IS GLUE PRODUCTION BY SEEDS OF SALVIA COLUMBARIAE A DETERRENT TO DESERT GRANIVORES?[1]

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With a few notable exceptions (Borchert and Jain 1978, Inouye et al. 1980, O'Dowd and Hay 1980, Hay and Fuller 1981), most ecological studies on seed-granivore interactions in arid communities have concentrated on the adaptations and ecology of the granivores and not on characteristics of the seeds that may deter granivory. Since a large portion of the annual seed crop of many desert ephemerals is lost to seed predators (Chew and Chew 1970, French et al. 1974, Nelson and Chew 1977, Brown et al. 1979), characteristics that significantly reduce losses to granivores should be strongly selected. In this paper we show that under natural conditions seeds of the desert annual *Salvia columbariae* produce a glue-like substance when wetted that strongly binds sand grains to the seeds, and that seeds thus covered by sand suffer significantly less loss to desert granivores.

Methods

Seeds of *Salvia columbariae* (Labiatae) were mixed with presifted sand, the sand was wetted with distilled water, and the mixture was dried for 24 h at 50°C, a common soil temperature in the study area (Capon and Brecht 1970). Presifted sand was used to insure that each clump of sand contained a seed and not some other organic matter. The dried mixture was then resifted to retrieve the sand-covered seeds (Fig. 1). All seeds became completely coated with sand. These seeds were used in all feeding tests involving sand-covered seeds. The amount of sand affixed to each seed was measured by separately weighing 20 sand-covered seeds and comparing their masses to the mean mass of clean seeds.

To determine if this method of obtaining a sand covering provided an abnormally thick coating, 18 sets of 20 seeds each were paired (i.e., 9 pairs) and placed on coarse sand in the field. Twenty seeds of each pair were lightly dusted with sand until the seeds were not visible; the other 20 seeds were left on the surface. Three pairs were then watered with a garden watering can to simulate a rain of 0.6, 1.8, or 3.5 mm. After the seeds dried, they were retrieved from the sand and returned to the lab for determination of mass.

Seed predation experiments were conducted in sandy washes running through a cresote bush scrub community (elevation ≈300 m) located within the University of California Deep Canyon Desert Preserve near Palm Desert, California.

Possible differential seed utilization by ants was evaluated by placing five paired depots of clean seeds and sand-covered seeds alongside the foraging columns of five colonies of the harvester ant *Veromessor pergandei*. Ten seeds of one type were placed in each depot, and each depot was monitored after 5, 10, 15, 25, 40, and 60 min to determine the number of seeds remaining. All colonies were watched continuously throughout the experiment to assure that no seeds were removed by birds or ground squirrels.

Vertebrate seed predators were grouped into nocturnal (heteromyid rodents) and diurnal (birds and ground squirrels) categories, and field tests were conducted during time periods when each group was active. Ants were excluded from seed depots by placing seeds in slick, glass Petri dishes (6 cm diameter, 1 cm height). The bottom of each dish was covered with sand, and 10 clean seeds or 10 sand-covered seeds were placed in each container. These dishes were paired by placing a dish containing clean seeds and a dish containing sand-covered seeds beneath shrub canopies along the border of a sandy wash. Paired dishes were placed <1 m from each other, while separate pairs were placed at 5–10 m intervals along the wash.

Tests involving nocturnal rodents were conducted on two separate nights between 2100 and 0700. Diurnal seed predation (doves, quail, and ground squirrels were observed in the area) was measured between 0700 and 1200 on 29 July 1980. Seed loss in each dish was recorded as the number of seeds taken.

The field tests assessing differential use by granivores of sand-covered or clean seeds were designed to measure the relative susceptibility of each seed type and not the absolute rate at which seeds would be removed under natural conditions. Since all seeds were purposely placed in microhabitats where maximal removal rates would be expected (i.e., on the surface and either a few centimetres from foraging ant columns or beneath shrub canopies where rodents concentrate their foraging), absolute removal rates reported here will be artificially high when compared to absolute removal rates for natural *Salvia* seeds.

To assess roughly the length of time a seed might go without being wetted, we used existing rainfall data from three gauges located at 350-, 415-, and 1330-m elevations within Deep Canyon Desert Preserve, which represents one of the most arid regions in which *Salvia columbariae* occurs. Five years of daily rainfall data
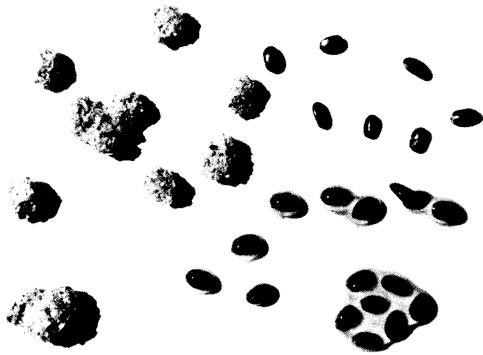
FIG. 1. Seeds of *Salvia columbariae* showing dry seeds, the mucilage produced by wetted seeds, and the sand covering that adheres to the seeds after the mucilage dries.

TABLE 1. Variation in the amount of sand affixed to seeds subjected to a range of experimental rainfalls. N equals three sets of 20 seeds for each treatment. Sand-dusted seeds were those that were slightly covered by sand before being subjected to the experimental rains.

Amount of precipitation (mm)	Mean sand mass (mg/seed)	
	Without sand dusting	With sand dusting
0.6	4	11
1.8	7	40
3.5	9	21

(1975–1979) were used to calculate mean number of rains per month in excess of 0.6, 1.8, and 3.5 mm.

Results

The mean mass of sand affixed by seeds used in our granivory experiments was 12.3 mg (sd = 2.7, n = 20) or about 11 times the mass of an average seed ($\bar{x}$ = 1.1 mg, sd = 0.2, n = 10). This mass was similar to that occurring in coarser desert soils where seeds only slightly dusted with sand were subjected to an experimental rain of 0.6 mm (sand mass = 11 mg/seed; Table 1). Our experimental seeds had only one-fourth to one-half the covering of sand found on seeds subjected to rains of 1.8 and 3.5 mm.

The sand covering significantly ($P <$ .05, Wilcoxon Paired-Sample Rank-Sum Test) decreased the rate at which seeds were taken by harvester ants and vertebrate seed predators (Fig. 2, Table 2). *Veromessor pergandei* removed 45% of the clean seeds and only 2% of the sand-covered seeds (Fig. 2) during the first 5 min of exposure. After 1 h, 96% of the clean seeds and 35% of the sand-covered seeds has been harvested.

For diurnal seed predators, the rate of seed loss was decreased by 77% ($P <$ .005, Wilcoxon Paired-Sample Rank-Sum Test) when seeds were sand covered (Table 2). In both trials where seeds were exposed to predation by nocturnal rodents, the loss of sand-covered seeds was ≈25% less than that for clean seeds, but this difference was significant (.025 > P > .01, Wilcoxon Paired-Sample Rank-Sum Test) only for the trial with the larger sample size.

Rainfall data (Fig. 3) show that during most months there was sufficient moisture to provide seeds with the protective sand covering but that May–July are the

months of least predictable rainfall, especially at lower elevations.

Discussion

The glue produced by the seed coat of *Salvia columbariae* affixes sand to the seeds (Fig. 1), thereby decreasing predation by both vertebrates (Table 2) and invertebrates (Fig. 2). Since ants and rodents (Brown et al. 1979) may destroy the majority of seeds produced in arid habitats, this should confer a significant advantage to seeds capable of producing this coating.

In California, *Salvia columbariae* occurs in low deserts, coastal valleys, and at elevations up to 2330 m in the mountains (Capon and Brecht 1970). Even in the most arid portions of the distribution of *S. columbariae*, the seeds mature by mid-April (Capon et al. 1978) and would usually be wetted shortly after maturation (Fig. 3) and thus gain the sand covering. During unusually dry years, seeds at the driest sites (350 m, Fig. 3) may not be adequately wetted until 4–5 mo after maturity. Thus, granivore damage to glue-producing seeds may be especially high during dry periods that follow dispersal from the parent.
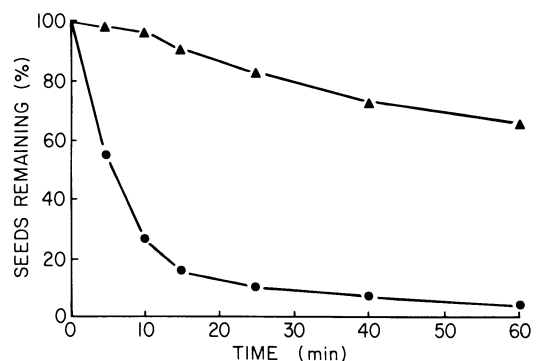

FIG. 2. The rate at which clean (●) and sand-covered (▲) seeds were harvested by colonies of *Veromessor pergandei*. For each sample interval, the ants removed significantly ($P <$ .05, Wilcoxon Paired-Sample Rank-Sum Test) more clean than sand-covered seeds.
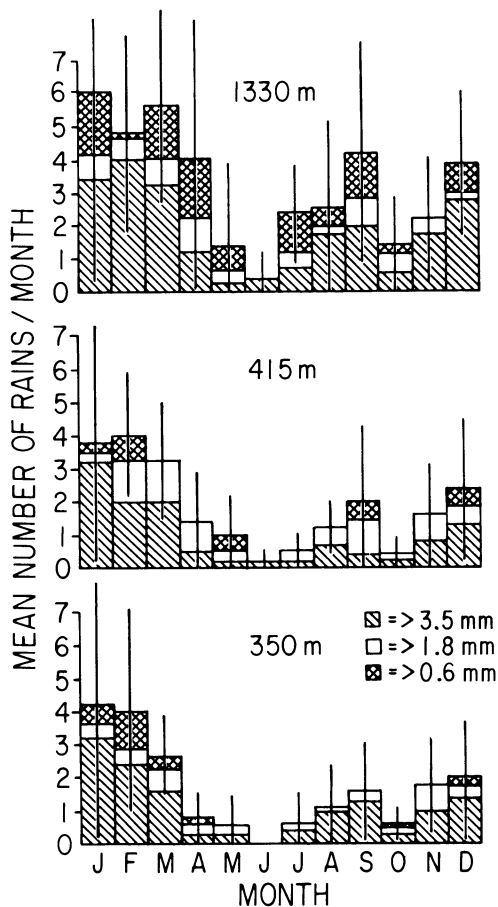
FIG. 3. The mean number of rains per month in excess of 0.6, 1.8, and 3.5 mm falling during each calendar month at elevations of 350, 415, and 1330 m in the Deep Canyon Desert Preserve near Palm Desert, California. Vertical bars represent ±SD for the mean number of rains in excess of 0.6 mm. Data are from years 1975–1979 inclusive.

The effectiveness with which the sand covering protects the seed is dependent upon the foraging modes of the seed predator. Since heteromyids can use olfaction to locate seed buried several centimetres be-

neath the soil surface (Reichman 1981), the sand covering was least effective against these granivores, decreasing seed loss by 25% (Table 2), as compared to a 94% decrease for harvester ants (Fig. 2) and a 77% decrease for diurnal vertebrates (Table 2). Many ants did not appear to recognize the sand-covered seeds as food items since most ants walked over sand-covered seeds without investigating them; almost all clean seeds contacted by ants were immediately harvested. When sand-covered seeds were recognized, they were much harder for the ants to move, and transport to the nest usually required the cooperative efforts of several ants. Since birds search by sight and have poor olfactory ability, the sand covering was very effective against these predators.

That the sand coating is acquired under natural conditions is demonstrated by such sand-coated seeds being found in soil samples from Dale Dry Lake in southern California (L. Day, *personal communication*) and also found in the cheek pouches of *Dipodomys deserti* (J. Brown, *personal communication*) collected in southern Arizona.

Glue production by seed coats is relatively common among desert plants in the southwestern United States (≈8% of the 233 species that have been investigated), having evolved in at least 12 genera representing five families (Young and Evans 1973), but this characteristic has generally been thought to function as a dispersal mechanism (Ridley 1930, Salisbury 1961, Stebbins 1971). Following rains, the seeds are thought to stick to passing animals or to leaves that will be blown great distances. In arid environments, dispersal may occasionally be enhanced in this manner, but since the seeds are damp for such a small proportion of the year and at those times quickly become covered by sand, this seems at best only a partial explanation for the evolution of mucilage production. Enhanced germination due to greater water retention has also been suggested as a factor selecting for the mucilaginous glue production (Young and Evans 1973). This explanation seems inadequate since the glue dries rapidly

TABLE 2. The differential utilization of clean vs. sand-covered seeds by vertebrate seed predators.

Seed predator	Date	No. of paired samples	% seeds removed/h ($\bar{X} \pm$ SE)		% decrease in loss due to sand covering	P value*
			Clean seeds	Sand-covered seeds		
Nocturnal rodents	28 June 1980	49	2.3 ± 0.6	1.7 ± 0.6	26	.025 > P > .01
Nocturnal rodents	28 July 1980	35	3.6 ± 0.6	2.7 ± 0.7	25	.25 > P > .10
Diurnal granivores	29 July 1980	35	7.0 ± 1.4	1.6 ± 0.8	77	<.0005

* Wilcoxon Paired-Sample Rank-Sum Test.

after light rainfall (P. J. Fuller and M. E. Hay, *personal observation*), and most desert ephemerals germinate only after winter rains (Shreve 1951) when water is relatively plentiful. As a working hypothesis, we suggest that seed predation by desert granivores has been the primary agent selecting for glue-producing seed coats in arid environments.

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