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GERMINATION RESPONSES TO TEMPERATURE
PRETREATMENT OF SEEDS FROM TEN POPULATIONS OF
SALVIA COLUMBARIAE IN THE SAN GABRIEL MOUNTAINS
AND MOJAVE DESERT, CALIFORNIA

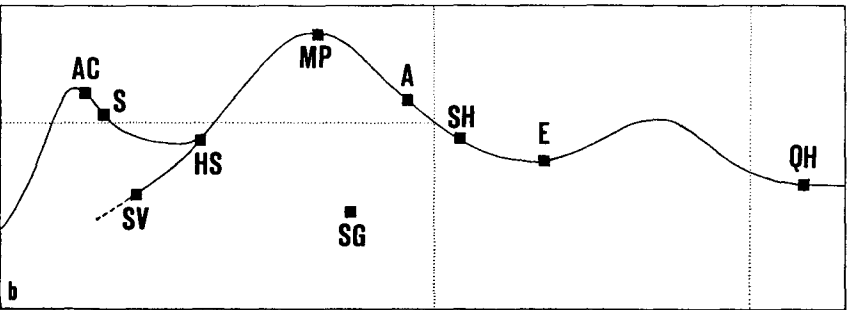
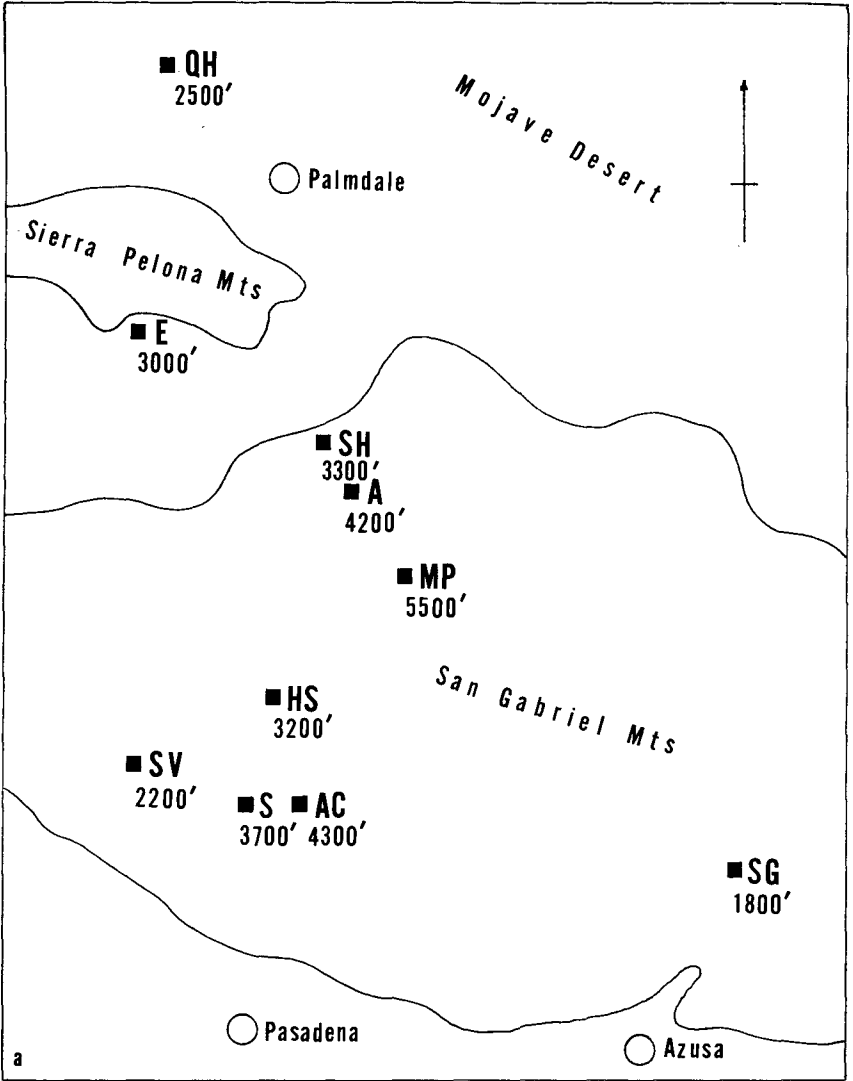
Brian Capon, Gary L. Maxwell, and Paul H. Smith

Introduction

In a study of 19 widely scattered populations of *Salvia columbariae* Benth. in southern California, Capon and Brecht (1970) showed the occurrence of a wide range of germination responses to high temperature pretreatment of the seed. The results of that study indicated the existence of possible ecotypes within the species that represent specific physiological adaptations to microenvironments at the collection sites. These findings aroused curiosity as to whether a related series of germination responses could be detected in plants growing along an environmental gradient within a more restricted geographic area than that considered in the previous study. Thus, seeds were collected from 10 populations along an approximate 30-mi (48-km) north-south transect across the San Gabriel Mountains and into the Mojave Desert in southern California, from sites that range in elevation from 1800 to 5500 ft (550 to 1675 m) above sea level. Comparative germination responses to both heat and cold pretreatment were studied in conjunction with variations in seed morphology between each of the isolated populations.

Methods

Seeds from the 10 populations of *Salvia columbariae* were collected as they matured on the parent plants. Collection of seeds from desert populations was accomplished by mid-April, 1971. Mountain populations were collected by mid-June. The seeds were stored in a dry condition in loosely stoppered vials in one of three constant temperatures: 20 C (controls), 50 C (heat pretreated), and 2 C in the presence of a desiccant (cold, dry pretreated). The initial germination percentage of each population was determined within 1 wk of seed collection. Thereafter, 100 seeds from each group were germinated at weekly intervals for 8 wk, then at monthly intervals for up to 6 mo of pretreatment. The effect of 1 mo of stratification (cold, moist pretreatment) was tested on seed that had been stored at one of the three temperatures for 6 mo. Seed viability after a period of long-term storage was tested in 1976 on samples that had been kept at 20 C for 5 yr. Germination was carried out in Petri dishes on moistened filter paper at 20 C in the dark. Germination percentages were recorded after 1 wk, a time period that had previously been found to be sufficient for maximum germination.



Morphological characteristics such as seed color, dimensions, and weight were also used to compare the populations. Color was evaluated by use of standard color charts (Maerz and Paul, 1950). Chromosome numbers in randomly selected seedlings from each population were determined as a possible indicator of polymorphism. Emerging radicles were treated with 0.004 M 8-hydroxyquinoline for 3 hr at 12 C to separate and coil the chromosomes. Hydrolyzation was carried out in 1 M hydrochloric acid for 5 min with gentle heating. Staining for 15 min in aceto-orcein preceded the preparation of squashes.

Collection Sites

The following are names assigned the 10 collection sites in Los Angeles County (Fig. 1):

Aliso Canyon.—Elevation 4200 ft (1280 m). South-facing granitic slopes on Angeles Forest Highway (N-3), 0.2 mi N of Aliso Canyon Road.

Angeles Crest.—Elevation 4300 ft (1310 m). Southwest-facing granitic slopes on Angeles Crest Highway, 3.4 mi E of junction with Angeles Forest Highway.

Escondido Canyon.—Elevation 3000 ft (915 m). South-facing gravel-clay disturbed roadside slopes on Escondido Canyon Road, 1.4 mi W of State Highway 14.

Hidden Springs.—Elevation 3200 ft (975 m). South-facing decomposed granitic slopes on Angeles Forest Highway, 3.5 mi N of Big Tujunga Canyon Road junction.

Mount Pacifico.—Elevation 5500 ft (1675 m). South-facing decomposed granitic slopes on Mount Pacifico Road, 1.5 mi S of Angeles Forest Highway at Mill Creek Summit.

Quartz Hill.—Elevation 2500 ft (760 m). South-facing sandy slopes on Avenue M, 4.6 mi W of Sierra Highway junction.

San Gabriel Dam.—Elevation 1800 ft (550 m). South-facing decomposed granitic slopes off Highway 39, 4.3 mi N of Angeles Forest boundary.

Sierra Highway.—Elevation 3300 ft (1000 m). Southwest-facing decomposed granitic slopes on Angeles Forest Highway, 2.4 mi S of Sierra Highway junction.

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Fig. 1. a. Location of collection sites with approximate elevations in feet above sea level. b. Population distribution according to altitude with division into four groups that reflect affinities in seed dimensions and germination responses. (A, Aliso Canyon; AC, Angeles Crest; E, Escondido Canyon; HS, Hidden Springs; MP, Mount Pacifico; QH, Quartz Hill; S, Switzer's Road; SG, San Gabriel Dam; SH, Sierra Highway; SV, Stonyvale.)



Fig. 2. Comparative effects of dry storage at 20, 50, and 2 C; 5-yr storage at 20 C; stratification after 6 mo at 50 C.

Table 1. Percentage germination of *Salvia columbariae* seeds following dry pretreatment for 6 mo and stratification for one month.

Population	Dry pretreatment temperature (C)		
	20	50	2
Quartz Hill	17	29	5
Escondido Canyon	17	60	30
Sierra Highway	2	15	4
Aliso Canyon	5	18	5
Mount Pacifico	6	14	7
Switzer's Road	10	6	10
Angeles Crest	17	45	33
Hidden Springs	76	88	70
Stonyvale	25	89	39
San Gabriel Dam	77	95	48

Stonyvale.—Elevation 2200 ft (670 m). South-facing decomposed granitic slopes on Big Tujunga Canyon Road, 7.2 mi W of Angeles Forest Highway.

Switzer's Road.—Elevation 3700 ft (1125 m). South-facing granitic soil slopes on Angeles Crest Highway, between intersection of Angeles Forest Highway and Switzer's Road.

Results

No appreciable improvement in germination over that of the controls was obtained as a result of cold, dry pretreatment (Fig. 2). Heat pretreatment, on the other hand, did increase germination percentages, mostly in the desert (Quartz Hill) and desert foothill (Escondido Canyon and Sierra Highway) populations. Conversely, long-term (5 yr) storage of the seed at 20 C resulted in the least improvement in germination in the Escondido Canyon and Quartz Hill populations while it seemed to benefit the others.

Stratification (moist, cold pretreatment) produced dramatic increases in germination percentages, particularly in seed that showed little or no response to heat or dry, cold treatment. In almost all cases (Sierra Highway population being the principal exception), stratification had a more pronounced effect than long-term storage. Seeds of 9 out of 10 populations responded most favorably to stratification after having received several months of heat pretreatment (Table 1).

Seed length and width, when plotted graphically, revealed further affinities between the 10 populations (Fig. 3) with seeds from Escondido Canyon and Quartz Hill appearing more distinctly different from the other eight groups. Seed weight and color, while varying from population to population (Table 2), had little value in establishing relationships between them. Chromosome counts for each population were identical, with $n = 13$.

Table 2. Weight, size and color of *Salvia columbariae* seeds.

Population	Weight/seed (mg) Mean of 100 seeds	Length (mm)		Width (mm)		Color* Plate section
		Mean of 10 seeds	Standard error	Mean of 10 seeds	Standard error	
Quartz Hill	0.102	2.108	0.030	1.333	0.018	14-6F
Escondido Canyon	0.100	2.093	0.028	1.283	0.022	15-10E
Sierra Highway	0.102	2.225	0.029	1.260	0.021	14-6D
Aliso Canyon	0.087	2.060	0.018	1.115	0.029	13-5B
Mount Pacifico	0.097	2.130	0.050	1.180	0.025	14-3B
Switzer's Road	0.098	2.222	0.049	1.230	0.021	14-6C
Angeles Crest	0.114	2.272	0.020	1.212	0.014	13-4C
Hidden Springs	0.083	2.065	0.027	1.138	0.016	14-3C
Stonyvale	0.080	1.985	0.035	1.108	0.018	14-6C
San Gabriel Dam	0.069	1.935	0.036	1.048	0.011	14-7B

* Maerz and Paul, 1950.

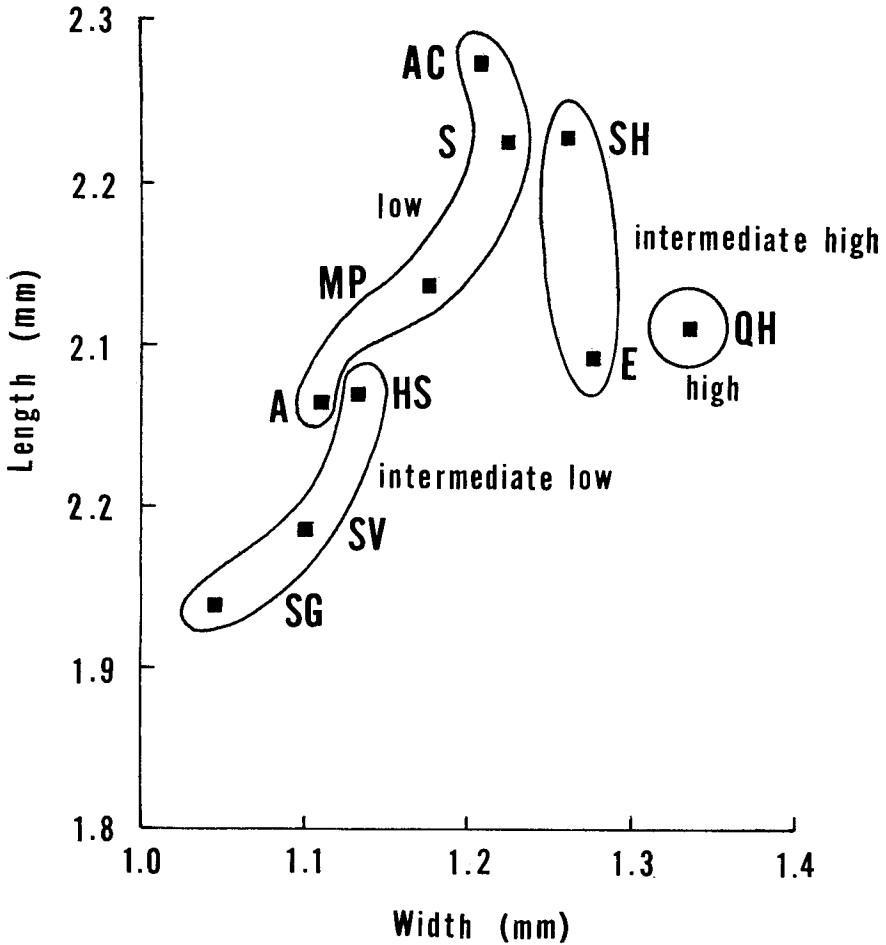


Fig. 3. Distribution of *Salvia columbariae* populations according to mean seed dimensions. Circled groups show populations having closest affinities in germination response to heat pretreatment. (A, Aliso Canyon; AC, Angeles Crest; E, Escondido Canyon; HS, Hidden Springs; MP, Mount Pacifico; QH, Quartz Hill; S, Switzer's Road; SG, San Gabriel Dam; SH, Sierra Highway; SV, Stonyvale.)

Discussion

Salvia columbariae has widespread distribution over a considerable range of environments throughout the southwestern United States and Sonora, Mexico (Munz, 1974). Data from this and a previous study (Capon and Brecht, 1970) suggest that such a distribution is not attributable to the adaptability of the species as a whole but to the species being composed of several

ecotypes, each characterized by having individual adaptability to a specific microclimate, particularly to prevailing seasonal temperatures as they correspond with various stages in the plant's life cycle. Geographic isolation of 26 populations in southern California studied to date, their relatively small sizes, and the uniformity of seed morphology within each lend support to the belief that they are genetically homogeneous units, maintained by inbreeding through self-pollination or localized cross-pollination (Visco and Capon, 1970). Collection of seed from several of the populations over a 10-yr period has assured us of the constancy of each. Hypothetically, new genotypes introduced into an area by occasional cross-breeding between populations or widespread seed distribution may be rapidly eliminated by the ineffectuality of ambient temperatures to break seed dormancy. On the other hand, long-term changes in local annual temperature conditions could conceivably shift the composition of a population from one ecotype to another by selection from the existing pool of physiological possibilities within the species.

Seeds of *Salvia columbariae* are shed from the plants by late spring and may germinate sometime after the first heavy rains of November or December. During the intervening dry summer-fall months of seed dormancy, temperature is understandably the principal factor in a seed's environment that affects its rate of afterripening. Mean summer temperatures are highest on the north side of the San Gabriel Mountains where foothills give way to the Mojave Desert. At mid-mountain collection sites and on southern slopes, temperatures are moderated by elevation and exposure to cooler maritime air that moves across the Los Angeles basin from the Pacific Ocean.

The relative response to heat pretreatment by the ten populations of seeds selected for this study appears to correspond with the normal temperature gradient along the approximate 30 mile transect. This ranges from a high germination percentage by the desert population at Quartz Hill to a low response by midmountain populations above 3500 ft (1070 m) elevation at Aliso Canyon, Mount Pacifico, Switzer's Road and Angeles Crest (Fig. 1b). As may be expected, desert foothill populations at Escondido Canyon and Sierra Highway showed an intermediate high response to heat pretreatment while their counterparts on the south slopes (San Gabriel Dam) and in sheltered midmountain valleys below 3500 ft (Stonyvale and Hidden Springs) showed an intermediate low response to the same treatment. Hopefully, it is more than coincidence that the 10 populations should fall into groups based on their degree of germination after heating and that these should parallel their groupings according to seed dimensions (Fig. 3). Yet the actual significance of seed size relative to germination response is unclear.

That cold, dry storage should, for the most part, be ineffective in promoting germination is not out of keeping with the prevailing conditions at the collection sites where dry soil and near-freezing temperatures are most likely

to occur in winter only in the desert and semidesert areas. The Quartz Hill population showed the most consistent, though minimal response to this type of treatment, suggesting that some ungerminated seeds at that site may undergo afterripening as a consequence of dry winter chilling. At mountain sites, particularly, the lowest annual temperatures occur after the soil has been thoroughly moistened by the November–December rains. Stratification, therefore, is a real possibility for seed that does not promptly germinate after the first seasonal rains. It is significant that seed from all populations responded to some degree to stratification in the laboratory, especially when it was preceded by heat pretreatment (Table 1)—in conformity with the normal summer to winter temperature pattern to which the seeds are subjected after being shed from the plants. Since occasional summer showers are not uncommon in the mountain areas, a stratification requirement may function as an effective mechanism to prevent germination at a season when prevailing conditions are unfavorable for seedling survival.

The lack of germination of seeds from Quartz Hill after long-term storage is somewhat surprising considering the supposed longevity of seed from “desert annuals” if, indeed, the desert ecotypes of *Salvia columbariae* may be classed as such. Attempts to germinate old seeds using heat, dry cold, and stratification techniques proved futile and lead us to believe that they had probably lost their viability. If this is the case, desert populations of this species must renew their viable seed reserves in the soil at fairly frequent intervals, a factor that may determine their distribution to sites that have a higher probability of regular winter rainfall than do most desert areas. There is no doubt that seed from most mountain collection sites (as well as Sierra Highway) remain viable for longer periods of time. In fact, their generally high percentages of germination after 5 yr showed that, in time, dormancy is ultimately broken even in the absence of heat and stratification pretreatments, a valuable alternative in nature where precise temperature requirements governing rapid afterripening may not always find annual fulfillment.

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