies are differentiated from each other by all three characters, in spite of considerable overlap, with *D. v. kinkiense* having mainly white, smaller flowers and *D. v. thornei* having mainly bright blue, larger flowers. Munz (1974), interestingly, had described *D. v. thornei* as having smaller flowers (sepals ca. 12 mm long) than *D. v. kinkiense* (which he recognized as a separate species, *D. kinkiense*; sepals 16–18 mm long). Current keys use sepal color to identify taxa (Warnock 1990b, 1993, 1997), although the most recent also uses density of hairs on the base of the stem to distinguish between *D. v. variegatum* and the island subspecies (Warnock 1997).

Casual observation of natural populations of *D. variegatum* on San Clemente Island suggests that hybridization may be occurring between *D. v. kinkiense* and *D. v. thornei* in some populations. At

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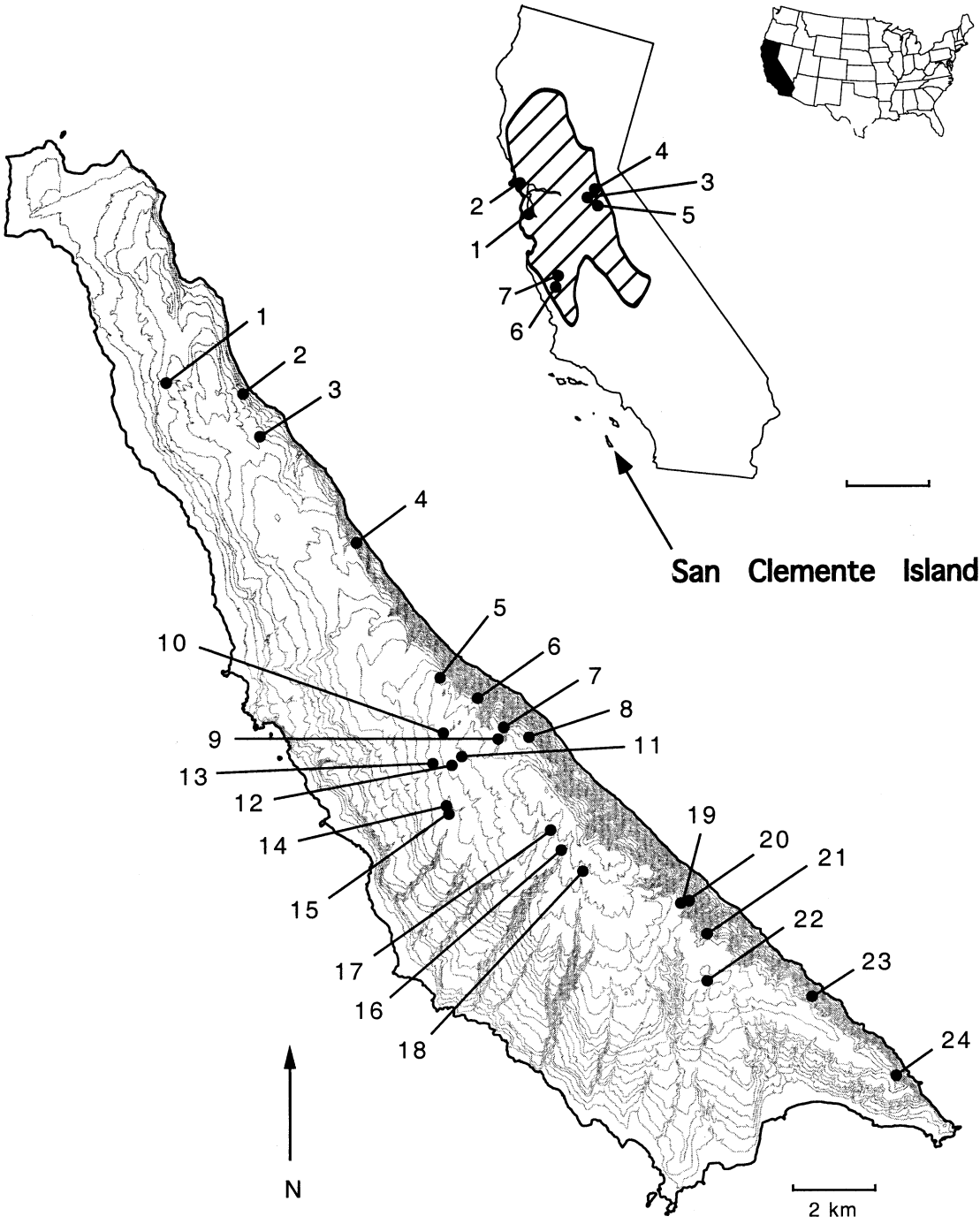

FIG. 1. Distribution and sampled populations of *Delphinium variegatum* from mainland California (ssp. *variegatum*) and from San Clemente Island (ssp. *kinkiense* and ssp. *thornei*).

the time this study was initiated, fewer than 15 populations of *D. variegatum* were known on San Clemente Island (along with scattered individuals), with *D. v. kinkiense* occurring in the northern half of San Clemente Island and *D. v. thornei* in the southern half. However, some populations in the central part of San Clemente Island include individuals exhibiting white, bright blue or intermediate flower colors. Natural hybridization has been documented to regularly occur among other taxa in the

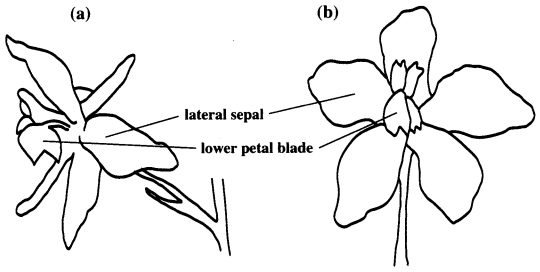

FIG. 2. Diagram of (a) side view and (b) front view of a *D. variegatum* flower.

genus *Delphinium* (Warnock 1990b, 1997); natural hybrids are known between *D. v. variegatum* and *D. hansenii, D. hesperium, D. parryi,* and *D. recurvatum* (Lewis and Epling 1954).

The goals of this study were (1) to document variation in floral morphology in natural populations of the subspecies of *D. variegatum,* (2) to evaluate the utility of the three floral characters for distinguishing *D. v. kinkiense* and *D. v. thornei,* and (3) to identify populations of *D. variegatum* on San Clemente Island as *D. v. kinkiense, D. v. thornei* or mixed populations.

MATERIALS AND METHODS

Study sites. Twenty-four populations of *D. v. kinkiense* and *D. v. thornei* were located and sampled from San Clemente Island in 1996 (Fig. 1; Table 2). This represents all known populations and probably all of the populations on the island; subsequent surveys have failed to reveal additional locations (Junak and Wilken 1998; S. Burckhalter, University of South Dakota, pers. comm.; K. Helenurm, personal observation). Seven populations of *D. v. variegatum* were sampled across its range, from Marin County in the north to southern Monterey County and east to Tuolumne and Mariposa Counties. All populations of the three subspecies occurred in open grassland habitat. Island populations were found only on west or northerly aspects, probably due to moister, cooler conditions in these areas.

Flower collection and measurements. Thirty to forty-four flowering individuals were haphazardly sampled from large populations (Table 2). In smaller populations, all flowering individuals were sampled. Two flowers from each sample individual were measured for sepal color, lateral sepal lengths, and lower petal blade lengths (Fig. 2). Sepal color was measured by matching lateral sepals to a color chart (Royal Horticultural Society 1986). Colors were quantified by matching the color chart patches to colors in Adobe Photoshop (1995) computer software using a calibrated monitor. We recorded their hue, saturation, and brightness values using the same computer system for all measurements. Values for brightness were used for analysis because brightness (quantifying the degree of lightness or darkness, ranging from 0 representing black to 100 representing white) best reflects Warnock's (1990b) descriptions of the subspecies and the range of variation in flower color we observed. Although differences in hue (the attribute of colors that permits them to be classed as blue versus lavender or purple, for example) and saturation (the degree of difference from a gray having the same lightness) occur, the quantifiable difference between white, light blue, bright blue and deep royal blue sepals is reflected in brightness values rather than hue or saturation.

In all, 775 individuals were measured for floral characters in all 24 San Clemente Island populations, and 242 individuals were measured in 7 mainland populations, for a total of 1017 individuals.

Analysis. Measurements of brightness and metric characters were averaged for different flowers of the same individual. Associations among the different floral characters in *D. v. kinkiense* and *D. v. thornei* were addressed in three ways. First, t-tests were used to test differences in lateral sepal and lower petal blade lengths in individuals with light versus dark sepal color. Second, correlations among the floral characters were tested using Pearson's correlation analysis. Third, grouping of floral characters was investigated using principal components analysis (PCA). All analyses were performed using SYSTAT (1992).

RESULTS

Variation in floral morphology. Box plots of floral variation in *D. variegatum* illustrate broad variation in most natural populations on San Clemente Island (Fig. 3). Sepal color is invariant, or nearly so, in some populations (populations 1–7, 10). The metric characters, lateral sepal length and lower

TABLE 1. FLORAL CHARACTERS USED TO DISTINGUISH THE THREE SUBSPECIES OF *DELPHINIUM VARIEGATUM* (SUMMARIZED FROM WARNOCK 1990B, 1993, 1997).

Floral character	*Delphinium variegatum* ssp. *kinkiense*	ssp. *thornei*	ssp. *variegatum*
Sepal color	white to light blue (or lavender)	light blue to bright blue	deep royal blue, rarely white or lavender
Lateral sepal length	11–18 mm	17–21 mm	10–25 mm
Lower petal blade length	4–9 mm	6–11 mm	4–11 mm

TABLE 2. POPULATION NUMBER, SUBSPECIES DESIGNATION, COLLECTION LOCATIONS, APPROXIMATE POPULATION SIZES (1996), AND SAMPLE SIZES OF DELPHINIUM VARIEGATUM. San Clemente Island populations are listed north to south.

Population number	Subspecies	Location	Population size	Sample size
Island				
1	*kinkiense*	Flasher Canyon	200	28
2	*kinkiense*	Nots Drive	200	41
3	*kinkiense*	Pelican Canyon	2500	44
4	*kinkiense*	Larkspur Canyon	150	40
5	*kinkiense*	Stone Canyon	500	37
6	*kinkiense*	Burns-Horton Canyon	>1000	40
7	*kinkiense*	Lower Twin Dams Canyon	16	9
8	mix	Boulder	200	40
9	mix	Upper Twin Dams Canyon	1000	39
10	*kinkiense*	Warren Canyon	200	37
11	*thornei*	Upper Middle Ranch Canyon	75	32
12	mix	Lower Middle Ranch Canyon	350	32
13	*kinkiense*	Waynuk Canyon	1000	41
14	*thornei*	North Norton Canyon	60	17
15	*thornei*	South Norton Canyon	500	36
16	*thornei*	Horse Canyon	16	6
17	*thornei*	Box Canyon	150	30
18	*thornei*	Cave Canyon	400	37
19	*thornei*	Eagle Canyon	150	38
20	*thornei*	Eagle-Bryce Canyon	7	6
21	*thornei*	Bryce Canyon	200	39
22	*thornei*	Malo	300	31
23	*thornei*	Canchalagua Canyon	3000	40
24	*kinkiense*	Guds	75	35
Mainland				
1	*variegatum*	Edgewood County Park	200	33
2	*variegatum*	China camp State Park	100	38
3	*variegatum*	Green Springs Road	40	22
4	*variegatum*	Chinese Station	200	40
5	*variegatum*	Route 49	150	39
6	*variegatum*	Nacimiento-Ferguson Road	200	31
7	*variegatum*	G14	250	39

petal blade length, are highly variable in most populations, with largely overlapping ranges.

Mainland populations show a similar pattern (Fig. 3). Sepal color is relatively invariant in mainland populations with the exception of China Camp State Park, in which many white-flowered individuals occurred (18 of the 38 sampled). Mainland populations also show variation in metric characters, but they generally have narrower distributions with fewer outside values. Edgewood County Park has longer lateral sepals and lower petal blades than the other mainland populations.

Histograms of the three floral characters indicate lighter-colored and larger flowers for the island populations (treated together because of the broadly overlapping distributions noted above) than for mainland populations (Fig. 4). Sepal color is distributed bimodally on the mainland only because of white-flowered individuals in China Camp State Park. The distribution of sepal color on San Clemente Island is clearly bimodal, with 375 of the 775 individuals sampled (48.4%) having white or very light blue flowers (henceforward "light-flowered"; brightness values from 88–100), 72 (9.3%) being intermediate (brightness values 56–87), and 328 (42.3%) having bright blue flowers (henceforward "dark-flowered"; brightness values 28–55). In contrast, the metric characters have unimodal distributions.

The overall bimodal distribution of sepal color on San Clemente Island shows a geographic pattern. Northern populations generally contain primarily light-flowered individuals and southern populations generally contain primarily dark-flowered individuals (Fig. 5). Central populations may contain substantial numbers of both flower types as well as intermediates.

Association among floral characters. The lateral sepal lengths of San Clemente Island individuals with light (brightness values 88–100) and dark (brightness values 28–55) sepal colors are significantly different ($t = -5.78$, $df = 698$, $P < 0.0001$), but their means (16.31 mm and 17.07 mm, respectively) and ranges (12.0–21.75 mm and 10.75–24.25 mm, respectively) are very similar. Likewise, lower petal blade lengths are significantly different for the two brightness classes ($t = -6.11$, $df = 689$,

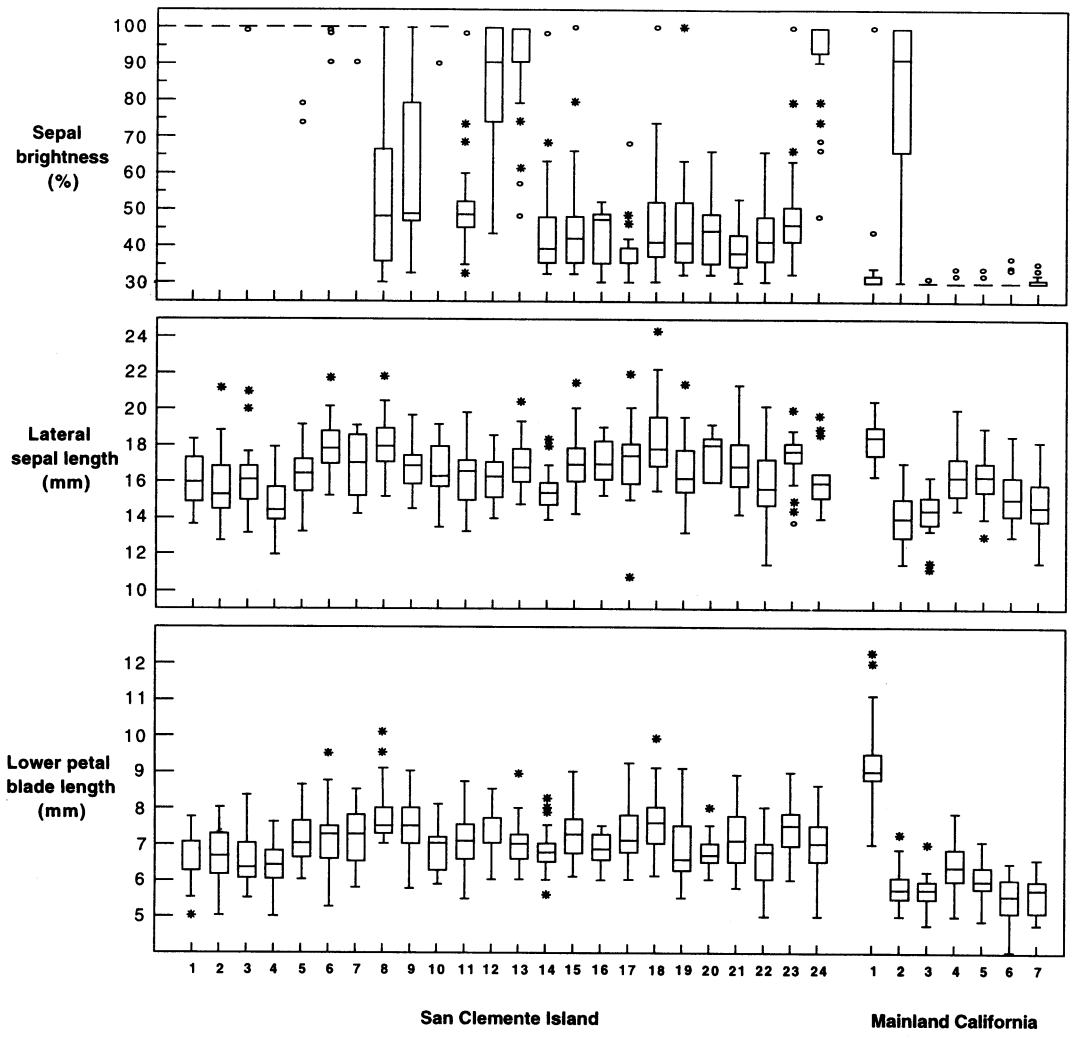

FIG. 3. Box plots of (a) brightness, (b) lateral sepal length, and (c) lower petal blade length in populations of *D. variegatum*. Median values (central line, defining the 50th percentile), upper and lower hinges (edges of the central box, defining the 25th and 75th percentiles), whiskers (extending to the farthest observation from the hinges not farther than 1.5 times the distance between the hinges), outside values (asterisks, observations farther from the hinges than 1.5 times the distance between the hinges), and far outside values (open circles, observation farther from the hinges than 3.0 times the distance between the hinges) are illustrated.

$P < 0.0001$), but their means (6.86 mm and 7.22 mm, respectively) and ranges (5.0–9.5 mm and 5.0–10.12 mm, respectively) are almost identical. Three of the four means fall within the overlapping portion of the ranges described for the two subspecies (Warnock 1990b, 1993, 1997).

A strong correlation exists between lateral sepal length and lower petal blade length (Pearson's $r = 0.619$, $P < 0.0001$; Fig. 6). Weaker correlations exist between brightness and lateral sepal length (Pearson's $r = -0.213$, $P < 0.0001$) and between brightness and lower petal blade length (Pearson's $r = -0.216$, $P < 0.0001$).

PCA groups individuals primarily by flower color with a broad range of lateral sepal and lower petal blade lengths for each color class (Fig. 7). The first two axes account for 58.11% and 29.20% of the total variation, for a total of 87.31%. Plots of the first and third and of the second and third axes (not illustrated) are dense clouds of points showing no structure.

The deep royal blue sepal color of *D. v. variegatum* is significantly different from both light-flowered and dark-flowered island plants (mean = 38.19, range = 30.0–100.0; $F = 1778.9$, df = 2, $r^2 = 0.798$, $P < 0.0001$; Tukey HSD multiple comparison $P < 0.0001$ for both comparisons). Lateral sepals in *D. v. variegatum* are significantly shorter than in light-flowered and dark-flowered island plants (mean = 15.66, range = 11.25–20.5; F =

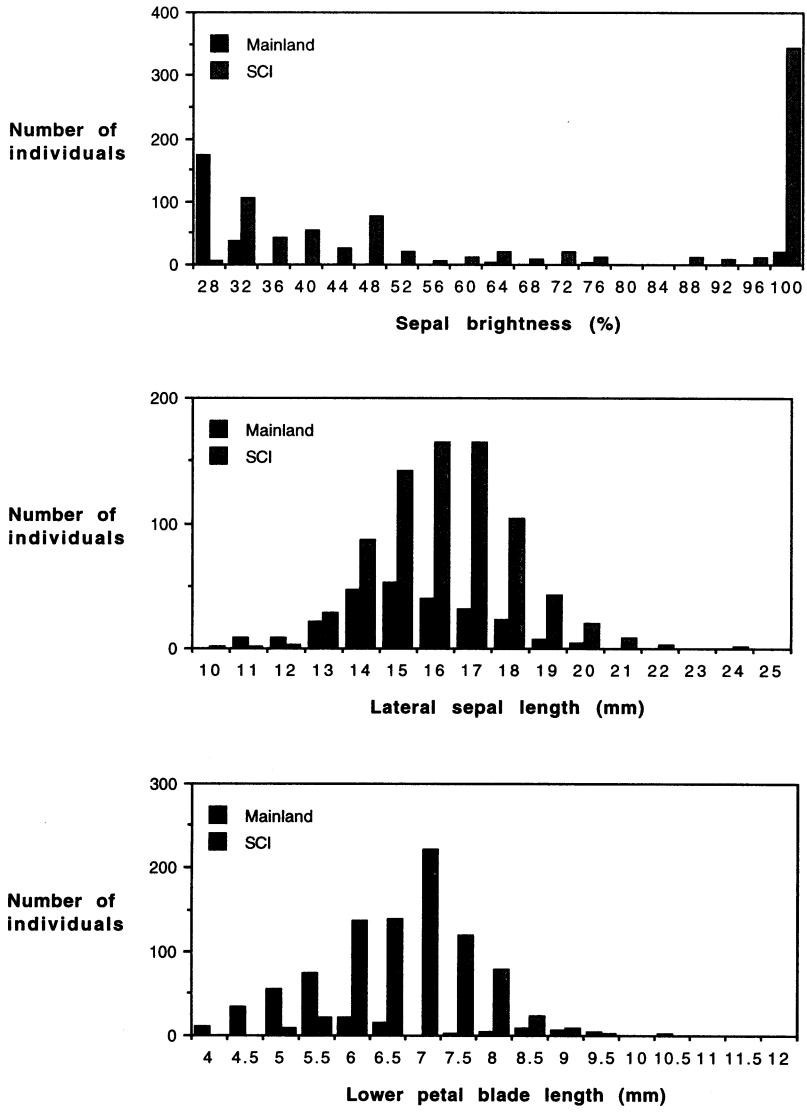

FIG. 4. Histograms of brightness, lateral sepal length, and lower petal blade length for populations of *D. variegatum* on San Clemente Island. X-axis values represent the minimum of a class.

37.2, df = 2, $r^2 = 0.076$, $P < 0.0001$; Tukey HSD multiple comparison $P < 0.0001$ for both comparisons). Lower petal blades are also significantly shorter in *D. v. variegatum* (mean = 6.34, range = 4.00–12.15; F = 47.7, df = 2, $r^2 = 0.097$, $P < 0.0001$; Tukey HSD multiple comparison $P < 0.0001$ for both comparisons).

DISCUSSION

Floral variation. All three floral characters exhibit substantial variation within populations. The metric characters, lateral sepal length and lower petal blade length, exhibit unimodal distributions both on the mainland and on San Clemente Island. Mainland populations have smaller flowers than island populations, with the exception of Edgewood County Park in which lower petal blades lengths even exceed those of San Clemente Island plants.

Sepal color is relatively invariant on the mainland, although it shows a bimodal distribution due to the high proportion of white-flowered individuals in China Camp State Park. In contrast, sepal color is clearly bimodally distributed on San Clemente Island. Most island populations of *D. variegatum* are highly variable in sepal color, although some consist primarily of white-flowered individuals.

Floral characters and taxonomy. Warnock (1990b) divided *D. variegatum* into three subspecies primarily on the basis of sepal color, lateral sepal length, and lower petal blade length. The

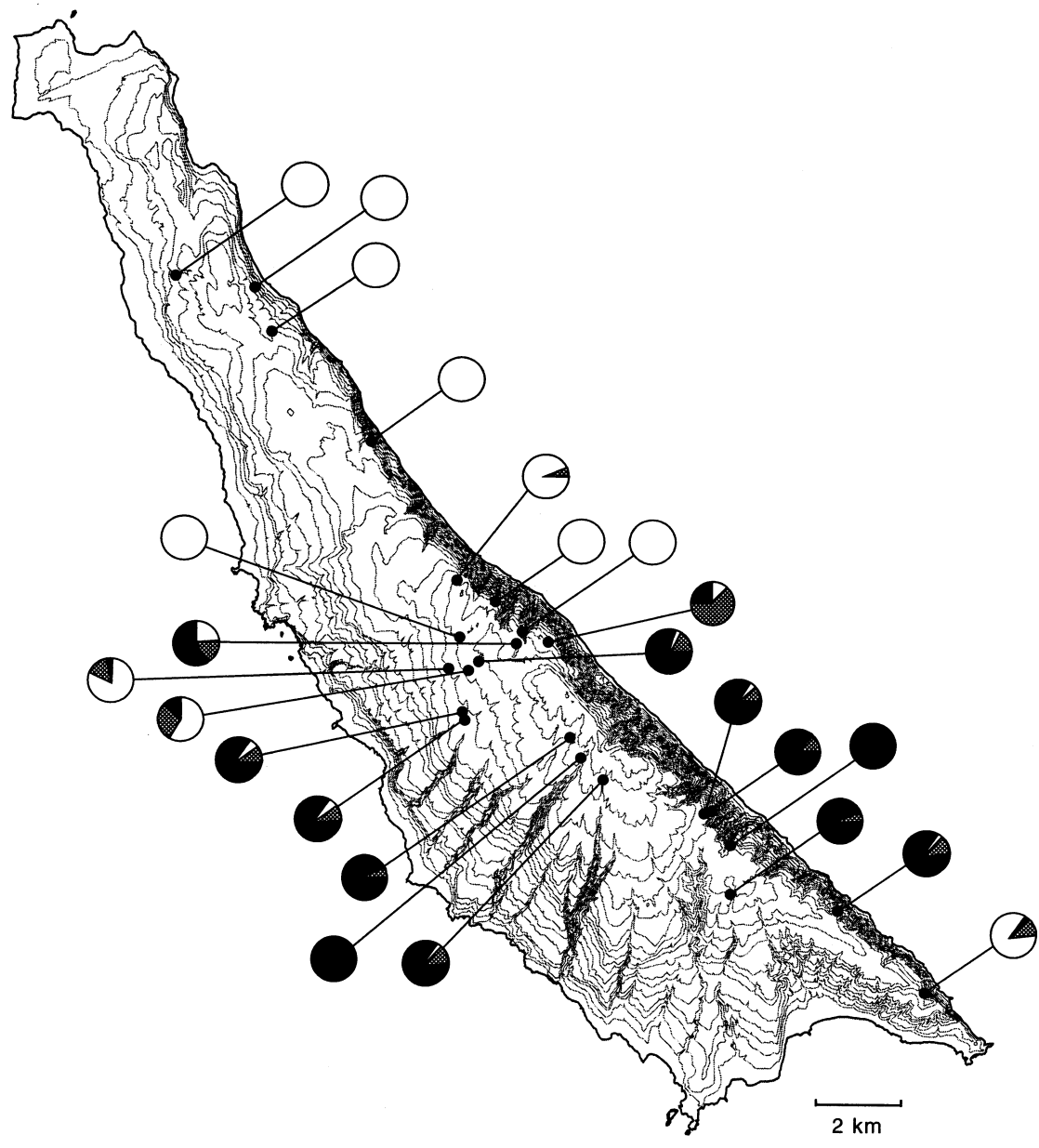

FIG. 5. Pie charts of flower color in San Clemente Island populations of *D. variegatum.* White areas represent proportion of individuals with white or light blue flowers (brightness values from 88 to 100), black areas represent individuals with bright blue flowers (brightness ≤55), and stippled areas represent individuals with intermediate colors (brightness values from 56 to 87).

mainland populations we sampled generally fit Warnock's (1990b) descriptions of *D. v. variegatum* (Table 1), although some individuals in Edgewood County Park have lower petal blade lengths exceeding the described taxonomic range. *Delphinium v. variegatum* differs from the two island subspecies in generally having darker (deep versus bright blue) flowers (except for many individuals in China Camp State Park) and shorter lower petal blades (except in Edgewood County Park).

Considerable population differentiation appears to exist within *D. v. variegatum.* Of the seven populations we sampled, two are morphologically distinct: China Camp State Park has a high proportion of white-flowered individuals (absent in the other populations we sampled), and Edgewood County

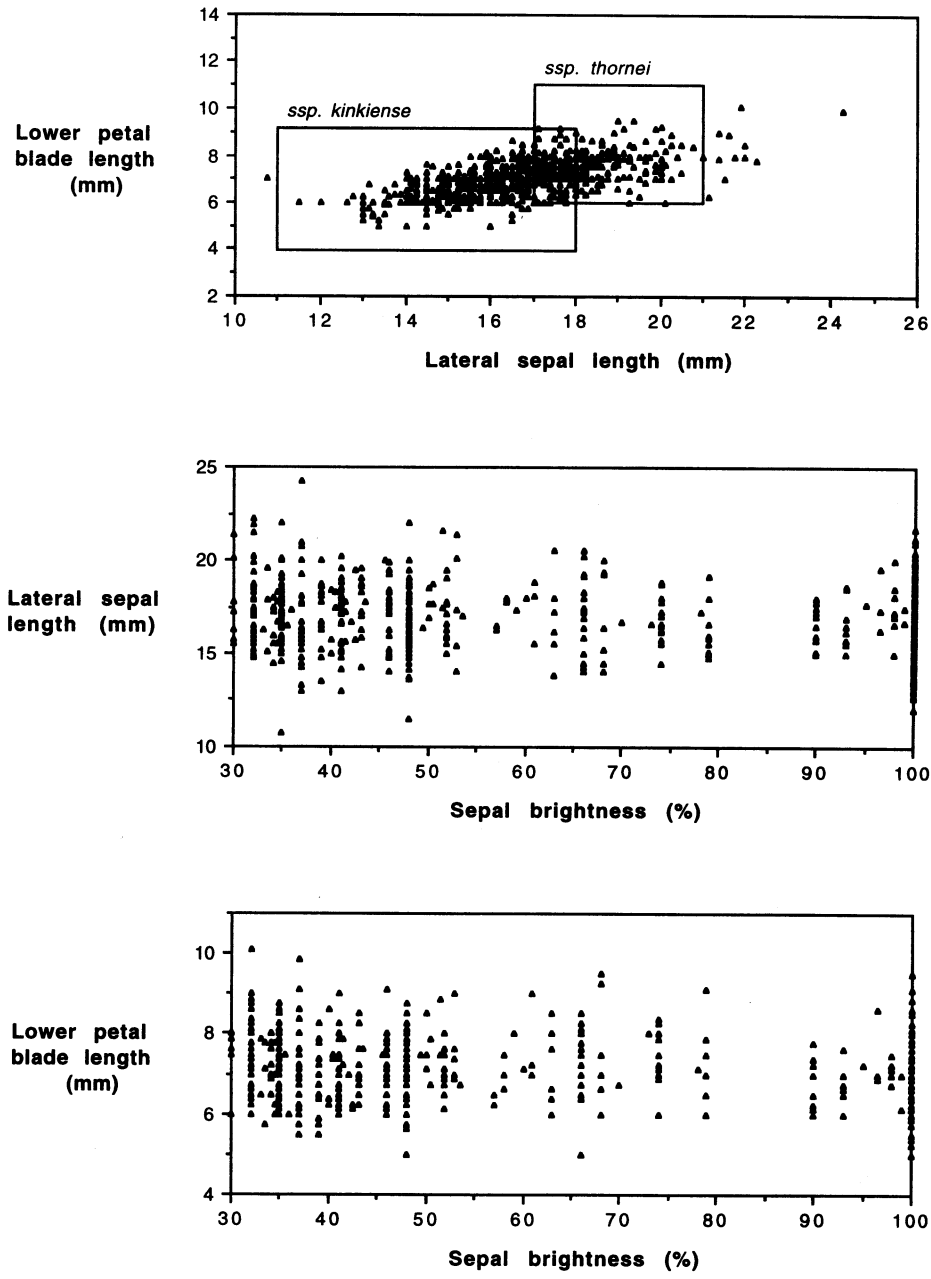

FIG. 6. Scatterplots of sepal brightness, lateral sepal length, and lower petal blade length for individuals of all populations of *D. variegatum* on San Clemente Island. Taxonomic designations shown are from Warnock (1990b, 1993, 1997).

Park has larger flowers than other populations. Subsequent to sampling, we discovered that Edgewood Park is the only population we sampled that occurs on serpentine soils. Warnock (1990b) considers serpentine soil populations of *D. v. variegatum* to be not well marked morphologically and did not recognize them as distinct taxa. Instead, Warnock (1997) comments that plants with large flowers are common in the San Francisco Bay area, either as scattered individuals or as populations made up largely of such individuals. In other species, plants growing on serpentine soils have often been documented to be morphologically and genetically distinct from plants growing on non-serpentine soils (Kruckeberg 1954; Mayer et al. 1994). Intensive sampling of additional natural populations of *D. v.*

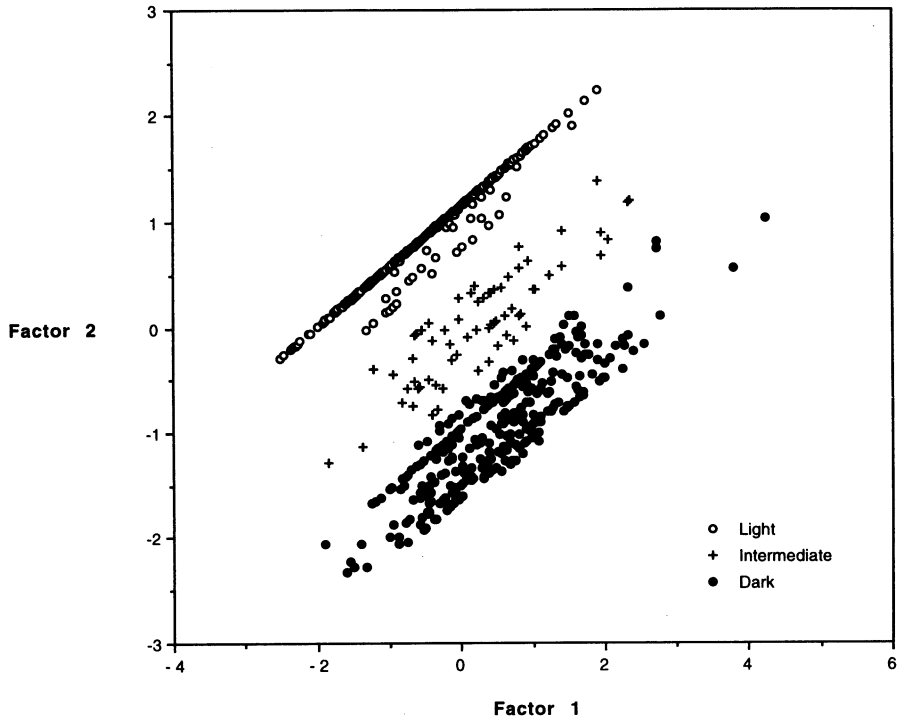

FIG. 7. Scatterplot of the first and second PCA axes for floral characters in *D. variegatum* on San Clemente Island. Individuals are coded as having light (brightness values 88–100), intermediate (brightness values 56–87) or dark (brightness values 28–55) flower color.

variegatum may clarify whether serpentine soil populations are differentiated morphologically from non-serpentine soil populations or whether variation is geographic in pattern.

Delphinium v. kinkiense and *D. v. thornei* also generally conform to Warnock's (1990b, 1993, 1997) descriptions, in spite of some individuals having lateral sepals exceeding the described taxonomic range (Fig. 6). However, our data do not support the separation of *D. v. kinkiense* and *D. v. thornei* on the basis of all three floral characters. Specifically, our results indicate that the two metric characters, lateral sepal length and lower petal blade length, provide no clear distinction between these taxa. Both exhibit a unimodal distribution on San Clemente Island so that any attempt to use them for delineating taxa is necessarily arbitrary. In addition, the majority of individuals fall within or near the area of overlap for these characters.

Both lateral sepal length and lower petal blade length show a statistically significant association with sepal color, indicating that light-colored flowers tend to be smaller than dark-colored flowers. These results are in agreement with Warnock's (1990b) descriptions. However, their significance should be considered an artifact of large sample size. The almost identical means and almost completely overlapping ranges of the metric characters for light- versus dark-colored flowers indicate that the statistical differences have little taxonomic significance.

The remaining floral character, sepal color, is the least ambiguous for differentiating between *D. v. kinkiense* and *D. v. thornei* but it is also problematic, exhibiting a more complex pattern of variation on San Clemente Island than previously suspected. Although northern populations generally contain primarily light-flowered individuals and southern populations generally contain primarily dark-flowered individuals, central populations may contain substantial numbers of both flower types as well as intermediates. Moreover, this is only a general trend as the southernmost population (Guds) is predominantly, although not exclusively, light-flowered. In addition, nearly half of the populations (11 of 24) contain both light- and dark-flowered individuals, thus having individuals with sepal colors considered to represent different subspecies. The complex pattern of variation observed for sepal color on San Clemente Island may be due to hybridization and subsequent introgression between the taxa. Genetic data may provide evidence regarding this possibility.

The discrepancy between our results and the taxonomic separation of *D. v. kinkiense* and *D. v. thornei* is probably due to our intensive sampling of all natural populations of *D. variegatum* on San Clemente Island. The taxonomic descriptions of these

taxa are based on examination of herbarium specimens (M. Warnock, University of Missouri, Columbia, pers. comm.) that may have represented only a fraction of the variation found in natural populations. This is clearly a potential problem with any taxon endemic to remote locations, especially in cases where access is highly restricted (permission of the U.S. Navy is required to visit San Clemente Island).

Classification of San Clemente Island populations. Because *D. v. kinkiense* is listed as endangered and *D. v. thornei* is merely considered a species of concern by the USFWS, it is necessary for practical reasons to identify populations on San Clemente Island. Since our analyses show poor separation between subspecies for lateral sepal and lower petal blade lengths, sepal color was used to classify populations as *D. v. kinkiense, D. v. thornei,* or mixed. Populations having at least 80% light-flowered individuals (brightness values between 88 and 100) were classified as *D. v. kinkiense,* and populations having at least 80% dark-flowered individuals (brightness values below 56) were classified as *D. v. thornei.* Populations with less than 80% of its individuals in either brightness range were classified as mixed. This criterion is based on the observed bimodal distribution of sepal color. Using this criterion, there are 10 populations of *D. v. kinkiense,* 11 populations of *D. v. thornei,* and 3 mixed populations (Table 2, Fig. 5).

Although an 80% criterion seems to be a weak basis for distinguishing taxa, it may be preferable to a stricter classification. If Warnock's (1990b, 1993, 1997) descriptions are interpreted in conjunction with the bimodal distribution we have documented, then individuals with brightness values from 88 to 100 may be classified as *D. v. kinkiense* (white to light blue flowers) and individuals with brightness values below 88 may be classified as *D. v. thornei* (light blue to bright blue flowers). Using this criterion, there are 7 populations of *D. v. kinkiense,* 5 populations of *D. v. thornei,* and 11 mixed populations (Fig. 5).

The results of this study indicate that *D. v. kinkiense* and *D. v. thornei* are, at best, currently separable only on the basis of sepal color. They may be more appropriately classified as varieties rather than subspecies or classified together as one subspecies (as defined by Stuessy 1990). However, it is not uncommon for plant taxa to be separated on the basis of morphological characters controlled by only one or two loci, such as flower color (Bachmann 1983; Gottlieb 1984; Hilu 1983). Moreover, other characters such as flowering time may clearly distinguish *D. v. kinkiense* and *D. v. thornei.* The northern populations of predominantly light-flowered individuals flower earlier than the southern, dark-flowered populations (S. Junak, Santa Barbara Botanic Garden, pers. obs.), although this may have an environmental rather than a genetic basis. Further taxonomic study using additional characters should be conducted to decide whether the island taxa have been appropriately designated as separate subspecies. Correct taxonomic designation has practical implications for the survival of these taxa because only *D. v. kinkiense* has legal protection.

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