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PRODUCTIVITY, DEPLETION, AND NATURAL SELECTION OF *SALVIA COLUMBARIAE* SEEDS

Robert D. Brayton and Brian Capon

Introduction

In an earlier report on variations in seed morphology among 19 populations of the annual *Salvia columbariae* Benth., it was noted that a high frequency of color matching occurs between seeds and soil at individual population sites (Capon and Brecht 1970). Seed and soil colors ranged from gray to light brown and red-brown. During an intervening 8-yr period, the constancy of seed color in 26 populations has been verified. Seed color is most uniform in relatively small populations (25–50 plants) that occupy sites with a single soil color. In large populations (over 500 plants) that cover patchy areas of mixed soil types, seed color is generally variable with no localized patterns of seed-soil color matching. Close correspondence between seed and soil color in small populations suggests that natural selection in favor of seeds least easily seen by granivores has been operative.

In the present work, some ideas of the extent to which the seed crop is depleted in a one-year period and the nature of the predators are given. The results of field and laboratory experiments offer support to the selection hypothesis.

Methods

Potential seed productivity at each of 11 sites in the San Gabriel Mountains and adjacent desert foothills, Los Angeles County, was calculated from the total number of plants, mean inflorescence numbers of 20–25 specimens, and the weight of seeds collected from known numbers of inflorescences. Seed weights were compared with the mean of 3 sets of 100 seeds. Foraging squirrels were found to remove immature inflorescences and thus play a role in the depletion of the potential seed crop at several sites. Estimates of seeds lost to these animals were made from numbers of peduncle stumps on plants in the populations. Subsequent to seed dispersal, their depletion from the soil surface was estimated from numbers present in periodically collected surface soil samples, 64 cm^2 × 1 cm deep. The results were compared with calculated seed production/m^2 at each population site. Seeds were removed from soil samples by flotation.

The comparative effects of ants *vs.* larger animals on seed depletion were studied at two sites, one of which had been selected for its abundant ant activity. Fifty seeds were scattered on local gray soil in 9-cm-diam dishes

Table 1. Mean numbers (out of 50) of *Salvia columbariae* seeds surviving predation in field experiments; examined with Two Way Analysis of Variance (n = 4).

	July 14 Population site		August 4 Population site	
Ant activity:	1 Maximum	2 Minimum	1 Maximum	2 Minimum
A. Type of predator involved:				
Daytime				
Ants only (seeds caged)	14.7	39.1	18.2	47.7
Ants + larger animals	8.0	38.7	29.2	47.2
	$P < 0.05$	NS	$P < 0.01$	NS
Nighttime				
Ants only (seeds caged)	42.4	45.7	47.2	47.2
Ants + larger animals	43.0	43.2	47.7	47.7
	NS	NS	NS	NS
B. Seed color (on gray soil):				
Daytime				
Gray seed	15.0	42.8	26.5	48.0
Red-brown seed	7.7	35.0	20.9	46.9
	$P < 0.01$	$P < 0.01$	$P < 0.05$	NS
Nighttime				
Gray seed	42.2	44.2	48.0	47.4
Red-brown seed	43.2	44.7	46.9	47.5
	NS	NS	NS	NS

which were buried with their surfaces flush with the surrounding substrate. Eight replicates were made, four of which were enclosed in 12-mm-mesh wire cages. Separate trials were made during the day and at night. The number of seeds used in each dish approximated the maximum seed density found in soil samples at the sites and, thus, did not constitute an unusually large concentration that may have changed the normal foraging habits of predators.

Selection experiments were performed with ants in the field and with birds in an aviary. In the field, 8 replicate mixtures of 25 gray and 25 red-brown seeds were left on gray soil for 8-hr periods, both day and night. In the aviary, mixtures of 100 each of gray, brown, and red-brown seeds were presented for daytime feeding by a mixed flock of 24 rock doves (*Columba livia*) and 4 Japanese quail (*Coturnix coturnix*). In each trial, seeds were scattered on soil of one of the above three colors. Feeding periods of 2, 10, 20, 30, and 60 min were allowed. Five replicates of each soil color/feeding time combination were made—a total of 75 trials—with the same group of birds on separate days. Replicates were randomized in regard to soil color

Table 2. Mean percentage of *Salvia columbariae* seeds surviving predation in an aviary; examined with Two Way Analysis of Variance (n = 5). R = red-brown; B = brown; G = gray.

	Feeding time (min)				
Seed-soil color	2	10	20	30	60
Matching					
R on R	53	23	6	3	4
B on B	65	24	21	9	3
G on G	63	40	27	11	5
Mean	60.2	28.1	16.8	6.6	4.5
Intermediate					
R on B	47	18	10	3	0.2
B on R	47	10	2	2	1
B on G	41	35	7	7	3
Mean	44.9	19.1	8.4	4.1	1.5
Contrasting					
R on G	10	7	2	2	0.4
G on B	20	3	4	1	1
B on R	24	6	1	0.6	0.3
Mean	17.9	5.2	2.1	1.1	0.6
Analysis of Variance					
Seed-soil color contrast	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.01$	$P < 0.001$
Soil color only	NS	$P < 0.01$	$P < 0.001$	NS	NS
Interaction	NS	NS	$P < 0.05$	NS	NS

and feeding time but factors such as light level and bird hunger were standardized as much as possible by conducting the experiments at the same time each day within regulated feeding schedules. Uneaten seeds were recovered by sieving.

Predation-selection experiments followed a standard Analysis of Variance design in which Bartlett's Test was used to test for homogeneity of variance. Whenever the variances were not homogeneous, the mean was always proportional to the variances, indicating a Poisson distribution. Square root transformations normalized the data and variances showed no statistically significant departure from homogeneity. The analysis was then run using transformed values.

Results

Eight of the 11 populations at which seed productivity was estimated were small in size (25–50 plants) with a potential average production of 25,000 seeds/population. Two intermediate-size populations (approx 300 plants each) had a potential production of 204,000 (1,521/m^2) and 205,000 (851/m^2)

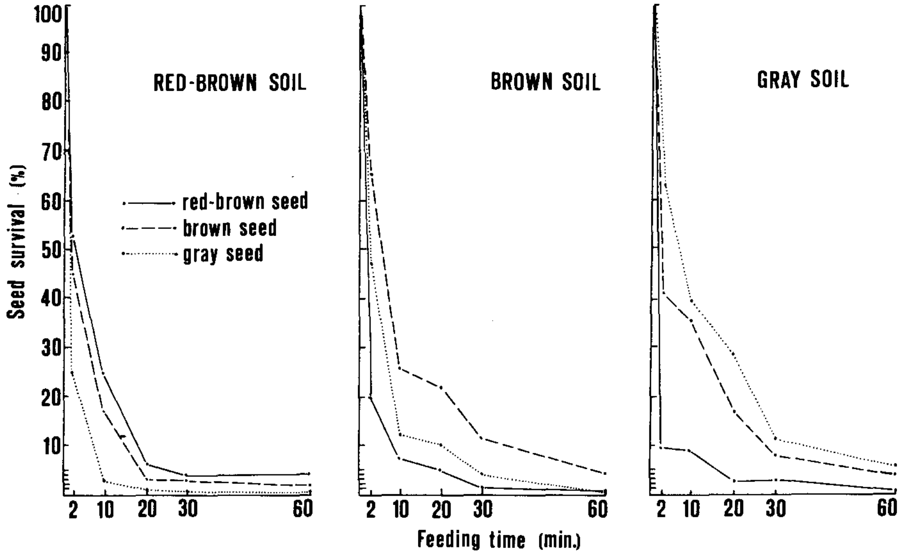

Fig. 1. Survival of *Salvia columbariae* seeds on different soil colors following predation by birds in an aviary. Means, n = 5.

seeds and the largest population (approx 500 plants) 550,000 seeds (3,315/ m^2). The two intermediate-size populations were selected for the seed depletion studies given in Table 1. Almost half of the potential production at these sites was removed in the form of immature seeds within inflorescences harvested by Beechy ground squirrels (*Spermophilus beechyi*). After the remaining seeds matured and were shed to the soil in spring, ants, birds, and small rodents decimated the seed population to as little as 2% of the original productivity potential. Ants accounted for the largest portion and most rapid rate of seed depletion. In Table 1A, the results show a significantly greater seed depletion at the site where maximum ant activity was observed, particularly during the day and in the period soon after seed dispersal. Two predatory ant species were identified: *Pogonomyrmex subnitidus* Emery and *Formica pilicornis* Emery. Of these, only small numbers of *Formica* individuals were seen to engage in nocturnal foraging. The results of seed color selection experiments in the field (Table 1B) show a significant daytime difference between matching and contrasting seed colors on gray soil. In each case, smaller numbers of red-brown seeds survived than did gray seeds. Likewise, consumption of seeds by birds in an aviary followed distinct patterns of selection based on the relative visibility of the seeds against each background color. Regardless of soil color, the least

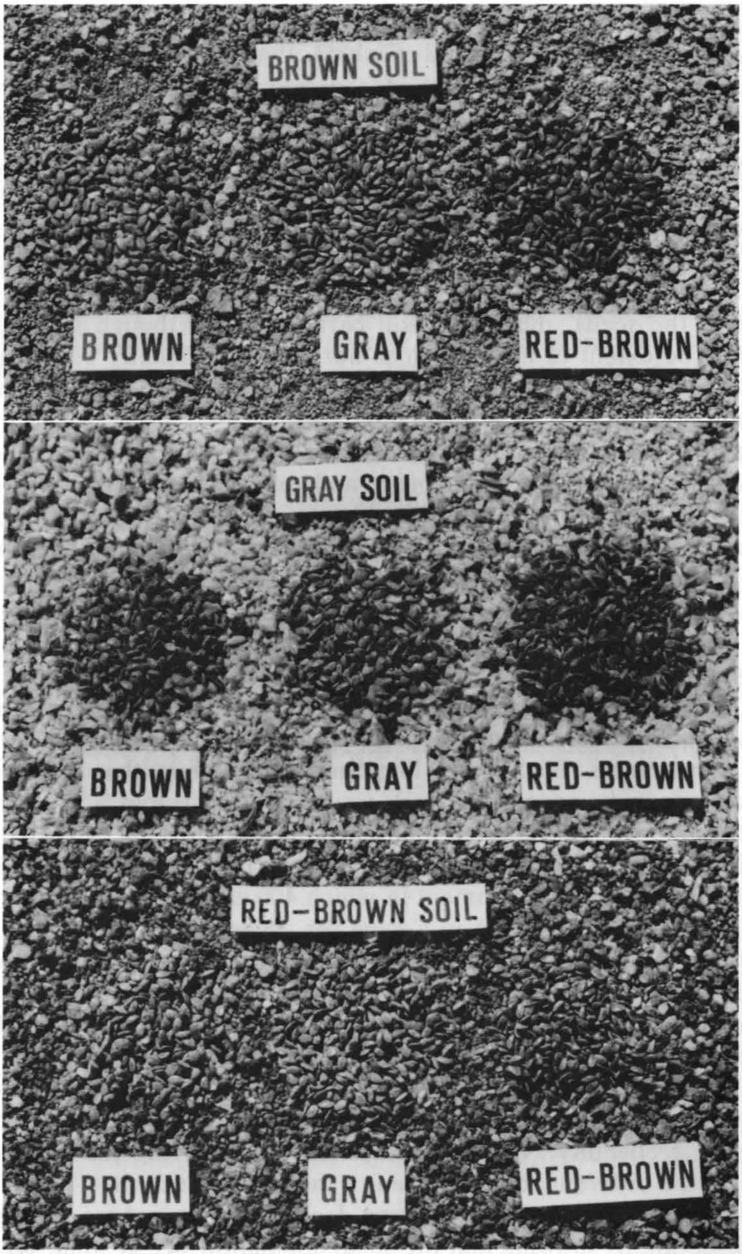

Fig. 2. Relative visibility of three colors of *Salvia columbariae* seeds on soils from different population sites.

contrasting seeds always had the greatest chance of survival, particularly within the shorter feeding periods (Table2, Fig. 1).

Discussion

Crypsis of *Salvia columbariae* seeds is derived from several characteristics. Their overall gray, brown, or red-brown colors closely match the range of soil colors in localized habitats studied to date. The seed coats (or correctly, the ovary walls since they are actually nutlets) are patterned with black mottlings and striations that convey the appearance of an irregular outline to the seeds, much like soil particles, even though the seeds are smooth. The extent of mottling does not vary significantly between populations. Size and shape of the seeds resemble coarse sand grains, the dominant soil fraction at typical population sites.

Crypsis is obviously an important factor in the survival of seeds such as these that are a desirable food source and subject to a heavy toll extracted by predators. The portion of the potential seed crop removed by squirrels is done on a nonselective basis when they carry away whole inflorescences during the spring flowering season. Color selection is most likely to occur during the 2–3 mo after seed dispersal in May and June. Visual clues to the seed's whereabouts are followed since predation mostly takes place during the daylight hours. As far as it is known, the seeds do not have characteristic odors. Thus, contrasts between soil and seed tones played an important role in the differential depletion of the various colored seeds used in field and aviary experiments. Black-and-white photographs show that sufficient contrast exists to make noncryptic seeds visible to animals that lack color vision (Fig. 2).

An indication of the intensity of ant activity in the field may be obtained from the results of an experiment in which 400 each of red-brown and gray seeds on gray soil were left in a cage for 24 hr. Only 5 gray seeds were recovered. In a second trial, using 1,000 each of the two seed colors, left uncaged for 24 hr, again only 5 gray seeds remained. In two similar experiments at a site where ant activity had not been seen, all of the seeds were left untouched. Significantly, on gray soil only gray seeds survived. In the aviary experiments, seeds that survived intensive feeding by birds were not simply those that became buried in the soil, since all colors were subject to that same probability. Without exception, seeds having the most cryptic colors on the different soils survived to the greatest extent.

The estimated extent of seed crop decimation given here is consistent with observations showing that the small population size at some sites hardly varies from year to year, although productivity of as many as 1,000 seeds/plant is not uncommon. The constancy of seed color at these sites may not only be attributed to the type of selection suggested by our experimental results but also to considerable inbreeding within the populations, encouraged by the capacity of these plants to self-pollinate in addition to or the absence of cross-pollination by insects (Visco and Capon 1970).

Seed color determination is believed to be strictly genetic and in no way is affected by soil composition. Plants of 12 populations, grown through 2 generations on a variety of native soils in the laboratory, produced seeds that were morphologically identical with those of the parents. The introduction of new seed colors into a population as a consequence of cross-pollination is possible since populations of diverse seed colors coexist within the normal range of observed insect visitors. Seed dispersal between sites could more directly introduce diverse seed colors into population sites. Whatever the means, it appears that forms of *Salvia columbariae* that produce cryptically colored seeds have the greatest chance of survival through several generations.

Acknowledgment

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