[Aliso: A Journal of Systematic and Floristic Botany](https://scholarship.claremont.edu/aliso)

Volume 7 | Issue 2 Article 9

1970

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ALISO

VOL. 7, No. 2, pp. 207-216 JUNE 22, 1970

VARIATIONS IN SEED GERMINATION AND MORPHOLOGY AMONG POPULATIONS OF *SALVIA COLUMBARIAE* BENTH. IN SOUTHERN CALIFORNIA

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INTRODUCTION

The finding that heat pre-treatment of the seeds of certain species of desert annuals quantitatively promotes their germination (Capon and Van Asdall, 1967) has led to a consideration of the relative effect of this factor on seeds from areas other than the desert. It was thought to be of particular interest to determine the comparative effects of heat pre-treatment on the germination of seeds of the same species from diverse habitats. *Salvia columbariae* Benth. is a plant ideally suited to such a study. Its distribution extends from the southern California deserts to coastal valleys, and mountains up to an altitude of 7000 feet. The seeds of S. *columbariae* are formed in late spring and, depending upon the locality, are subjected to a wide range of temperatures after they fall to the ground. In desert areas, for example, soil surface temperatures in excess of 50° C prevail during the summer months whereas considerably lower temperatures occur at high elevations in the mountains.

In the present study, variations in both morphology and response to heat pre-treatment of *Salvia columbariae* seeds from nineteen widely scattered populations are discussed.

METHODS

Fresh seeds of *Salvia columbariae* were collected from nineteen populations of this species in southern California during the Spring of 1969. The seeds were gathered from fully mature inflorescences, flower parts were removed, and the seeds were stored in loosely-stoppered vials. One hundred seeds from each population were initially removed to determine the percentage germination of untreated seeds. Of the balance of the seeds, one half were stored in a dry condition at a constant temperature of 20° C in the dark and the remainder were stored at 50° C, also in the dark. The selection of these two temperatures was based upon previous studies with S. *columbariae* from the Joshua Tree area (Capon and Van Asdall, 1967). At weekly intervals over an eight-week period, 100 seeds were removed from each population stored at each of the two temperatures and divided into four equal portions of 25 seeds each. Replicates made in this manner provided an opportunity to note possible biological diversity within each sample. Germination of the seeds was carried out in Petri dishes on filter paper moistened with 2 ml of distilled water and maintained at 20° C in growth chambers, set on an 8-hour photoperiod. Illumination was provided by "Cool White" fluorescent lights. One week after planting, the seeds were examined for germination. A seed was considered germinated when a radicle emerged.

Color, weight, and dimensions of the seeds of each population were recorded. Color was determined by comparison with standards given in color charts (Maerz and Rea Paul, 1950). The average weight of representative seeds in each population was determined from the total weight of 100 seeds. The length and width of each of ten representative seeds from each population were measured with an ocular micrometer and the mean and standard error of the mean were calculated.

COLLECTION SITES

The following are the names given to the nineteen collection sites in southern California.

ANGELES CREST, Angeles National Forest, Los Angeles County. Southwest-facing gravel slopes on south side of Angeles Crest Highway, 3.4 miles east of the intersection of Highway N-3. Elevation: 4300 feet.

ANZA, Riverside County. South-facing sandy slopes across from the Anza Community Church on Highway 71. Elevation: 3920 feet.

BADLANDS, Riverside County. Steep east-facing firm, clay slope on Highway 60, 2.2 miles northeast of Jackrabbit Trail. Elevation: 2400 feet.

ELSINORE, Cleveland National Forest, Riverside County. Steep, gravelly, northeast-facing slopes 250 feet west of 2000 feet marker on Highway 74. Elevation: 2100 feet.

JOSHUA TREE, Riverside County. South-facing sandy slopes off Park Boulevard, 1.8 miles southeast of the intersection with Highway 62. Elevation: 3200 feet.

LAKE MATHEWS, Riverside County. South-facing gravel slopes on the north side of Cajalco Road, 1.0 miles west of Lake Mathews. Elevation: 1200 feet.

LANDERS, San Bernardino County. Banks of a wash near the intersection of Old Woman Springs Road and Lucky Strike Mine Road. Soil varies from fine sand and silt to rock and gravel. Elevation: 3500 feet.

ORD MOUNTAINS, San Bernardino County. Sandy and rocky banks of washes along and near the intersection of Barstow Road and Taylor Springs Road. Elevation: 4000 feet.

PALM DESERT, Riverside County. Southwest-facing gravel slopes of a wash off Highway 74, 1.5 miles south of the intersection with Highway 111. Elevation: 500 feet.

QUARTZ HILL, Los Angeles County. South-facing sandy slopes on Avenue M, 4.6 miles west of the intersection with Sierra Highway. Elevation: 2500 feet.

RIVERSIDE, Riverside County. Southeast-facing red clay slopes along Canyon Crest Drive between Country Club Drive and Allesandro Boulevard. Elevation: 1000 feet.

SAN JACINTO MOUNTAINS, San Bernardino National Forest, Riverside County. East-facing steep, rocky slopes on Highway 74, 0.25 mile inside National Forest, between San Jacinto and Santa Rosa Mountain Ranges. Elevation: 3800 feet.

SAN JUAN CREEK, Orange County. Southeast-facing gravel slopes on Highway 74, 0.25 mile southwest of San Juan Bridge and 1.0 mile northeast of San Juan Guard Station on west side of Santa Ana Mountains. Elevation: 820 feet.

SANTA MONICA MOUNTAINS, Los Angeles County. Gravelly, steep south-facing slope on north side of Mulholland Highway. 1.0 mile west of Las Virgenes Road. Elevation: 1000 feet.

SANTIAGO, Los Angeles County. South-facing sandy slopes along roadside on Santiago Road, 0.25 mile south of the intersection with Highway 14. Elevation: 2900 feet.

SHAMROCK RANCH, Cleveland National Forest, Riverside County. Steep south-facing gravel slope 1.0 mile west of Radec on north side of Highway 71. Elevation: 1500 feet.

SWITZER'S ROAD, Angeles National Forest, Los Angeles County. South-facing gravel slopes on south side of Angeles Crest Highway, between the intersection of Highway N-3 and Switzer's Road. Elevation: 3700 feet.

TEMESCAL, Riverside County. Southeast-facing grassy slope, 1.0 mile east of railroad underpass on Highway 71 in Temescal Valley. Elevation: 1100 feet.

WHITE WATER CANYON, Riverside County. South- and southwest-facing gravel slopes of a wash off White Water Canyon Road, 3.4 miles north of the intersection with Interstate Highway 19. Elevation: 2100 feet.

RESULTS

Within each population, considerable homogeneity in seed weight and dimensions was found. This is indicated by the standard errors shown in Table 1. Likewise, seed color was generally consistent within each population with the exception of that from the Ord Mountains in which the color ranged from light tan (13-4C in the color charts) to dark brown (chart 16-3C). In the germination studies, there was a notable uniformity in percentage germination among the four 25-seed replicates per population per temperature treatment made each week. In view of this, it was felt that the possibility of genetic variability within a population was a factor which need not be considered in interpreting the germination results.

In an attempt to determine the possibility of genetic relationships among, or discontinuities between the various populations, the nineteen collection sites were initially divided into six geographic areas—the Santa Monica Mountains area (Santa Monica Mountains collection site); the area encompassing the San Gabriel Mountains and foothills to the north (Angeles Crest, Switzer's Road, Quartz Hill and Santiago sites); the Ord Mountains area (Ord Mountains site); the high eastern Mojave Desert area (Joshua Tree and Landers sites); the Colorado Desert and eastern slopes of Mount San Jacinto (Palm Desert, White Water Canyon, and San Jacinto Mountains sites); and the inland valley and Santa Ana Mountains area (Anza, Badlands, Elsinore, Lake Mathews, Riverside, San Juan Creek, Shamrock Ranch, and Temescal sites). Geographic proximity of populations and the presence of isolating, intervening high mountain ranges and broad deserts were factors used in making these tentative divisions.

Possible similarities in seed color among populations within such geographic groupings was next considered. A color resemblance was found among the eastern Mojave Desert populations (light tan), among the Colorado Desert populations (tan), and among all of the inland valley populations except Badlands and Temescal (red-brown). Badlands and Temescal seeds possessed the tan color of the Colorado Desert group. The variable seed color of the Ord Mountains population lent additional support to the placement of that population into a group by itself.

Seed dimensions were considered next as a possible indication of existing relationships among the populations. In Fig. 1 the populations have been distributed graphically according to the mean dimensions of the seeds. Interestingly enough, the distribution closely correlated with the previously determined approximate geographical and color groupings. Again, Badlands seeds more closely resembled the Colorado Desert group. Seed weight was also analyzed in terms of the geographic areas and by statistical analysis of various possible groupings.

Six morphological groups were established on the basis of seed color, dimensions and weight, and of the previously defined geographic areas. These were numbered as shown in Table 1 and Fig. 1. Group means and standard errors for seed size and weight are shown in Table 2.

After the data on the effects of heat pre-treatment of the seeds were ob-

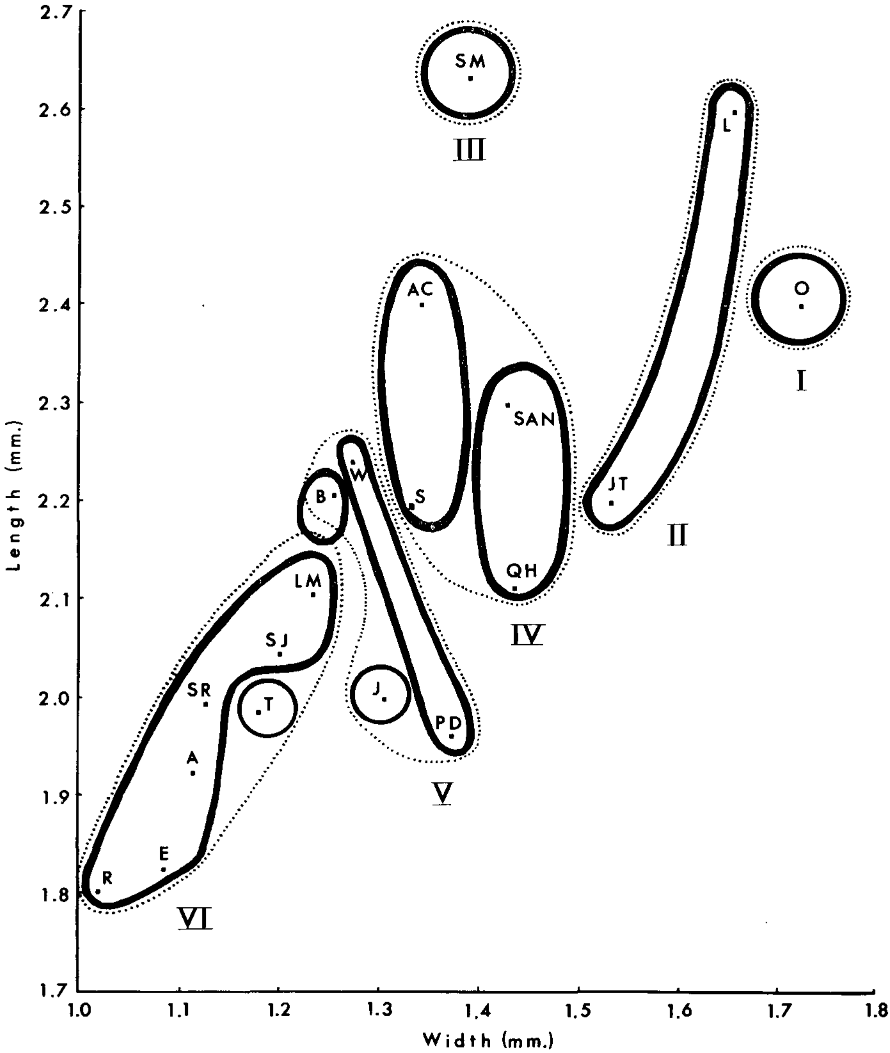

TABLE 1. *Weight, size and color of* Salvia columbariae *seeds.*

MORPHOLOGICAL GROUPS AND POPULATIONS	WEIGHT/SEED (mg) MEAN OF 100 SEEDS	LENGTH (mm) MEAN OF 10 SEEDS	LENGTH (mm) STANDARD ERROR	WIDTH (mm) MEAN OF 10 SEEDS	WIDTH (mm) STANDARD ERROR	COLOR* PLATE/SECTION
GROUP I						
Ord Mountains	1.56	2.400	0	1.718	0	13 – 4C to 16 – 3C
GROUP II						
Joshua Tree	1.30	2.198	0.031	1.531	0.031	13 – 4C
Landers	1.34	2.596	0.031	1.651	0	13 – 4B
GROUP III						
Santa Monica Mountains	1.16	2.635	0.044	1.387	0	14 – 5D
GROUP IV						
Quartz Hill	0.90	2.116	0.031	1.435	0.031	13 – 5C
Santiago	1.04	2.299	0.031	1.425	0	14 – 6B
Angeles Crest	1.06	2.409	0.033	1.339	0	14 – 3C
Switzer's Road	0.99	2.198	0	1.324	0	13 – 5C
GROUP V						
Palm Desert	0.85	1.963	0	1.372	0	14 – 6B
White Water Canyon	1.00	2.241	0.031	1.272	0	14 – 3B
San Jacinto Mountains	0.87	2.001	0.031	1.305	0	14 – 5C
Badlands	0.94	2.208	0.031	1.252	0	14 – 3B
GROUP VI						
Anza	0.64	1.924	0.031	1.113	0	15 – 7E
Elsinore	0.58	1.828	0	1.084	0	15 – 4C
Lake Mathews	0 83	2.107	0.031	1.233	0	15 – 8E
Riverside	0.60	1.804	0	1.022	0	15 – 7C
San Juan Creek	0.83	2.044	0	1.200	0	15 – 8C
Shamrock Ranch	0.78	1.996	0	1.128	0	15 – 2C
Temescal	0.71	1.987	0	1.180	0	14 – 6D

* Maerz and Rea Paul, 1950.

Fig. 1. Distribution of *Salvia columbariae* populations according to the mean dimensions of the seeds. Geographic and morphological groups are shown within dotted lines, physiological groups within solid lines.

Group 1 — O – Ord Mountains

Group II — L – Landers; JT – Joshua Tree

Group III — SM – Santa Monica Mountains

Group IV — QH – Quartz Hill; SAN – Santiago; AC – Angeles Crest; S – Switzer's Road

Group V — PD – Palm Desert; W – White Water Canyon; J – San Jacinto Mountains; B – Badlands

Group VI — A – Anza; E – Elsinore; LM – Lake Mathews; R – Riverside; SJ – San Juan Creek; SR – Shamrock Ranch; T – Temescal tained (Table 3), the results were considered in the light of the above morphological groups. In many instances, the physiological response to treatment further justified such divisions. For example, the Ord Mountains population (Group I) showed a pronounced difference between the 20° and 50° treatment when compared with its most closely allied populations in Group II—Landers and Joshua Tree (Fig. 2). The Santa Monica Mountains population (Group III) was geographically closest to the populations in the region of the San Gabriel Mountains (Group IV). Color and width of the seeds within these two groups were similar. Physiologically, however, the germination of the Santa Monica Mountains seeds was most comparable to the desert foothill populations within Group IV—Santiago and Quartz Hill. It was felt that the differences in seed length, weight, and actual geographical isolation of the Santa Monica Mountains population warranted its placement into a separate group. Within the inland valley populations (Group VI), a relatively weak response to heat treatment occurred in all except Temescal (Fig. 2), which, as has already been mentioned, also showed seed color inconsistent with the other members of Group VI. The Badlands population, on the other hand, showed a morphological affinity to Group V, although its physiological behavior was most comparable to those populations in Group VI. In light of the above, the Badlands population was designated a member of Morphological Group V and of Physiological Group VI. In Table 3, Morphological Groups IV, V and VI are shown subdivided into Physiological Subgroups to further emphasize the differences in germination responses to heat pre-treatments.

TABLE 2. *Mean weight and size of morphological groupings of* Salvia columbariae *seeds.*

MORPHOLOGICAL GROUPING	WEIGHT/SEED (mg)		LENGTH (mm)		WIDTH (mm)	
(NUMBER IN TABLE 1)	MEAN	STANDARD ERROR	MEAN	STANDARD ERROR	MEAN	STANDARD ERROR
I	1.56	–	2.400	–	1.718	–
II	1.32	0.020	2.397	0.199	1.591	0.060
III	1.16	–	2.635	–	1.387	–
IV	1.00	0.001	2.256	0.063	1.381	0.282
V	0.92	0.033	2.103	0.070	1.300	0.244
VI	0.71	0.040	1.956	0.041	1.137	0.264

DISCUSSION

A significant variation in seed germination response to heat pre-treatment among the nineteen populations of *Salvia columbariae* has been shown. In addition, distinct differences in seed morphology between populations were revealed. Such differences may indicate the existence of ecotypes within the species. Environmental conditions prevailing at the various collection sites are sufficiently diverse to support such a view. Apart from differences in seed morphology and physiology, no obvious variations in the plants themselves were noted from one collection site to another except for the size differences attributable to local soil moisture and temperatures.

Collections of *Salvia columbariae* seeds were grouped into geographic areas for ease of comparison of one population with another. It has been shown that the size, weight and color of the seeds vary from one selected geographic group to another. Morphological and physiological groupings were determined in relation to these geographic areas. Each group is discussed separately below.

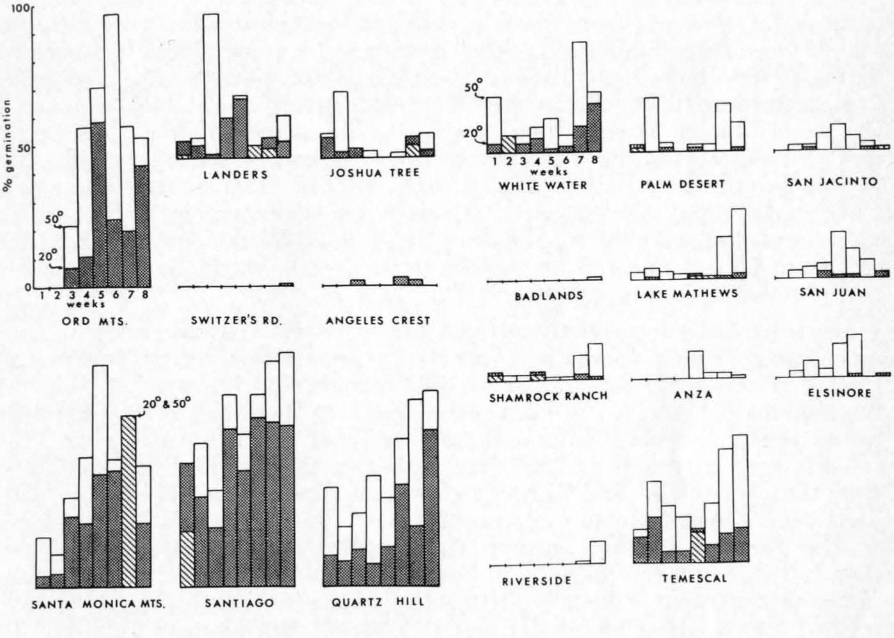

Fig. 2. Comparative effects of storage at 20° and 50°C on the percentage germination of *Salvia columbariae* seeds. The actual difference in seed germination between the experimental and control is indicated by the unshaded portion of appropriate bar graphs.

The Ord Mountains are located in the high Mojave Desert, where, during the summer, soil temperatures may reach 75° C. Seeds exposed to such conditions, after being released from the plants, predictably would respond to heat pre-treatment in the promotion of germination. In the sixth week of the experimental period, 97% of the seeds germinated in response to 50° treatment compared with 24% germination by the control group (Table 3; Fig. 2). This was the most definite response to heat pre-treatment found in any of the populations. Morphologically, the Ord Mountain population lacked homogeneity of seed color, showed the heaviest weight per seed, and the greatest overall dimensions. These factors reveal the exclusiveness of this population of plants and justify its placement into a single group (I).

Seeds of Group II populations from Joshua Tree and Landers indicated a striking uniformity in morphology and physiological response to heat pre-treatment. This is indicative of the fact that these populations fall within the same geographic area and altitude in the Mojave Desert north of the Little San Bernardino Mountains. Here, high summer daytime temperatures and cool nights are prevalent. A moderate response was shown to heat pre-treatment. In fact, the Landers population in the third week showed the second greatest contrast between the experimental and the control groups (51% experimental, 1% control).

The Santa Monica Mountains population, Group III, is separated geographically from all other populations and is located only six miles from the Pacific Ocean. Physiologically, there appears to be a substantial resemblance to the desert foothill populations at Santiago and Quartz Hill. A possible explanation for this similarity may be in the nature of the local climate at the Santa Monica Mountain collection site. Local rain shadows, the occurrence of moderately high temperatures in the valley during the summer, and as described by Bailey (1966), heat radiating from south-facing slopes causing the rapid dissipation of clouds lying against them, create an environment similar to that of the desert foothills. Morphologically, the seeds of Group III appeared to be sufficiently unique to merit the placement of this population in a separate group.

Seeds from the four populations in Group IV showed uniformity in their morphology, which, it was felt, reflected a genetic relationship fostered by their close geographic proximity. Physiologically, however, Group IV populations fell into two subgroupings, possibly stemming from differences in elevations. Switzer's Road and Angeles Crest populations (Group IVa) were located as much as 1800 feet higher in the San Gabriel Mountains than the Quartz Hill and Santiago collection sites (Group IVb). The complete lack of response to heat pre-treatment by Group IVa is significant. At the higher altitudes, summer temperatures are understandably lower than in the desert foothills. Thus, in the populations of Group IV the effect of the environment influencing natural selection is strongly suggested. It is curious that seeds of Group III and IVb populations showed a marked response to *both* the 20° and the 50° treatment. This condition is not easily explained.

A similar situation to Group IV with respect to physiological subgroupings existed among members of Group V. The Palm Desert and White Water Canyon populations revealed a greater germination response to heat pre-treatment than did the San Jacinto Mountains population, which is located 3300 feet above Palm Desert. Morphologically, the members of Group V, which includes the Badlands population, showed close affinities.

A great deal of uniformity was exhibited in the morphology of the inland valley populations (Group VI). These seeds were the smallest of all the groups examined and, excepting Temescal, they had remarkable homogeneity of color (Table 1). Physiologically, all of these populations, again with the exception of Temescal, were relativelv the same with the seeds showing only a slight response to heat pre-treatment. The Temescal population's response was much more pronounced than any of the other representatives of Group VI, for no obvious reason.

Seeds from the Badlands population possessed mixed qualities of Groups V and VI. Their larger seed weight and dimensions and their lighter color are characteristics akin to those possessed by seeds from the Colorado desert populations (Group V). In germination response to heat pre-treatment, the

TABLE 3. *Percentage germination of* Salvia columbariae *seeds with temperature pretreatment.*

PHYSIOLOGICAL GROUPS AND POPULATIONS	UNTREATED	PERCENTAGE GERMINATION 20° C TREATMENT – WEEKS								50° C TREATMENT – WEEKS							
		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
GROUP I																	
Ord Mountains	6	0	0	7	11	59	24	20	43	0	0	22	57	71	97	57	53
GROUP II																	
Joshua Tree	12	7	2	3	0	0	0	7	2	8	23	0	2	0	1	4	8
Landers	0	6	5	1	14	21	4	7	6	1	7	51	0	22	4	3	15
GROUP III																	
Santa Monica Mountains	9	4	5	25	23	40	41	61	23	18	12	32	46	79	45	61	43
GROUP IVa																	
Quartz Hill	8	11	9	13	8	14	36	21	55	35	21	26	39	31	52	66	69
Santiago	37	44	32	21	56	41	60	58	57	20	51	34	68	54	68	80	83
GROUP IVb																	
Angeles Crest	2	0	0	2	0	0	3	2	0	0	0	0	0	0	0	0	0
Switzer's Road	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
GROUP Va																	
Palm Desert	1	2	0	1	0	1	0	0	1	1	19	3	0	2	2	17	10
White Water Canyon	7	3	6	3	5	1	2	9	17	20	6	6	9	12	6	39	21
GROUP Vb																	
San Jacinto Mountains	0	0	1	0	0	0	0	1	1	0	2	2	6	9	5	3	1
GROUP VIa																	
Badlands	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
GROUP VIb																	
Anza	0	0	0	0	0	0	0	0	0	0	0	0	0	10	2	2	1
Elsinore	0	0	0	0	0	0	1	0	1	0	2	6	3	12	15	0	0
Lake Mathews	3	0	1	0	0	2	1	1	2	3	4	3	2	1	1	15	25
Riverside	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8
San Juan Creek	0	0	0	0	2	1	1	0	2	0	3	4	5	16	10	6	0
Shamrock Ranch	2	3	0	0	3	0	0	2	1	2	2	2	2	1	1	9	13
GROUP VIc																	
Temescal	14	9	16	4	4	12	6	10	12	12	29	20	16	11	21	40	45

Badlands seeds were more similar to seeds of Group VI from the inland valley (Fig. 2). The Badlands collection site is situated geographically between the inland valley and the Colorado Desert. A pass between Mt. San

Gorgonio to the north and Mt. San Jacinto to the south connects these two areas. Dispersal of diaspores of *Salvia columbariae* between the valley and the desert conceivably would be facilitated in time by the strong winds which prevail in the pass. Comparing the size and weight of the seeds from the Riverside, Badlands, and White Water Canyon populations, a progressive increase in seed size was noted to follow the ecological gradient from valley to desert. A detailed study of other populations in what seems to be a transition zone between the two areas would be worthwhile.

The question arose concerning seed morphology and color in the individual habitats in which the nineteen populations were found. For instance, large seeds containing substantial food reserves were common to desert populations. In such localities the growing season is limited to the relatively short period (three months) between the annual winter rains and the onset of the late spring drought. Black (1958) has pointed out that larger seeds with more stored food may have a selective advantage in a situation in which short growing seasons are prevalent.

A comparison was made between the color of the seeds and of the soil samples collected at the base of the plants. In many instances, an obvious correlation existed. It is interesting to speculate that a heterogeneity of seed color, such as that found in the Ord Mountains group, may have been characteristic among the progenitors of our present populations. Emigration of diaspores bearing such a genetic potential conceivably could have subjected the progenies to natural selection in favor of seeds not easily detected by herbivorous animals as they laid on the soil surface.

Evolution of the diverse physiological responses noted in the results is also worthy of speculation but more information is definitely needed. A degree of correlation has been found between germination response to heat pre-treatment and elevation of the collection sites—in Groups IV and V, for example. But although heat pre-treatment may perform a definite role in preparing seeds in some of the populations for germination, particularly those in the deserts, other factors are influential in breaking seed dormancy in *Salvia columbariae* established in different habitats. Further experimental work will hopefully define these factors.

Even from the relatively small amount of data presented here, it is obvious that a complex pattern of intraspecific variation exists in *Salvia columbariae* in southern California. The present paper represents only an initial survey of the possibilities for study that this species has to offer.

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