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# IN MEMORIAM — MICHAEL EVENARI AND HIS DESERT

# SEED DISPERSAL AND GERMINATION STRATEGIES OF *SPERGULARIA DIANDRA* COMPARED WITH SOME OTHER DESERT ANNUAL PLANTS INHABITING THE NEGEV DESERT OF ISRAEL

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## ABSTRACT

The late Professor Michael Evenari was a leader and a great scientist with a very wide view and varied interests. Throughout the 26 years that I studied desert plants with Professor Evenari in the deserts of Israel and the Sinai Peninsula, he liked to summarize the seasonal field observations of seedling emergence with the words, "this particular year is a very special year."

What are the reasons for such species' diversity, and what are the survival strategies of desert annuals? Some species are common and others emerge only once in several years under unpredictable seasonal precipitation and massive seed consumption by ants. Escape dispersal strategies after maturation of the tiny, long-living seeds, and partial "opportunistic" germination strategies after only 10 mm of rain, are found in some common annuals such as *Schismus arabicus* and *Spergularia diandra.* Day length during seed maturation, and light and temperatures during seed wetting and germination, also affect their germinability. In *S. diandra,* nine types of seeds have been found (3 genotypes and 3 color phenotypes), which differ in coat structure, color, and germinability, and in *Mesembryanthemum nodiflorum* a position effect was found (3 groups of seeds in a capsule). The more opportunities for a small portion of seeds from the seed bank to germinate after several rainfalls, the greater the chances to germinate at suitable rain distribution. This enables these plants to develop and produce large numbers of seeds, even after a number of small rainfalls.

## INTRODUCTION

The late Professor Michael Evenari was a great scientist with a very wide view and varied interests. He was the Vice-President of the Hebrew University of Jerusalem for 7 years, and Head of the Department of Botany for 16 years. He was one of the initiators of the Desert Research Institute at Sede Boker, and the first Head of the Unit for Ecology of that Institute. He reconstructed the farms of Avdat, Shivta, and Meishash, and developed them to be research stations in order to study and develop agriculture in the desert based on

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runoff water, using the floods which occur in the desert. Professor Evenari loved the desert and spent half of each month at the research station at Avdat and the other half at the Hebrew University in Jerusalem.

During his scientific career he published more than 228 scientific papers and reports, including 7 books. He received 4 honorary doctorates, and was a Fellow or an Honorary Member of 10 scientific societies. He received the Israel Prize in 1986 and the Balzan Prize in 1988.

Seed dispersal, germination, and flowering in desert plants were some of the subjects which we studied together over about 26 years in the deserts of Israel and the Sinai Peninsula. When we summarized the field trips to observe seedling emergence, Professor Evenari liked to say, "this particular year is a very special year."

These findings were a result of the environmental factors such as (a) the unpredictable amounts and distribution of rain as well as the beginning, length, and end of the growing season in different years (Fig. 1) and (b) massive seed consumption (Evenari and Gutterman, 1976; Evenari et al., 1982; Gutterman, 1993). Also involved are (a) plant survival strategies, such as the "escape" or "protection" strategies avoiding massive seed consumption, and (b) the history of each seed in the long-living seed populations, which

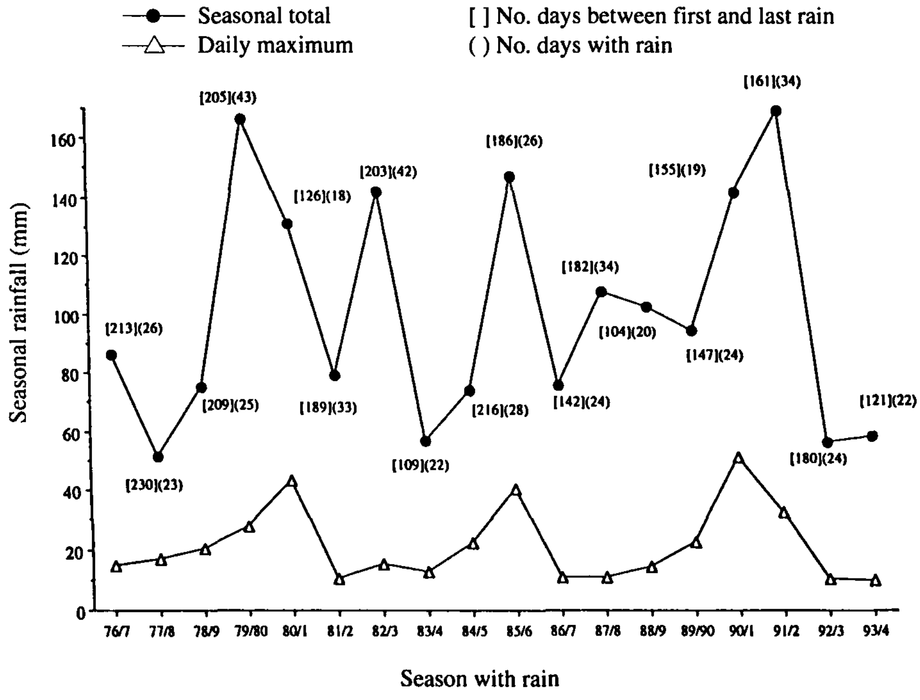


Fig. 1. Seasonal total and maximum daily rainfall for the years 1976–1994 at Sede Boker. [..] number of days between first and last rain; (..) number of days with rain (Zangvil and Druian, 1983 and Unit of Meteorology, Jacob Blaustein Institute for Desert Research; adapted from Gutterman, 1993).

may have an influence on the number of seeds at the stage of "readiness to germinate" during or after a particular rain. This includes (1) genotypic and phenotypic maternal effects, such as seed position on the plant, or in the inflorescence or fruit, (2) environmental effects such as day length and temperatures during seed development and maturation while still on the mother plant, (3) post-maturation conditions, and (4) the conditions of water, temperature, and light during the time of seed wetting and germination which also regulate the low percentage of germination (Gutterman, 1973, 1980/81a, 1993, 1994a, in press a, b; Gutterman and Nevo, 1994; Gutterman et al., in press).

Partial seed germination of the seed bank (Ellner and Shmida, 1990) is a very important strategy, especially in plant species inhabiting the more extreme deserts. Heteroblasty (Evenari, 1963; Datta et al., 1970, 1972; Wurzburger and Koller, 1976) is important to spread the risk to seedling survival when further rain does not follow (Evenari et al., 1966; Gutterman, 1973, 1978, 1980/81b; Angevine and Chabot, 1979; Venable and Lawlor, 1980; Silvertown, 1981, 1985; Westoby, 1981). *Schismus arabicus* Nees (Poaceae) and *Spergularia diandra* (Guss.) Heldr. et Sart. (Caryophyllaceae) are examples of annual plants which produce very large numbers of tiny seeds which are dispersed after maturation into cracks in the soil, and thus "escape" and avoid massive seed consumption. They also show an "opportunistic" seed germination strategy, germinating after about 10 mm of rain to very low percentages. The more opportunities there are for a very small percentage of the species seed population to germinate after several small rainfalls, the greater the chances of some of the seeds to germinate after suitable rain distribution for plant development and massive seed production. This is in spite of the unpredictable and small amounts and distribution of rain such as occur in the Negev Desert (Evenari and Gutterman, 1976; Loria and Noy-Meir, 1979/80; Gutterman, 1993, 1994a, in press a, b, submitted).

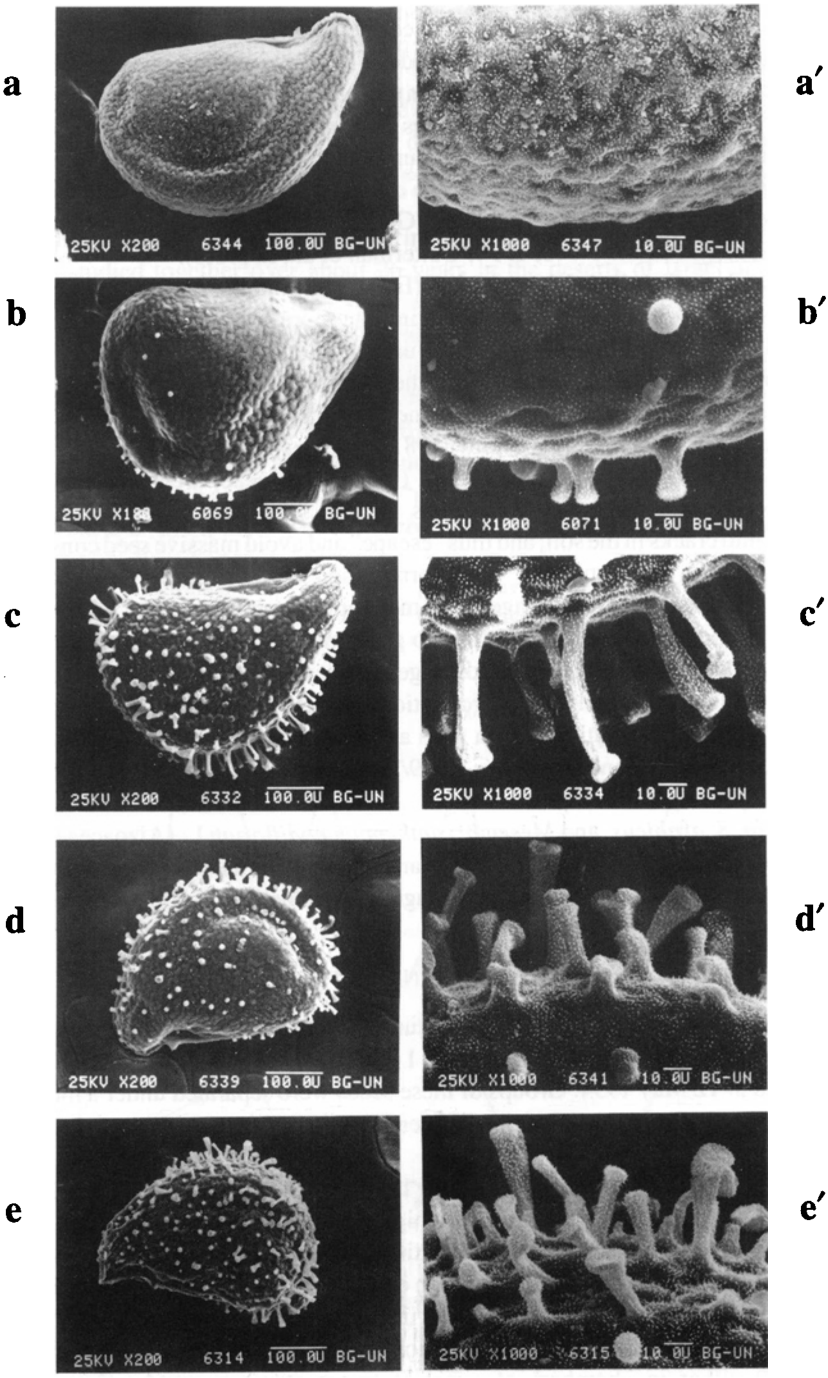
*S. diandra*, *S. arabicus*, and *Mesembryanthemum nodiflorum* L. (Aizoaceae), may be examples of plants influenced by genotypic and phenotypic maternal and environmental factors that are involved in the low percentage of germination.

## MATERIALS AND METHODS

Seeds of *S. diandra* were collected from natural populations near Sede Boker (34°46′E 30°52′N, 460 m asl) between 13 April and 1 May and on 27 June 1989, as well as on 13 April and 5–12 May 1994. Groups of these seeds were separated under a microscope to study the seed coat structure of the different "hairyness" genotypes and the different seed color phenotypes.

1) The seed coat structure was studied by light microscopy and by scanning electron microscopy (SEM) at low (×180–200) and high magnification (×1000) (Plate I).

2) Seed germinability was tested by wetting groups of 50 seeds, in 4 replicates per treatment, in 50-mm-diameter Petri dishes on one Whatman No. 1 filter paper with 1.3 ml of water, incandescent and fluorescent light intensity of 100 $\mu$ E $m^{-2}$ $s^{-1}$, or in dark with short illuminations of 5 min when germination was counted. The groups of Petri dishes were placed either in chambers of constant temperatures or outdoors at naturally


a
25KV X200 6344 100.0U BG-UN
a′
25KV X1000 6347 10.0U BG-UN
b
25KV X100 6069 100.0U BG-UN
b′
25KV X1000 6071 10.0U BG-UN
c
25KV X200 6332 100.0U BG-UN
c′
25KV X1000 6334 10.0U BG-UN
d
25KV X200 6339 100.0U BG-UN
d′
25KV X1000 6341 10.0U BG-UN
e
25KV X200 6314 100.0U BG-UN
e′
25KV X1000 6315 10.0U BG-UN

fluctuating temperatures in 20% shade of sunlight intensity, or in dark with short illuminations (5 min) when germination was checked. During all treatments, seeds were covered with transparent PVC bags to prevent water loss. More details of particular experiments will be found under Results.

## RESULTS

*S. diandra*, which inhabits the Mediterranean, trans-Turanian, and Saharo-Arabian geographic plant distribution areas, is one of the common annuals that may emerge in very large numbers in many habitats of the Negev Desert highlands and neighboring deserts. This plant produces very large numbers of long-living tiny seeds that are dispersed by wind after maturation, and thus escape and avoid massive seed consumption.

## MECHANISMS AFFECTING PARTIAL GERMINATION

### *GENOTYPIC AND PHENOTYPIC INFLUENCES OF SEED COAT STRUCTURE AND COLOR*

Among seeds harvested from one plant population of *S. diandra* near Sede Boker on 27 June 1989, nine types of seeds were found, differing in color, seed-coat hairiness, and structure when observed by light microscope and SEM (Plate I). Three plant genotypes were observed when seeds in capsules of each individual plant were examined: one group of plants produced only smooth seeds, others produced only "partially hairy" seeds, and the third group produced only hairy seeds (Plate I, a–c). Each genotype produced black, brown, or yellow seeds, depending on the maternal and environmental influences during seed maturation (Plate I, c–e). The seeds which matured in the first capsule that appeared on a plant were black. Capsules that appeared later contained brown seeds, and when the plant was in senescence at the end of the season, the last capsules to appear contained yellow seeds. No yellow seeds were found among those harvested between 13 April and 1 May 1989. The different phenotypes and genotypes differed in their size and weight (Fig. 2) and displayed different germinability (Fig. 3).

### *GERMINATION OF BLACK, BROWN, AND YELLOW SEEDS*

Among the seeds harvested between 13 April and 1 May 1989, the black and brown seeds, or hairy and smooth seeds differed in their germinability. No yellow seeds were found among the earlier harvests. In an experiment which began on 13 April 1994, significant differences were found in germination percentages between genotypes after 11

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Plate I. Facing page. Magnification of seed coat structure of different *Spergularia diandra* seeds harvested from a natural population near Sede Boker between 5 and 12 May 1994 (original photos reduced to 41%).

(a) Low (×200) and (a′) high (×1000) magnification of black smooth *S. diandra* seed.

(b) Low (×180) and (b′) high (×1000) magnification of black partially hairy *S. diandra* seed.

(c) Low (×200) and (c′) high (×1000) magnification of black hairy *S. diandra* seed.

(d) Low (×200) and (d′) high (×1000) magnification of brown hairy *S. diandra* seed.

(e) Low (×200) and (e′) high (×1000) magnification of yellow hairy *S. diandra* seed.

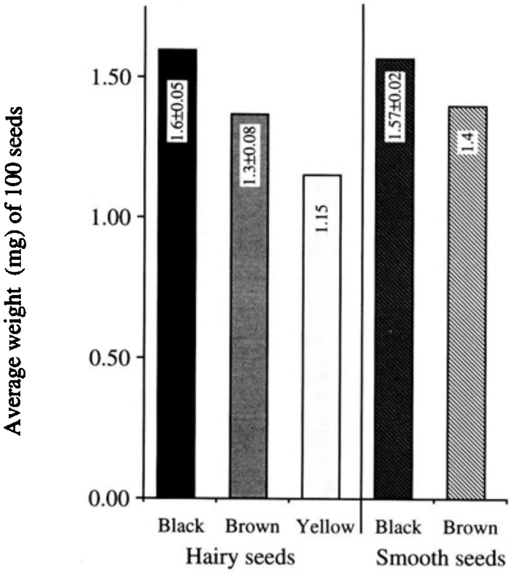

Fig. 2. Average weight of 100 seeds of black, brown, and yellow hairy seeds and black and brown smooth seeds harvested near Sede Boker on 27 June 1989.

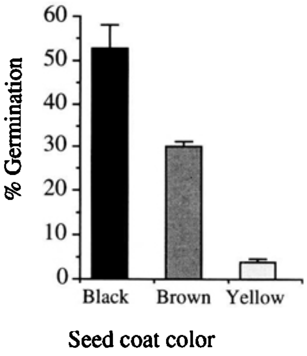

Fig. 3. Comparison of germination after 9 days of wetting (Average % of 4 × 50 ± standard error) of black, brown, and yellow hairy *Spergularia diandra* seeds harvested on 27 June 1989 from a natural population near Sede Boker. Seeds were wetted on 2 May 1994 at 15 °C in dark for 6 days and then transferred to continuous light.

days of wetting at 15 °C: 25 ± 2.5 brown hairy vs. 52 ± 1.2 brown smooth. After 15 days under the same conditions, significant differences were found between color phenotypes (58 ± 3.2 black hairy vs. 20 ± 2.6 brown hairy and 55 ± 9 smooth black vs. 33 ± 3.4 smooth brown).

Seeds of all three color phenotypes, black, brown, and yellow, were found among seeds harvested at the end of the growing season.

In the germination experiment started on 1 March 1994, seeds collected on 27 June 1989 were separated according to their color (Plate I, c–e) and germinated. After 6 days in dark the seeds were exposed to light. Between 8 to 39 days of wetting, the black seeds germinated to significantly higher levels (41.5–87.5%) than the brown (28–68.5%), which germinated to significantly higher levels than the yellow seeds (16.0–35.5%).

In another experiment which began on 2 May 1994, seeds from the same harvest were wetted for 6 days in dark and then transferred to continuous light. Germination of the hairy black seeds was significantly higher than the hairy brown seeds, which was significantly higher than the hairy yellow seeds. Germination of smooth black seeds was also significantly higher than that of the smooth brown seeds 9 days after wetting (Fig. 3).

### *GERMINATION IN A RANGE OF CONSTANT TEMPERATURES*

*S. diandra* seeds harvested on 13 April 1994 near Sede Boker were stored dry at 20–25 °C and wetted on 6 August 1994, at constant temperature between 10 and 35 °C (Table 1). Even after 17 days of wetting at the optimal temperature of 15 °C in light, the percentage of germination was low (33.5%). There were significant differences between the percentage of germination in light under different temperatures, as well as between the percentage of germination in light and dark. At temperatures of 10–20 °C the percentage of germination in light was much higher than in dark.

*S. diandra* seeds harvested on 27 June 1989 near Sede Boker were stored dry at 10–25 °C and wetted at constant temperatures between 10° and 25 °C on 5 September 1993, in light or dark (Table 2).

At constant temperatures from 10 to 25 °C, germination in light was significantly higher than in dark. The highest germination level was observed at 15 °C in light after 4 days, but later the highest level of germination (38%) was at a constant temperature of 10 °C. At 5 °C the start of germination was delayed until day 9, and after 17 days of wetting the levels were low (10%) in light and dark. The highest percentage of germination in dark with short illuminations occurred at 15 °C, but was significantly lower (22%) than in light at that temperature as well as at 10, 20, and 25 °C. At 30 and 40 °C, there was very low germination in light and dark. There was a significant difference in the percentage of germination when comparing treatments of 10, 15, and 20 °C with treatments of 5, 25, 30, and 40 °C. (Table 2).

### *GERMINATION AT NATURAL SUMMER OR WINTER TEMPERATURES*

Seeds harvested on 27 June 1989 were also germinated in Petri dishes at naturally fluctuating summer temperatures (14–37 °C) in the experiment that started on 5 September 1993 (see daily temperature measurements in Table 3). Germination in light started 7 days after wetting. Germination in the dark started after 9 days, and remained at the same level of 2.5% and 0.5% in light and in dark, respectively, even after 17 days (Table 3).

In experiments which began on 20 January 1994 in naturally fluctuating winter temperatures of 3–17 °C, after 7 days of wetting in light or in dark, germination reached 37% in light and only 9% in dark. After 17 days of wetting at 3–20 °C, the level of germination reached 47.5% in light, and 25% in dark with short illuminations. There was a significant difference between germination in light and dark from day 4 to day 17. No seeds germinated during the first 3 days after wetting (Table 3).

## DISCUSSION

Of the 110 annual plant species observed in 1974 near Sede Boker in the Negev Desert, not even two were found to be identical or closely similar in distribution and population behavior (Loria and Noy-Meir, 1979/80), nor any of the 40 plant species whose seeds are dispersed by rain (Gutterman, 1990a). Some plant species emerge every year and others only once in several years (Evenari and Gutterman, 1976; Gutterman, 1993, 1994a, in press a, b). In spite of the great diversity of rain, amounts, and distribution (Fig. 1), some of the annual plant species emerge almost every year, and the question is: what are the strategies of seed dispersal and regulation of germination of some dominant annuals of the Negev Desert which enable them to emerge almost every year in large numbers?

The more common plant species seem to produce large numbers of tiny seeds which "escape" from massive seed consumption by dispersal after maturation, and have

Table 1

Germination (% ± standard error) after wetting for 3,4, 6, 10, 11, and 17 days of *Spergularia diandra* seeds harvested on 13 April 1994 and stored in laboratory conditions. Germination experiment started on 6 August 1994, at constant temperatures of 10–35 °C in light (L) and in dark (D) with short illuminations (5 min) during daily observations after 11 days of wetting; 4 × 50 seeds for each treatment in 50-mm-diameter petri dishes

| | Germination (%) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Temp. | 3 days | | 4 days | | 6 days | | 10 days | | 11 days | | 17 days | |
| °C | L | D | L | D | L | D | L | D | L | D | L | D |
| 10 | 0 | — | 0 | — | 9.5 ± 1.3 | — | 13.5 ± 1.3 | — | 13.5 ± 1.3 | 2.0 ± 0.8 | 15.0 ± 2.1 | 3.0 ± 1.3 |
| 15 | 5.0 ± 1.3 | — | 12.0 ± 0.8 | — | 20.0 ± 1.4 | — | 30.5 ± 4.5 | — | 31.5 ± 4.4 | 1.5 ± 1.0 | 33.5 ± 5.1 | 9.5 ± 1.3 |
| 20 | 7.0 ± 1.7 | — | 11.0 ± 0.6 | — | 16.5 ± 1.9 | — | 17.5 ± 1.5 | — | 18.0 ± 1.4 | 2.0 ± 1.2 | 19.0 ± 1.7 | 4.0 ± 1.4 |
| 25 | 0.5 ± 0.5 | — | 0.5 ± 0.5 | — | 0.5 ± 0.5 | — | 1.0 ± 0.6 | — | 1.5 ± 0.5 | 1.5 ± 1.5 | 2.0 ± 0.8 | 1.5 ± 1.5 |
| 35 | 0 | — | 0 | — | 0 | — | 0 | — | 0 | 0 | 0 | 0 |

Significant at 95% by 2-way ANOVA after angular transformation: at temperatures 10–25 °C; light and dark (see Results).

Table 2

Germination (% ± standard error) of *Spergularia diandra* seeds, harvested on 27 June 1989 near Sede Boker and wetted by water on 5 September 1993, at constant temperatures of 5–40 °C in light (L) and in dark with short illuminations (D)

| | Germination (%) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Temp. | Day 4 | | Day 7 | | Day 9 | | Day 17 | |
| °C | L | D | L | D | L | D | L | D |
| 5 | 0 | 0 | 0 | 0 | 1.5 ± 0.9 | 0.5 ± 0.5 | 10.5 ± 2.6 | 10.5 ± 2.2 |
| 10 | 0 | 0 | 30.0 ± 4.0 | 3.5 ± 1.5 | 35.0 ± 4.8 | 9.5 ± 2.9 | 38.0 ± 4.2 | 15.5 ± 3.5 |
| 15 | 22.5 ± 3.4 | 1.5 ± 0.9 | 29.0 ± 3.4 | 6.5 ± 2.0 | 30.0 ± 2.8 | 13.0 ± 2.6 | 33.0 ± 2.6 | 22.0 ± 3.2 |
| 20 | 16.5 ± 0.5 | 0.5 ± 0.5 | 21.0 ± 0.5 | 2.0 ± 0.8 | 27.5 ± 2.7 | 4.5 ± 1.7 | 30.5 ± 2.0 | 6.5 ± 2.5 |
| 25 | 5.5 ± 1.7 | 0 | 7.0 ± 1.7 | 0 | 9.0 ± 1.7 | 1.5 ± 0.9 | 9.0 ± 1.7 | 2.0 ± 1.1 |
| 30 | 0.5 ± 0.5 | 0 | 1.0 ± 0.6 | 0 | 1.0 ± 0.6 | 0 | 1.0 ± 0.6 | 0 |
| 40 | 0.5 ± 0.5 | 0.5 ± 0.5 | 0.5 ± 0.5 | 0.5 ± 0.5 | 0.5 ± 0.5 | 0.5 ± 0.5 | 0.5 ± 0.5 | 0.5 ± 0.5 |

Significant at 95% by 2-way ANOVA after angular transformation: Temperatures; light vs. dark (see Results).

Table 3

Germination (% ± standard error) of *Spergularia diandra* seeds, harvested on 27 June 1989 near Sede Boker and wetted by water on 5 September 1993 in a range of natural summer temperatures (NST) of 14 to 37 °C and on 20 January 1994 at natural winter temperatures (NWT) of 3 to 21°C, in light (L) and in dark with short illuminations (D)

| | Germination (%) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Day 4 | | Day 7 | | Day 9 | | Day 17 | |
| Season | L | D | L | D | L | D | L | D |
| NST | 0 | 0 | 2.0 ± 1.2 | 0 | 2.5 ± 0.9 | 0.5 ± 0.5 | 2.5 ± 0.9 | 0.5 ± 0.5 |
| °C* | 16–34 | | 15–36 | | 14–33 | | 15–37 | |
| NWT | 5.5 ± 1.7 | 0 | 37.0 ± 2.0 | 9.0 ± 1.0 | 46.5 ± 4.6 | 25.0 ± 2.6 | 47.5 ± 4.3 | 25.0 ± 2.6 |
| °C* | 7–15 | | 3–17 | | 5–21 | | 6–20 | |

WL vs. WD significant at 95% by one-way ANOVA.
*Min/max daily temperatures.

"opportunistic" strategies of germination. After even small rainfalls a small percentage of the seed population may germinate. Germination after more rains increases the chance to germinate at the suitable distribution of rain (even small rainfalls) which will enable them to produce large numbers of seeds. In different plant species, various mechanisms are involved in the low percentage of germination even under optimal conditions.

It was found during this study, and by Gutterman (unpublished), that in *S.diandra* the diversity of seed dispersal mechanisms and germination is a complex of survival mechanisms and strategies of long-living seeds with only a small portion that are ready to germinate after one wetting (Tables 1, 2).

There are three genotypes and three phenotypic maternal influences that create nine types of seeds in one population near Sede Boker. These seeds differ in their weight (Fig. 2), hairiness, dispersability, seed coat structure (Plate I), color, and germinability (Fig. 3). Day length during seed maturation affects seed germinability (Fig. 4). *S. diandra* seeds are long living. After more than 4 years of dry storage at temperatures from 10 to 35 °C, germination is higher and faster (Table 2) than in seeds of the current year (Table 1). The low level of germination is also affected by temperature and light during wetting of seeds and the germination process (Tables 1–3).

One of the most important results of this study showed that even under the most favorable germination conditions (constant light at 10 °C) the level of germination only reached 38% after 17 days of continuous wetting. At 15 °C the highest level of germination reached in dark after 17 days of wetting was 22% (Table 2).

The naturally fluctuating winter temperatures and natural day length are more favorable for seed germination in *S. diandra* (47.5%) than constant temperatures after 17 days of wetting (Table 3). At the same temperature and time, but in dark with short illuminations, only 25% of the seeds germinated.

*S. diandra* seeds emerged in their natural habitats in winter even after very little rainfall (10 mm), after which the soil was only wet enough for germination for a short time. In Petri

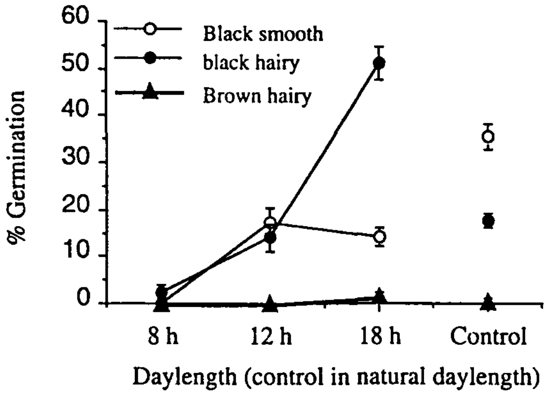

Fig. 4. Comparison of germination (% ± standard error), after 47 days of wetting, of black and brown hairy, and black smooth *Spergularia diandra* seeds matured under 8h, 12h, and 18h day lengths outdoors and under natural day length and temperatures in the growing season (control). Seeds were collected between 7 and 9 March 1994 from mother plants that had developed from seeds harvested on 27 June 1989 near Sede Boker. The germination experiment began on 10 March 1994. There were significant differences in germination percentages between phenotypes ($p = 0.0001$) and genotypes ($p = 0.0001$) (at 95% in 3-way ANOVA after angular transformation among seeds matured under different daylengths.

dishes, when water was not a limiting factor, germination started after 3 to 9 days, depending on temperature; the percentage of germination at this stage was very low (Tables 1–3).

Under naturally fluctuating summer temperatures, very low germination was observed (0.5–2.5%) (Table 3). This was also found at constant high temperatures of 25 °C (Table 1), and at 30 and 40 °C (Table 2).

Experiments with summer irrigation were carried out in 1977 near Avdat and in 1985 near Sede Boker. Only a few *S. diandra* plants emerged and flowered in an area of 2000 $m^2$ of natural habitats near Sede Boker when soil moisture was not a limiting factor after irrigation throughout the hot and dry summer (Gutterman, 1986). In this area many *S. diandra* plants emerge in winter. During the hot season, in August and September 1977, after irrigation of 16 $m^2$ near Avdat, *S. diandra* seedlings did not emerge (Gutterman and Evenari, 1994), but in winter they emerged in great numbers (Evenari and Gutterman, 1976). From these results, it seems that *S. diandra* is a winter annual with very low ability to emerge in areas receiving summer rains.

This may not be the case for *Reboudia pinnata* (Viv.) Täckh. et Boulos (Brassicaceae) (Gutterman, 1990b) or *S. arabicus*, plants that are very common in the Negev Desert highlands. *S. arabicus* seeds are capable of germinating at high summer temperatures, and 506 seedlings/16 $m^2$ emerged after summer irrigation of a natural desert habitat. In winter *S. arabicus* seedlings emerge after less than 10 mm of rain, but in summer, as the amount of irrigation increased from 90 to 200 mm, more seedlings emerged and survived (Gutterman and Evenari, 1994). In another year in the same habitat, after summer irrigation, as many as 3849/16 $m^2$ seedlings emerged (unpublished data).

As with *S. diandra*, for *S. arabicus* there are also a complex of mechanisms and strategies which regulate the low percentage of germination: (1) day length during caryopses maturation (Gutterman, unpublished), (2) temperatures during dry storage, and (3) light and temperatures during wetting of caryopses and germination. Older seeds germinate to the same levels as seeds of the last growing season (Gutterman, 1994a, in press a, b).

Another plant species with long-living seeds, but which appears in mass germination once in several years, is *M. nodiflorum*. The seeds are dispersed by rain and adhere to the soil crust for many years until they germinate in very large numbers. This mass emergence was observed in 1972 between Jericho and the Dead Sea (Gutterman, 1980/81b). *M. nodiflorum* inhabits soils on which salts accumulate during the dry and hot summer. Germination is affected by the dilution of the salts by (1) a number of rains; (2) an annual rhythm of germination (Gutterman, 1980/81b); (3) the influence of light and temperatures during seed wetting and the germination process; and (4) a position effect in which the terminal group of seeds germinates even after 22 years of storage to higher percentages than the basals and centrals (Gutterman, 1994b).

The position effect in which the terminal seeds germinated to higher percentages than the centrals and basals after 8 years (Table 4, A and B) also occurred after 16, 19, and 22 years. However, the relative levels of germination of the centrals and basals increased with time, and after 19 and 22 years they germinated to higher levels than 8 or 16 years after maturation. There are also changes in light sensitivity of the seeds, and after 19 and 22 years germination in dark was higher than in light.

Common to the dominant plant species displaying escape seed dispersal strategies and "opportunistic" strategies of germination is the production of many tiny, long-living seeds. Plants with the "protection" strategy of seed dispersal, such as *Blepharis* spp. (Acanthaceae) (Gutterman, et al., 1967, 1969, 1973; Witztum et al., 1969; Gutterman,

Table 4

The position of terminal, central, and basal seeds matured in *Mesembryanthemum nodiflorum* capsules affecting their germinability after about 8, 16, 19, and 22 years of dry storage

| Seed position | Light condition* | Germination (% ± SE) | | | | | |
|---|---|---|---|---|---|---|---|
| | | 8 y | | 16 y | 19 y | 22 y | |
| | | A (12d) | B (8d) | 22 d | 35 d | 16 d | 57 d |
| Terminals | L | 61.0 | 57.5 ± 4.0 | 29.0 | 22.0 ± 2.5 | 31.0 ± 3.3 | 58.5 ± 3.1 |
| | D | — | — | 17.0 | 54.0 ± 3.5 | 48.0 ± 2.9 | 64.5 ± 2.2 |
| Centrals | L | 5.5 | 9.0 ± 1.3 | 15.0 | 16.5 ± 2.9 | 18.0 ± 2.2 | 30.0 ± 2.6 |
| | D | — | — | 9.0 | 21.5 ± 1.0 | 27.0 ± 2.5 | 51.0 ± 8.2 |
| Basals | L | 1.0 | 8.7 ± 2.4 | 10.0 | 16.0 ± 2.5 | 8.5 ± 2.6 | 14.5 ± 3.3 |
| | D | — | — | 12.0 | 32.5 ± 6.0 | 16.5 ± 3.1 | 35.0 ± 6.6 |
| °C† | | 25 | 25 | 15 | 15 | 20 | 15 |

Plants with dry capsules contain mature seeds harvested near the Dead Sea in summer 1972. Seeds were separated from capsules and germinated after 8 years (two experiments: A and B), 16 years, 19 years, and 22 years (adapted from Gutterman, 1980/81, 1990b, 1993, 1994a, b, in press a, b). *Light condition during wetting. —: Similar results in light and dark. †Temperature during time of wetting.

1972, 1988, 1989, 1993, 1994a, in press b; Gutterman and Witztum, 1977), produce relatively large seeds in small numbers. In spite of the very sophisticated dispersal mechanism which ensures that only some of the seeds explode from their capsules after a promising rain, with germination occuring after the same rain, these plants are rare and occur in limited areas. Therefore, these sophisticated strategies of seed dispersal and germination might not be the most successful survival strategies under the unpredictable precipitation existing in the Negev Desert.

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