ECOLOGY OF DESERT PLANTS. IV. COMBINED FIELD AND LABORATORY WORK ON GERMINATION OF ANNUALS IN THE JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA

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In the studies of the annuals of the Joshua Tree National Monument, Death Valley, and the Coachella Valley, made prior to 1948, it appeared that the temperatures which prevailed at the time of the infrequent rainfalls were a critical factor in determining which species would germinate. The difference in summer and winter flora was shown to be due to this factor (Went 1948, 1949, Went and Westergaard 1949).

The extension of these observations in the present paper consists of the attempt to define in more detail the correlation between rainfall and temperature, and germination. The study has extended from the fall of 1948 to the fall of 1953.

It was thought that temperature, in combination with rainfall, might explain other differences than those of summer and winter, for it is a conspicuous feature of the flowering of the desert annuals that a rather small portion of the number of native species will blossom in any one year. At one time, two or three species may dominate, appearing most profusely; the following year these may scarcely appear at all, quite different species predominating. Yet three, five, or even seven years later the first ones may appear again, and in the same locations. The present study is directed toward the question whether their appearance might be due to recurrence of favorable rain-temperature

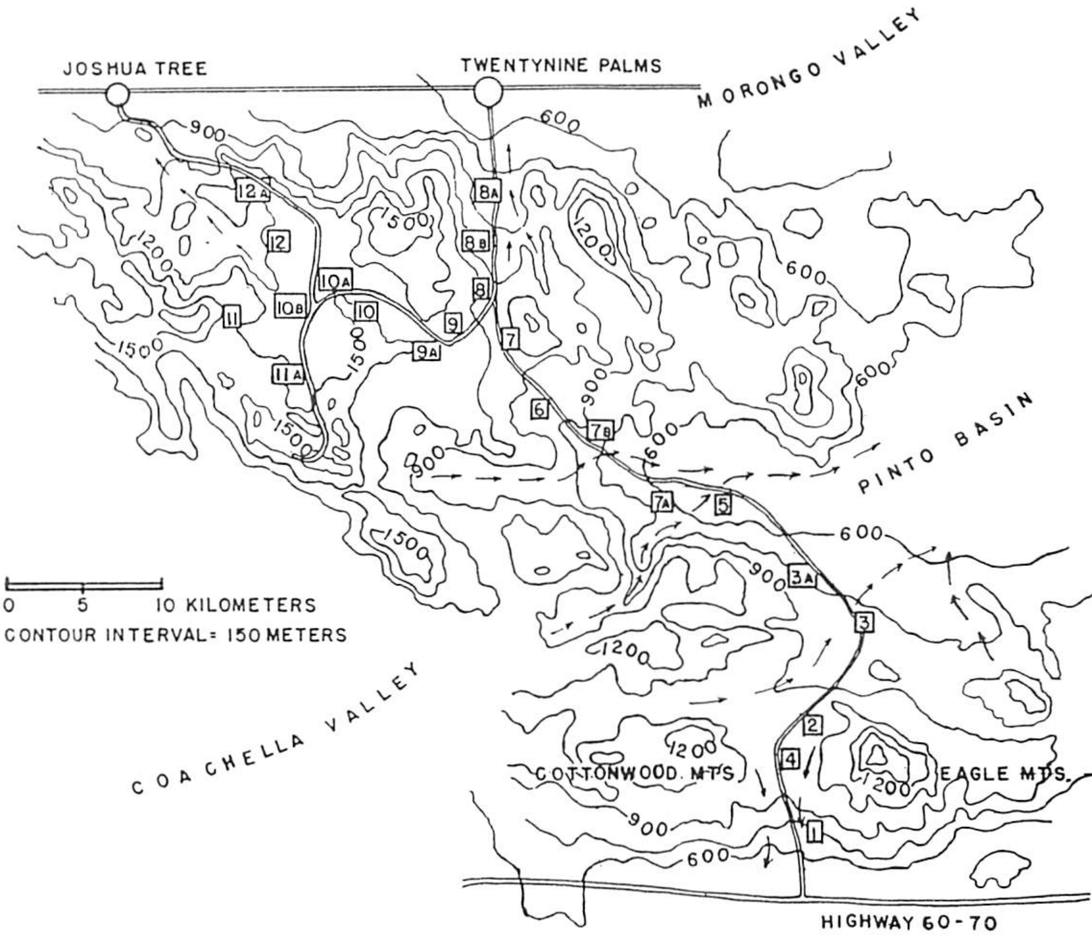

Fig. 1. Map of the Joshua Tree National Monument.

combinations. It might be that there are not in any one year enough temperature-moisture combinations during and after the few rains, to cause germination of all species if each has its own different and rather narrow requirements.

Accordingly, 17 stations were selected at approximately 3 mile intervals along the roads in the Joshua Tree National Monument. This number was later increased to 23 (Fig. 1). The altitudinal range is from 610 m. (2,000 ft.) to 1,600 m. (5,275 ft.). At each station was placed a rain gauge and a quadrat. The gauges were read after every rain by the Park Rangers.[1] Quadrats were placed on level ground, well away from shrubs.

Temperature records were furnished by the Cooperative Weather Station at Twentynine Palms. As reported previously (Went 1948), there was a mean difference of about 6° C. for an altitudinal difference of 750 meters. In tables and figures the temperatures are corrected for elevation. Preliminary experiments showed that soil temperatures were reasonably proportional to air temperatures while the soil was wet which was the only time germination was taking place.

Quadrats were visited after each rain of sufficient magnitude to cause germination, and germination counts were made. The quadrats were revisited at suitable intervals to complete identification and observe survival. When seedlings could not be identified, they were transferred to Pasadena and grown to maturity. As a preliminary study, the seedlings of the commonly occurring plants had been sketched, at the cotyledon stage and when showing the first pair of leaves. In most cases the genus can easily be recognized at this stage and very frequently the species. A few of these seedlings are shown in Fig. 2. Seedlings were transplanted from the desert with less than 1% of loss by placing them in an airtight container with a litle moist earth or paper, replanting them in sand, and watering with nutrient solution. It seemed to be more important to protect the leaves from water-loss, than to be careful of the roots, unless it was a taproot.

In 1952-53, a method of counting quadrats from stereoscopic photographs was tried. Cement bases were poured for a tripod of fixed height so that the camera could be set up in exactly the same position and height each time. All quadrats could be photographed in less than a day. This method provides a permanent record. Skill must be developed to count from photographs, and even then some species cannot be distinguished. Color might solve the problem. Herbarium specimens were taken from near the quadrat of each species found on the quadrats. These were deposited in the Pomona College Herbarium.

Soil samples were taken from the vicinity of 17 quadrats after the first rain in 1948, and were placed in various controlled conditions in the Clark or Earhart Laboratories.

[1] We gratefully acknowledge the help of Supt. S. A. King, former Supt. Frank Givens, and Supervisory Park Ranger H. L. Earenfight, whose untiring cooperation has been invaluable.

TABLE I. Germination of the more abundant annuals in the soil samples placed in various conditions of the laboratory. "Cool" = day 10°, night 3°. "Moderate" = day 17°, night 10°; day 23°, night 10°; and day 23°, night 17°. "Warm" = day 30°, night 17° and day 30°, night 23°. C = Day temp. 10°C; M = Day temp. 17°C and 23°C; W = Day temp. 30° C.

Sta.	Elev. in meters	*Eriophyllum*			*Chaenactis fremontii*			*Salvia*			*Gilia aurea*			*Euphorbia setiloba*			*Bouteloua*			*Monoptilon*			*Portulaca*			*Amaranthus*			*Pectis*		
		C	M	W	C	M	W	C	M	W	C	M	W	C	M	W	C	M	W	C	M	W	C	M	W	C	M	W	C	M	W
5	600	7	3	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	1	..	..	..	..	..	1	..	..	..	..	1	2
7a	670	..	1	..	..	..	..	..	..	..	..	2	..	..	..	..	..	2	3	..	..	..	..	1	..	..	..	..	..	..	..
1	670	..	..	..	..	..	..	..	1	..	2	..	..	..	..	..	..	2	2	..	..	..	..	..	..	..	..	..	..	1	..
7b	800	..	1	..	..	..	..	..	..	..	..	..	1	..	..	3	..	1	2	..	..	..	..	1	..	..	..	..	..	1	..
3	850	7	1	..	..	..	..	..	..	..	3	..	1	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	1
8a	900	2	2	..	..	..	..	..	..	..	1	..	..	..	..	..	..	2	5	..	..	..	..	..	..	..	..	..	..	..	2
4	900	..	..	..	2	..	..	3	1	..	..	..	..	..	..	..	..	..	1	9	3	..	..	..	..	..	..	..	..	3	1
8b	1100	..	..	..	..	..	..	..	..	..	2	1	..	..	..	2	..	..	3	..	..	..	..	..	..	..	..	..	..	3	..
6	1150	24	13	..	..	..	..	2	..	..	..	9	8	..	..	..	..	1	3	..	..	..	..	..	..	..	..	..	..	11	28
8	1200	22	13	3	..	..	..	..	..	..	2	1	1	..	..	4	..	1	5	..	..	..	..	..	..	..	..	..	..	..	..
7	1220	8	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	3	..	1	..	..	..	..	..	..	..	..	20	38
12a	1220	..	1	..	..	3	..	..	..	..	..	..	..	..	..	..	..	7	20	..	..	..	..	..	..	..	..	..	..	27	16
9	1220	..	..	..	6	1	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	1	5	..	28	52
12	1300	..	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	6	20	..	..	..	..	..	..	..	..	..	..	..	..
9a	1370	..	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	2	..	..	..	..	13	41	..	..	..	..	4	..
10b	1370	..	2	1	..	..	..	..	..	..	..	4	..	..	..	..	..	3	9	..	..	..	..	3	22	..	1	..	..	..	..
Totals		70	51	4	8	4	0	5	2	1	10	18	11	0	1	10	0	29	80	9	4	0	0	18	64	0	2	5	0	79	140

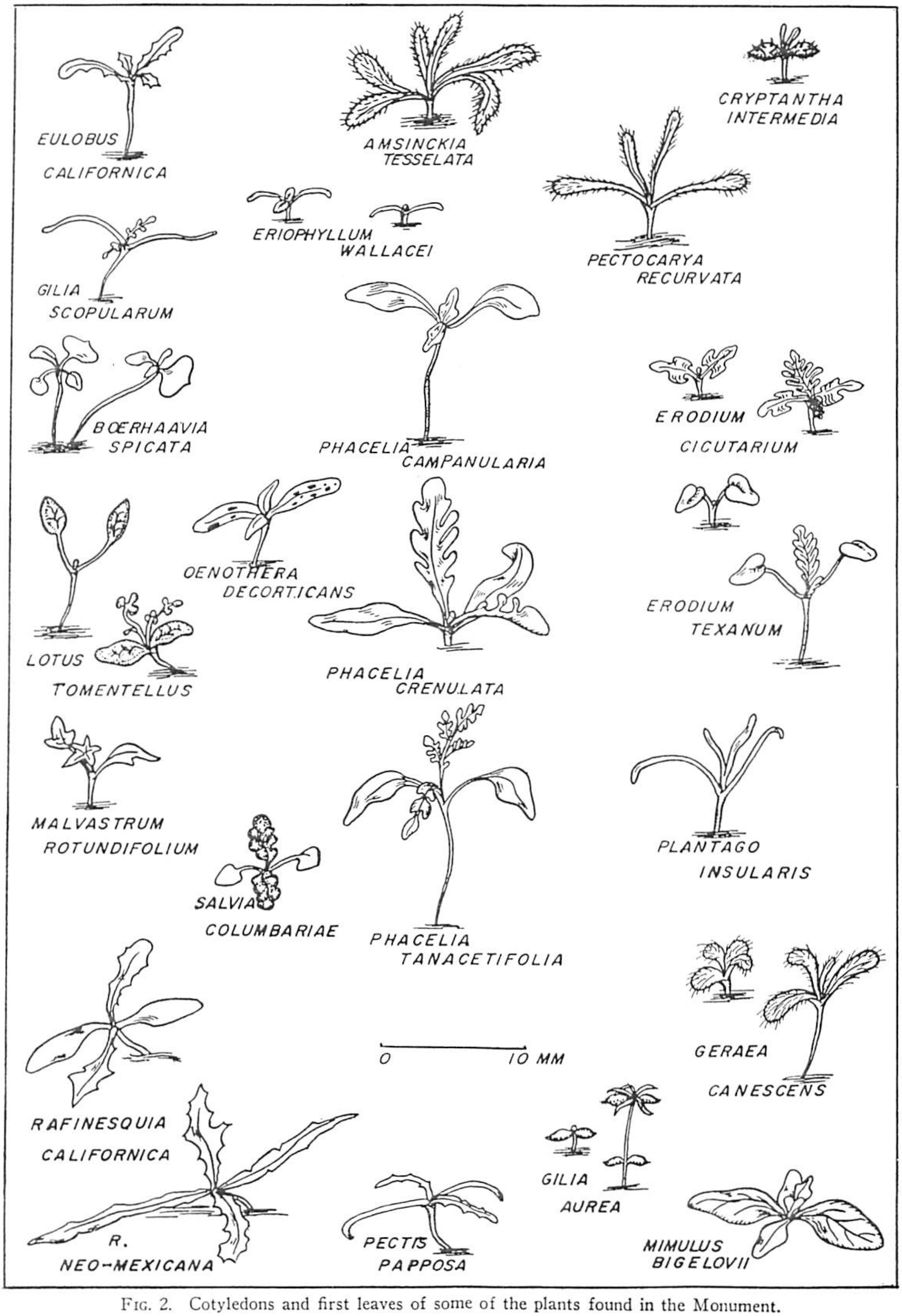

FIG. 2. Cotyledons and first leaves of some of the plants found in the Monument.

On December 30, 1948, 50 cc. of each soil sample was placed in a 4 x 18 cm. wooden flat previously filled with sand, and 100 cc. of washed sand was sprinkled over the top. Each sample was prepared in duplicate. They were then placed under a fine spray for 24 hours, outdoors. The weather was cool at this time (max. 17° C, min. 6° C) with no sun or wind. They received 550 mm. of "rain." They were then brought into the Clark temperature-controlled greenhouses and placed in 6 temperature combinations. Daily observations of the germinations were made, and each seedling marked with a colored toothpick, the color signifying the date. This simplified the daily counting of new germinations. They were sketched occasionally and identified when mature.

On July 26, 1949, after the Earhart Laboratory was in operation, either 50 or 100 cc. of soil sample (the amount depended on the estimated amount of seed in the soil from the location) was placed in a 4" x 8" plastic container previously filled with sand, and 40 cc. of sand was sprinkled over the top. All were placed in an artificial rain at a temperature of 20° C day and night. The "rain" lasted 15½ hours and amounted to 1 cm. per hour. There was a set of samples from 5 of the stations, which was not given rain; each set was kept at the same temperature and watered regularly. The containers were then placed in nine different temperature combinations (Table I) and at an 8 hr. photoperiod. The light intensity was about 400 f.c. There were two replications for each treatment for each of the samples. They were watched daily for the appearance of seedlings and a toothpick was inserted next to each new seedling.

After 11 days, when the peak of germination had been passed, some containers of seedlings in the cold conditions were moved to warm ones, and vice versa, to see if additional species would germinate. Somewhat later all were placed in daylight, in temperatures approximately the same as those in which they had germinated, so that they could flower and their identification be completed.

Results of Laboratory Work

The species whose seeds germinated in the soil samples are presented in the following lists.

I. Winter germinators (as determined by field observation).

Achyronychia cooperi T. & G.
Baeria chrysostoma F. & F. var. *gracilis* (DC) Hall
Bromus rubens L.
Chaenactis carphoclinia Gray
Chaenactis fremontii Gray
Chaenactis stevioides H. and A.
Chorizanthe brevicornu Torr.
Chorizanthe rigida Torr.
Chorizanthe thurberi Wats.
Cryptantha intermedia Gray
Cryptantha spp.
Eriogonum, small annual forms
Eriophyllum wallacei Gray
Erodium cicutarium L'Her. (introduced)
Eschscholtzia glyptosperma Greene
Eschscholtzia minutiflora Wats., var. *darwiniensis* Jones
Eulobus californicus Nutt. (*Oe. leptocarpa* Greene)
Euphorbia micromera Boiss.
Euphorbia setiloba Engelm.
Festuca octoflora Walt.
Filago californica Nutt.
Gilia scopulorum M. E. Jones
Gilia aurea Nutt.
Gilia eremica (Jeps.) Craig
Gilia matthewsii Gray
Gilia spp.
Glyptopleura setulosa Gray
Lepidium lasiocarpum Nutt.
Lepidium nitidum Nutt.
Lepidium other unidentified species, probably *L. fremontii* Wats.
Monoptilon bellioides (Gray) Hall
Oenothera decorticans (H. & A.) Greene
Oenothera spp., probably *californica, deltoides, brevipes, clavaeformis*
Pectocarya spp., probably *recurvata* Johnston; *penicillata,* (H. & A.) A. DC and/or *setosa* Gray
Phacelia crenulata Torr.
Phacelia tanacetifolia Benth.
Phacelia campanularia Gray
Plantago insularis Eastw.
Poa annua L.
Salvia columbariae Benth.

II. Summer annuals

Amaranthus fimbriatus (Torr.) Benth.
Bouteloua aristidoides (H.B.K.) Griseb.
Bouteloua barbata Lag.
Boerhaavia spictata Choisy var. *torreyana* Wats.
Boerhaavia intermedia Jones
Pectis papposa Gray
Portulaca oleracea L (introduced).
Euphorbia micromera Boiss.
Euphorbia setiloba Engelm.

After this, the plants will be referred to by the genus name alone, when only one species has been listed.

Of those soil samples which were given rain and placed in different temperatures in the Clark greenhouse, a comparison was made between the number which germinated per square meter of

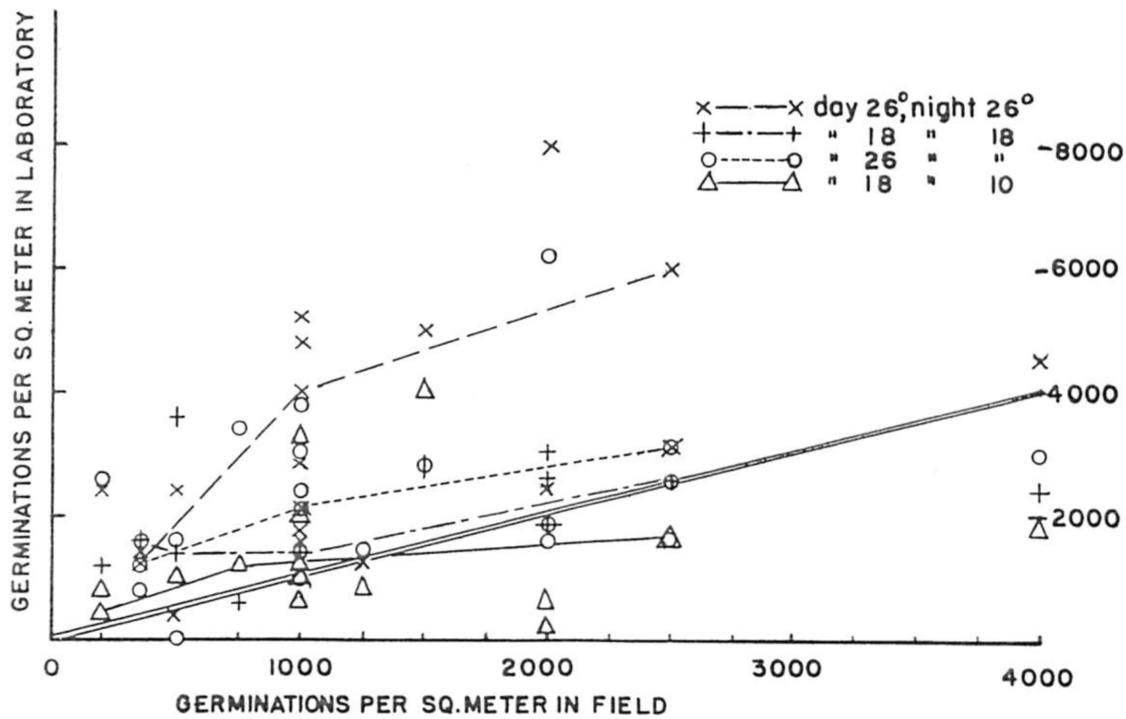

FIG. 3. Comparison of germination per square meter in the field and in the laboratory. The double line represents the ideal curve that would be obtained if there were 1 germination per sq. m. in the laboratory for every 1 in the field, in the season of 1948-49. The curves obtained for the cold temperature in which the winter annuals appeared, approximate the ideal curve fairly well. Curves obtained in the warm conditions, in which the summer annuals appeared, diverge greatly because there was little germination in the field that summer, due to lack of rain.

desert soil in the greenhouse and the number which germinated in the field in 1948-49.

At the lower temperatures (day 18°, night 10° and day 18°, night 18°), the ratio is close. At the higher temperatures (day 26°, night 18° and day 26°, night 26°) there was a large germination in the greenhouse but none in the field, because of the absence of summer rain. (See Figure 3.)

It should be borne in mind that these soil samples were taken after a rain. This rain of October, 1948, was followed by large germination in the field. Nevertheless, much viable seed must have remained ungerminated in the soil, since large numbers of seedlings appeared when the soil samples were placed in various temperatures in the laboratory.

Table I presents a condensation of the laboratory soil sample germination results. The division into cold, medium, and warm is made according to the phototemperatures, which seemed to be critical for some of the species. Nothing but winter annuals germinated in the cool temperatures; both summer and witner ones germinated in the medium temperatures. Summer annuals germinated predominantly in the warm temperatures. Of winter annuals, only a few *Eriophyllum*, never more than one to a sample, germinated in warm conditions.

Where many seedlings were expected, only 50 cc. of soil was used in the germination tests. By doubling the figures obtained, the estimated number of viable seeds per 100 cc. was obtained. All other soil samples consisted of 100 cc.

In the samples which were given no initial rain but which were watered thereafter, from one-fourth to three-fourths as many seedlings appeared in the medium temperature conditions as in control samples, in the same conditions but with the initial rain. Whereas *Pectis, Portulaca,* and *Gilia aurea* were plentiful in the controls, they did not appear in the sample which received no rain. There was a single exception to this; in the sample from Station 5, which is the lowest and hottest of all and consisted of almost pure sand, there were an equal number of germinations with and without rain, and *Eriophyllum* and *Gilia aurea* were among them.

In the warm conditions, germination in the samples without rain was in no case greater than half of the germination with rain. In one sample, there was no germination, while its control had 32 germinations. Few of the seedlings which germinated survived, even from Station 5. Species which appeared plentiful in the duplicate samples were, again, *Pectis, Gilia aurea,* and *Portulaca;* of these only *Gilia aurea* appeared in the sample without rain. This confirms the field observations on the need of *Pectis* for a rainfall of at least 20 mm. (Went 1948). After light summer rains in 1953, a few *Pectis* seeds germinated after 15 mm. precipitation, but not after 10 mm. or less.

In growing the annual seedlings to maturity, it was found that given sufficient light intensity and proper photoperiod in the case of long-day plants, temperatures best for germination are also best for survival and flowering. This is what we should expect if the faculty of germination only within certain temperature limits has survival value. In the case of some species (*Pectis* and *Eriophyllum*), a change of temperature (to low or high) shortly after germination is followed by dwarfing and early flowering both in the laboratory and in the field.

In 1951, for example, there were 2 rains with the same temperatures prevailing, one in July and one at the end of August. Some *Pectis* germinated after both rains. After the July rain temperatures remained high and the seedlings developed into large plants. After the August rain, the temperature dropped and the plants were dwarfs. In the laboratory, both *Pectis* and *Eriophyllum* were dwarfed if transferred to lower temperatures.

In the Earhart Laboratory experiments, when containers were first placed in low temperatures and then placed in higher temperatures after germination semed to have ceased, *Bouteloua* (a summer annual), germinated. There was also some further germination of *Portulaca,* an introduced summer annual. When those placed first in high temperatures were changed to lower ones, *Gilia aurea* and *Eriophyllum* (winter annuals) appeared.

Not only germination, but also survival was observed both in the field and in the laboratory. As Figure 4 shows, the winter annuals not only germinated, but also survived better at the lower

Table II. Germination, temperature, and rainfall at Station 8, a station typical of medium elevation (1189 m.) toward the center of the Monument

Date	mm. rain	Temp. °C. day	Temp. °C. night	Species which germinated
Oct. 17, 1948	43.5	21°	9°	*Eriogonum, Erodium, Filago, Gilia matthewsii, Mentzelia* sp., *Oenothera clavaeformis, Pectocarya* sp., *Salvia*
May 31, 1949	12.0	19°	4°	1 *Bromus,* 106 *Calyptridium,* 48 *Chaenactis carphoclinia,* 50 *Cryptantha,* 250 *Eriophyllum,* 1 *Malacothrix,* 35 *Nama,* 106 *Bromus,* 1 *Anisocoma,* 400 *Erodium,* 13 *Eriogonum,* 10 *Gilia aurea,* 10 *Lupinus,* 42 *Salvia*
Nov. 10, 1949	6.2	14°	8°	No germination
Dec. 8, 1949	10.9	10°	4°	4 *Lupinus,* (germ. in Feb. There had been 4 showers since Dec.)
July 7, 1950	8.3	35°	19°	No germination
Aug. 25, 1950	5.6	39°	21°	No germination
Sept. 5, 1950	43.4	31°	17°	210 *Aristida,* 1 *Bouteloua,* 10 *Eriophyllum,* 5 *Erodium,* 30 *Euphorbia setiloba,* 20 unidentified
Jan. 11, 1951	6.3	12°	−2°	No germination
Jan. 29, 1951	11.2	16°	−1°	2, unidentified, died
April 3, 1951	8.0	24°	9°	No germination
April 18, 1951	19.5	24°	10°	No germination
May 14, 1951	9.2	20°	11°	2 *Aristida,* 2 *Bromus,* 6 *Chorizanthe,* 8 *Erodium,* 3 *Gilia* sp. *Pectis* and *Salvia* near quadrat.
Aug. 28, 1951	11.3	28°	11°	No germination
Sept. 28, 1951	6.7	31°	13°	No germination
Oct. 30, 1951	10.4	22°	3°	No germination
Nov. 22, 1951	11.9	14°	0°	No germination
Dec. 12, 1951	7.3	11°	−2°	No germination
Dec. 29, 1951	7.0	8°	−6°	1 *Delphinium,* 33 *Erodium,* 150 *Eriophyllum,* Near quadrat: *Amsinckia tesselata, Chaenactis fremontii, Monoptilon, Oenothera decorticans, Oe. clavaeformis, Salvia*
Jan. 17, 1952	41.7	14°	1°	No germination
March 8, 1952	7.7	12°	−2°	No germination
March 15, 1952	6.0	16°	0°	31 *Eriophyllum*
April 27, 1952	5.3	29°	11°	No germination
Nov. 8, 1952	6.5	19°	2°	No germination
Nov. 14, 1952	18.1	14°	1°	No germination
Dec. 17, 1952	39.6	9°	0°	40 *Chaenactis fremontii,* 17 *Coreopsis bigelovii,* 300 *Eriogonum,* 500 *Eriophyllum,* 300 *Filago,* 130 *Gilia matthewsii,* 10 *Oenothera decorticans.*
Feb. 24, 1953	9.2	16°	0°	22 *Cryptantha*
July 11, 1953	7.2	38°	22°	No germination
July 18, 1953	9.3	40°	21°	No germination
Aug. 12, 1953	11.5	33°	15°	5 *Bouteloua*

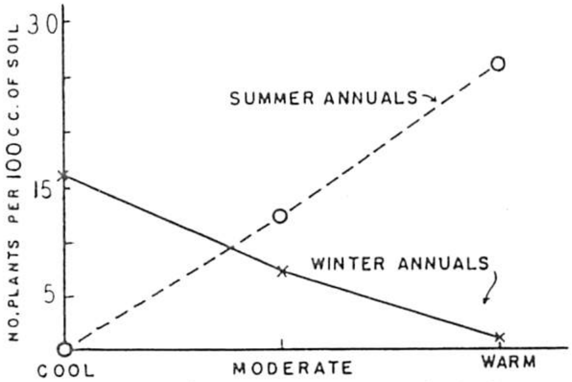

FIG. 4. Comparison of temperature optimals for summer and winter annuals when germinating in the laboratory.

temperatures, whereas the opposite was true for summer annuals. Tables IV and V give typical survival records.

RESULTS OF FIELD WORK

In reporting the field observations, it is not possible because of their extent to give the entire tabulation. Neither does it seem wise to group the stations, since the chief value is the segregation of factors. Hence it was thought best to show the full data for one station. As a typical example, the germination at Station 8 is shown in Table II. All data, however, have been considered in discussing the individual species, and are available.

Rainfall for the various stations is given in Table III. Estimated temperatures for all stations were calculated from those taken at Twentynine Palms on the basis of a decrease of 1° C for each rise of 125 meters, which seemed to be justified by previous temperature observations in various parts of the Monument.

TABLE III. Winter rainfall for various stations during each of the 5 years

Station	1948-49	1949-50	1950-51	1951-52	1952-53	Elevations
5.......	49.7	18.2	19.0	97.3	47.3	610 m.
1.......	43.5	21.8	15.1	80.4	55.2	671 m.
3a......	—	22.1	26.2	96.4	61.9	762 m.
3.......	—	19.5	—	72.0	64.4	854 m.
8a......	53.5	27.0	61.2	—	—	915 m.
4.......	—	27.2	19.8	—	—	915 m.
2.......	—	19.5	24.6	127.3	89.5	1067 m.
8b......	55.8	28.0	53.3	—	—	1098 m.
6.......	53.6	31.6	33.2	123.3	72.5	1159 m.
8.......	57.7	30.8	60.4	120.5	84.7	1189 m.
7.......	55.1	36.1	—	—	73.0	1220 m.
9.......	59.8	38.3	43.6	136.6	84.8	1220 m.
12......	80.7	58.8	60.9	158.4	—	1312 m.
11......	57.4	53.0	78.1	143.4	94.3	1311 m.
9a......	59.4	41.1	69.1	—	—	1372 m.
10a.....	72.8	54.5	87.1	186.6	94.9	1372 m.
10......	50.5	58.6	85.2	165.2	92.9	1403 m.
Twenty nine Palms...	93.3	44.7	39.3	61.1	49.7	650 m.

The winter rains (September through April) have been compiled in Table III. The summer rains are even more irregular, and there were very few in the years 1949-1953. These 5 seasons have been exceptionally dry, as indicated by a comparison with the average winter rainfall of 100 mm. in Twentynine Palms, which is just outside the Joshua Tree National Monument at 700 m. elevation. In Figure 5 the winter rainfall values of 3 to 5 stations are averaged for the different altitudinal ranges. This figure shows clearly the increase in precipitation with altitude; at 1,370 m. almost twice as much rain fell as at 650 m. In the driest years, the highest stations received 2.5 and 3.8 times as much rain as the lowest, but in the wetter years, only from 1.4 to 1.9 times as much. The stations below 1,100 m. had 5.0 times as much rain in the wettest years as they had in the driest. The higher stations had only 3.3 times as much. This shows that the yearly aberrations from station to station are greater when the precipitation is less.

In general, the quadrats typified the germination of the area as a whole. This was true particularly in the years of wide-spread germination. In the more barren years, species which occasionally occurred in an area often failed to be represented in its quadrat. Their presence in the neighborhood of the quadrat was then recorded.

It may be of interest to describe briefly the general character of each of the 5 winters.

The season of 1948-1949 began with a general rain of over 40 mm. In late December, there was a heavy snowfall which covered the ground for weeks. This was not recorded by the gauges but amounted to about 50 mm. of precipitation. Therefore, moisture was probably not a limiting factor. Although nights were below freezing, plants were protected by snow. By the time the snow melted, temperatures were moderate. Rainfall for the year, exclusive of the snow, varied from 50 mm. at Station 5 to 73 mm. at Station 10a. There was a large germination. Species which were conspicuous in the blossoming period were *Gilia aurea, Gilia matthewsii,* and *Eriophyllum wallacei.* The infrequently found *Nemacladus* and *Eschscholtzia glyptosperma* were also present.

In 1949-1950, there were only two rains of any consequence, one in October and one in December. Rainfall at Station 5 totaled 18 mm.; that at station 10a, 55 mm. Average monthly temperatures range from day 16° C, night —1° in

January, to day 25°, night 7° in March. There was little germination, mostly borages and *Salvia columbariae,* with a few *Chaenactis fremontii, Achyronychia,* and *Gilia eremica.*

The winter of 1950-1951 was equally dry, and was very cold. The average minimum temperature for the first 3 weeks of January was below 0° C. Night temperatures at the higher stations were as low as —11° C. There was no snow to mitigate the effect of these temperatures. *Eriogonum, Gilia eremica,* and *Erodium cicutarium* germinated. Although at the higher stations a few seedlings were killed by frost, in the main the plants proved remarkably hardy. Many survived a period of being encased in ice, with the ground frozen.

In 1951-1952, there was a late August and a late September rain, both with temperatures of approximately day 29°, night 13°. This brought about the unusual appearance of summer and winter annuals at the same time, the former blooming while the latter were germinating. There were good rains later. Station 5 received 98 mm., Station 10a had 187 mm. There were also heavy frosts. Temperatures were moderate in the daytime (16° to 24°) and low during the night (0° to 4°). There was a very large germination and plants grew so vigorously that there was a great display of flowers. Large areas were covered with *Malacothrix californica, Eschscholtzia minutiflora* var. *darwiniensis* (very large), *Rafinesquia* (both species), *Oenothera decorticans* and *Oe. clavaeformis.* There were many patches of *Phacelia campanularia, Phacelia tanacetifolia, Monoptilon, Nama demissum, Amsinckia,* and *Draba.* For the first time since the winter of 1947, *Thelypodium cooperi, Mimulus bigelovii,* and *Glyptopleura* were noted. *Layia* and *Baileya* were more common than usual.

In 1952-1953, Station 5 received 47 mm. of rain, and Station 10a, 95 mm. There was one good general rain in February. Night temperatures were below freezing much of the time in November and December. The most abundant species were *Chaenactis carphoclinia, Erodium, Eriophyllum, Gilia matthewsii,* and *Eriogonum.*

There were good summer rains in 1951, and one in 1953. The other summers were rainless or nearly so, consequently were without germination. In 1951, all the typical summer annuals were found. In 1953, there was barely sufficient rainfall in August, at Station 8, 5, and 11 to cause the germination of the usual species. There was less *Pectis* and more annual *Boerhaavia* than usual. *Mollugo* germinated along washes but died.

Distribution of seed

As a general rule, the seed of various species are well-distributed over the area. The different stations do not have species peculiar to them; rather, the appearance of a species was correlated with the conditions accompanying a particular rain. If found germinating plentifully at any station, it was usually found at all stations where climatic conditions were similar.

An exception to this rule was Station 11b, the highest one, on a windy promontory. The stations richest in both number of specimens and of species were 10a, 10b, and 8. These were intermediate in elevetation and rainfall, located toward the center of the Monument. Stations 8a, 12a, and 1, though they contained the same species, did not show as large numbers of seedlings. These stations are around the outer slopes which rise toward the central area of the Monument. These slopes face the Coachella and Morongo Valleys, and are subjected to more wind.

Effect of heavy precipitation

The greatest total precipitation does not necessarily produce the greatest germination. In 1948-49 especially, when rainfall was very good, the best germination was correlated with the intermediate amounts of rain. This has been confirmed in the laboratory, where it was shown that the optimal artificial rain for *Baileya* is 50 mm. Soriano (1954) has shown that in the laboratory, 15-25 mm. precipitation is optimal for the germination of *Pectocarya* and certain other winter annuals.

Duration of rainfall

It has also been observed that a long rain is more effective than the same amount of precipitation in a short time. In the summer of 1951, very little germination was found following a brief torrential rain near Rancho Mirage in the Coachella Valley, while in a nearby area, there was a large germination subsequent to a slow rain of no greater total precipitation. This has been shown in laboratory experiments also (Soriano 1954). Soil samples known to contain seed of *Amaranthus retroflexus, Erodium, Malva,* etc., yielded very little germination after an artificial rain of 2 hours, whereas duplicate samples at the same temperature and receiving the same total amount of rain but over a period of 8 hours, gave excellent germination (Went, Juhren, and Juhren 1952).

Correlation of germination with season

Many species germinated when temperatures met their requirements regardless of the time of year. For example, the rain of September 5, 1950, brought forth the winter annuals *Eriophyllum, Erodium, Cryptantha, Gilia,* and *Oenothera de-*

corticans and the summer annuals, *Bouteloua* and *Aristida adscencionis*. Temperatures were 32°-17°. *Eulobus* and *Salvia* germinated in August, 1951, when the temperatures were day 28°, night 10°. *Amaranthus* was found beside the usually winter-germinating *Eschscholtzia minutiflora* and *Phacelia tanacetifolia* after the September 28 rain, at temperatures of day 28°, night 12°.

Effects of first rain on germination for the year

A great variety of species was brought forth by the first rain in October, 1948. This was a general rain which caused the Monument gauges to overflow, so was over 43 mm. There were about 10 species at most stations, with plants numbering in the hundreds and thousands. At the lower stations (day 26°, night 14°), *Phacelia campanularia* and *Dithyrea* germinated in abundance.

The first rains of the autumn of 1949 varied from 5.2 to 12.5 mm. at each station; 4 species appeared at the one station which had 12 mm. but there were only 3 or 4 plants of each. These were *Bromus, Pectocarya, Salvia,* and a *Chaenactis. Erodium,* which is not a native, germinated to the extent of 250 plants at Station 12a after 9.4 mm. of rain. Otherwise there was no germination at all. Even after the second rain there was little germination.

In the fall of 1950, there were again rains of 5.2 to 14 mm. and no germination whatsoever, even after the second rain.

The 1951-1952 season began with somewhat better rain between 8 and 15 mm., with 23 mm. at Station 5 (the sandiest and hottest), but there was no germination before the third rain, except a few *Erodium,* and an *Abronia.* Between Stations 1 and 4 there was extensive germination of *Mentzelia involucrata, Phacelia campanularia, Oenothera clavaeformis,* and other autumn-germintors. At Stations 4 and 2 a total of 20 mm. precipitation was recorded in the end of October. Later in this season there was much rain, also hoar frost (so presumably dew) and then there was very extensive germination.

Ordinarily 10 mm. of rain in the beginning of the winter season did not cause germination, but once there had been a heavy winter rain, a subsequent rain of 5 or 6 mm. would produce germination, even if the ground had dried out thoroughly in the interim. Presumably leaching of an inhibitor had occurred in the first rain; the following low temperatures had prevented the formation of new inhibitors.

Relation of individual species to rain-temperature combinations

In order to establish limits of tolerance for the various species, all the appearances of each species were listed, with the accompanying weather data. If more than 15 seedlings of the species appeared on a quadrat after a rain, conditions at the time of the rain were considered favorable. If none appeared in or near the quadrat, conditions were considered unfavorable. It was thus possible to determine limits within which a species germinates. Once a plant had appeared on a quadrat and borne seed, it was assumed that seed was present in or near the quadrat. Subsequent occasions were studied to find out whether there were rains which supplied conditions within those limits, yet were not followed by germination of the species. Both the conditions accompanying the individual rain, and those which were characteristic of the season as a whole, were considered. The results of such studies on some of the species follow. All temperatures are Centigrade.

Chaenactis fremontii appeared when day temperatures were between 12° and 30°, with night temperatures of 10° and 4°. Once only, it appeared after the night temperature had been 0°. Rainfall was always above 10 mm. unless there had been a previous rain or rains that season, when a 5.6 mm. rain was sufficient. Table I shows that in the laboratory it is a cold germinator.

Chaenactis carphoclinia was usually found when day temperatures had been between 15° and 19°, night temperatures between 1° and 4.5°. It appeared many times after the night temperatures had been below 0°. The lowest temperatures at which it germinated were 4.5° day and —3.9° night. It never germinated after a first rain of less than 10 mm., but once appeared after a 2 mm. rain preceded by snow. Intermittent germination occurred, that is, the species that appeared in November, did not appear after January rains, but germinated again after a March rain. Temperatures in November and in March were optimal for it, but in January they were lower than any which have accompanied its appearances. *C. fremontii* and *C. carphoclinia* were found only once growing simultaneously in the same quadrat; on this occasion the former appeared a month later than the latter, which was in harmony with their temperature preferences.

Calyptridium monandrum germinated when the day temperatures were between 14° and 25°, night temperatures between 1° and 9°. On 2 occasions, 1 or 2 plants appeared when the night temperature was 0°. It germinated after the first rain of the season only once, when the rain was of over 40 mm., at other times only after later rains of not less than 11 mm. It always appeared when optimal conditions were satisfied.

Eriophyllum wallacei usually occurred when day temperatures were 19° or 20°, night temperature from 3° to 8°. It germinated occasionally when day temperatures were as high as 30° or as low as 11°, with corresponding night temperatures of 2° to 16°. It was never found after a rain of less than 12 mm. unless there had been previous rains in which case 7mm. sufficed. On many occasions, these conditions were satisfied, yet *Eriophyllum* did not appear. The enormous germinations which occur at times, the many areas that are covered, and the frequency with which it comes up in soil samples, indicate that there is plenty of seed. *Eriophyllum* is at its best when there has been snow, and succeeds well in the greenhouse, where it is watered frequently. These considerations point to leaching as a critical factor. In the laboratory, it germinated predominantly in the cold conditions.

Amsinckia vernicosa appeared only when night temperatures were very low, —1° to —6°, and 7 mm. was the minimum rainfall. It was an intermittent germinator. On a few occasions, it failed to appear when temperatures were optimal for it.

Coreopsis bigelovii germinated when day temperatures were between 11° and 21°, night temperatures between 1° and 5.5°. It has come up after a first rain of 12 mm., a fourth rain of 6.6 mm. The large germinations, however, appeared after rains of 30 to 43 mm.

Plantago insularis occurred when day temperatures were between 4° and 20°, night temperatures between 0° and 9°. It did not appear when nights were below —1°.

Gilia aurea germinated when day temperatures were between 9° tnd 26°, night temperatures between 0° and 10°. Rainfall was always 10 mm. or more.

Baileya pauciradiata and *multiradiata*. No difference in climatic response was observed in these species. They both germinated when the day temperature was between 16° and 29°, night temperatures between 5° and 9°. It is possible that the day temperature could be higher. Seven mm. of rain was sufficient. In the Monument, *Baileya* has not been found below 1200 m.

Salvia columbariae was found when day temperatures were from 10° to 31°, night temperatures 0° to 11°, but most of its appearances followed day temperatures of about 18°, night temperatures of 2° to 4°. A rain of 12.5 mm. was sufficient to cause germination.

Amaranthus fimbriatus was found when day temperatures were between 28° and 35°, night temperatures between 12° and 20°. First rains of only 6 mm. were sufficient for it. It sometimes germinated for a second time in a summer, but did not do so when the second rains were heavy, of 23 to 50 mm. This seems to agree with the other evidence that large amounts of rain are deterrent to its germination.

Pectis papposa appeared after any of the summer temperatures, day temperatures of 28° through 40°, night temperatures of 13° to 21°. Only when the first rain was of as much as 12.5 mm. did *Pectis* appear; and if subsequent rains were of at least 9.5 mm. A 22 mm. rain brought forth enormous numbers of seedlings at Station 9 when a previous rain of 9.3 mm. and similar temperatures, had not been followed by germination.

Occasionally (though by no means frequently, and not in our quadrats) *Pectis* has germinated in early fall when temperatures were definitely lower than summer temperatures; in the laboratory also it has come up in soil samples placed in moderate temperatures. Both in the field and in the laboratory it is then much dwarfed. In the laboratory it germinated predominantly under warm conditions (Table I).

Boerhaavia spicata and *intermedia* appeared under widely differing conditions, rains of from 6 mm. to 51 mm., with day temperatures between 21° and 39°, night temperatures between 12° and 30°. In spite of this wide tolerance. it did not appear after every summer rain, when these conditions were offered. On 4 out of 5 appearances, it germinated after the second rain of the summer, not after the first. However, on one occasion it did germinate after the first rain, which was of only 6 mm. The scarcity of summer rains, and especially on the same quadrat, prevented the obtaining of much evidence. The species is not a prolific seeder, and it may be that this is the reason for its non-appearance under favorable germinating conditions.

Discussion

In this investigation, an attempt has been made to correlate laboratory results and field data in a dual effort to explain field observations with quantitative and controlled experiments, and to show that behavior of plants in the laboratory parallels that in the field provided laboratory conditions duplicate the significant factors controlling development of the plant in nature.

The principal factors which determine the germination of annuals in any given season in this area are the amount and duration of precipitation and the temperatures which prevail while the soil is wet. Each species has definite and rather narrow limits of tolerance and is not found in quantity except when conditions are within these limits. In consequence, much viable seed remains ungerminated in the soil from year to year, even after heavy rains, which can be induced to germinate if placed in suitable conditions. Leaching is also an important factor. It is brought about best by slow rains, or by a heavy initial rain followed by light sprinkles at intervals, or in the case of winter germinators by snow remaining on the ground.

While species are not found germinating outside of their limits of tolerance, they are not always found when seemingly, conditions within these limits have prevailed. This failure to appear could be due to absence of seed in the particular areas, or to factors as yet unknown.

In previous work, it was shown that desert annuals can be segregated into winter and summer germinators (Went 1947, 1948). This distinction was made by Shreve (1951) for Sonoran Desert plants. It also was shown that a definite amount of precipitation was necessary before these plants germinated. Both these facts were confirmed and extended in the present investigation. From Table I and Figure 3, it is clear that desert annuals can be divided according to the temperatures at which they germinate and at which they survive. The low temperature germinators (*Eriophyllum, Chaenactis, Gilia aurea*) survived best at the lowest temperatures at which they were tested in the greenhouse (10° C day, 3° C night), and when they had germinated at all at the higher 30° C day and 17° C or 23° C night temperature, they later died. Exactly the opposite is the case for summer germinators (*Pectis, Bouteloua, Portulaca* and *Euphorbia*). In the field plots, the distinction between summer and winter germinators was more pronounced than in the laboratory, where at intermediate temperatures (day 17° C and 23° C with night at 10° C-17° C) both groups germinated in equal numbers. This was never observed in the field. Although once in autumn a few summer annuals germinated with large numbers of winter annuals, and in the late summer a few *Eriophyllum* were found in shaded spots together with much *Pectis* and *Bouteloua*, on the whole there is no doubt that the difference between summer and winter germinators is primarily a question of temperature during germination. The reason that some summer germinators appeared in cool conditions in the laboratory, may have been that during the 12-24 hour rain period all seedling flats were exposed to the same temperature (17° C-20° C). Only afterward were they brought into different temperatures. Also, neither warm nor cold temperatures are so extreme in the laboratory as in the field.

There was no yearly rhythm in germination such as Bünning has observed with several plants or Barton in *Amaranthus* (Barton 1945), for our germination tests have been carried out at different times of the year and each time the same two groups of warm and cold germinators developed.

The collected data are most interesting in connection with the rain observations. On account of the irregularity of rains in the desert, both in respect to space and time, it was necessary to have a rain gauge installed next to each ecological station. These gauges were distributed over an altitudinal range from 600-1300 m. above sea level, and as Fig. 5 indicates, the amount of precipitation is greater at higher altitudes. The Joshua Tree National Monument lies east of the San Bernardino and San Jacinto mountains, which are over 3,000 meters high, and relatively little moisture is left in the atmosphere after the moist air from the Pacific has passed over them. At 100 m. elevation west of these mountains, the average annual rainfall is 400 mm. At 100 meters in the Monument, it is likely to be only 25 mm. (See Fig. 5). The measurements were made in dry years. Precipitation at this elevation would be about 50 mm. in normal years. (In Death Valley further northeast, at sea level, annual winter precipitation amounts to 30 mm. per year.)

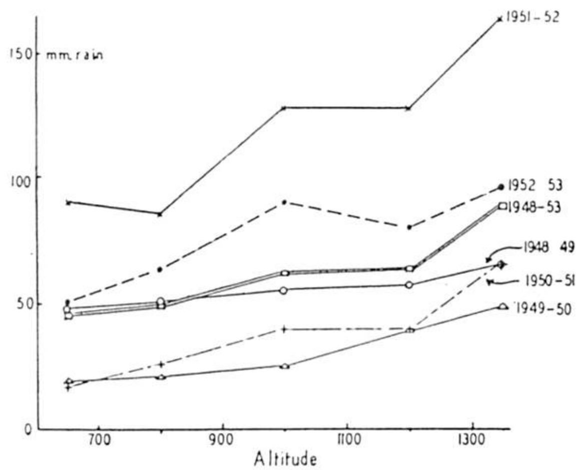

FIG. 5. Correlation of precipitation with altitude.

The years over which the project has ranged (1948-1953) were exceptionally dry, all but 1951-52. This can be seen in the field by the many dying or dead shrubs of *Larrea* (*e.g.*, near Station 4a), *Dalea spinosa* (near Station 5), *Juniperus* and especially (near Station 3) smaller plants like *Franseria dumosa* and *Hymenoclea*. Summer rains, coming as local thunderstorms, were almost completely absent, and the splendid display of *Pectis* and other summer annuals in 1945 has not been repeated. In the summer of 1953, a rain of 9-12 mm. occurred at Stations 8 and 9, and in both places a few *Pectis* and *Bouteloua* germinated (about 5-10 per m.^{2}). They flowered and set seed, even though the plants remained very small. At Station 11, in that same summer, no rain occurred, but on a nearby slope precipitation was barely sufficient to have some water stream down a few washes. There a few seedlings germinated, but there was not enough water on the soil to carry them through, and consequently they died before flowering.

After the winter rains, the amount of germination was proportional to the amount of precipitation. The first rain of the winter season had to be well over 10 mm., preferably 20 mm. or more, before germination would occur. Also, the night temperature had to remain at or above freezing. Heavy rains or snow at lower temperatures were ineffective in causing germination. When the first rains were accompanied by moderate temperatures but were of only 10 mm., another rain of 10 mm. or more would be required to bring about further germination.

If, however, the first rains were accompanied by very low temperatures, a subsequent rain of as little as 5 mm. could result in germination. This could be explained by assuming that a germination inhibitor is released by a rain of 10 mm. or more, but if the temperatures are not suitable for germination, the inhibitory factor is reconstituted again, so that another rain of 10 mm. or more is again required for germination. If, however, temperatures during and after the first rain are very low, the inhibitory factor is not reconstituted. Consequently, the seeds can germinate with much less rain, given suitable temperatures.

Once sufficient germination had taken place to produce a closed cover of plants, subsequent rains at various temperatures did not produce any further germination within the existing thick vegetation. In nearby areas where there was not a closed cover, more germination occurred. In soil samples taken from the thickly covered areas, further germination took place in the laboratory. Competition for moisture by the plants already germinated could hardly have been the reason for the nonappearance of new ones in the field, for the seedlings already up were small and by no means exhausted the soil moisture, nor did they create shade of an extent which could be limiting. The phenomenon is believed to be due to germination inhibition by an existing vegetation. This conclusion was first based on counts of seedlings and successive visits to the plots, and later confirmed by counts made from photographs. Further investigations are being carried out in the laboratory.

TABLE IV. Number of seedlings which germinated and number of surviving seedlings at various stations in the season of 1948-1949

Station	Elev. in meters	No. of seedlings Dec. 12	Mar. 13	Apr. 30	Identified species germinating at rates from 50 to 600 seedlings per m^2.
5........	600	500	22	18	None identified
7a.......	670	2000	364	244	*Chorizanthe, Monoptilon*
7b.......	800	1000	128	62	*Chorizanthe, Salvia*
8a.......	900	500	—	251	*Cryptantha, Eriophyllum, Pectocarya*
8b.......	1100	1200	—	1008	*Cryptantha, Filago, Chorizanthe, Coreopsis, Eriophyllum*
6.......	1150	1500	3140	766	*Chaenactis, Coreopsis, Eriophyllum, Pectocarya*
8.......	1200	1000	—	966	*Bromus, Chaenactis, Erodium, Eriophyllum*
7.......	1220	1000	—	872	*Amsinckia, Chorizanthe, Eriogonum, Eriophyllum, Pectocarya*
9.......	1220	1000	—	512	*Chaenactis*
12.......	1300	200	64	93	*Eriophyllum, Gilia aurea, Gilia scopularum*
9a......	1370	800	—	298	*Cryptantha, Eriophyllum*
10b......	1370	2000	1450	1492	*Eriophyllum, Gilia aurea, Gilia scopularum, Pectocarya*

TABLE V. Typical survival figures, obtained in the season of 1951 and 1952. By means of 3-dimensional photographs, it was possible to tell that the plants surviving in April were the same individuals that germinated in February or March.

Station elevations (m)	Number germinating	Number surviving seedlings	% survival
600-800......	3,500	324	9
900-1150.....	4,840	2,025	42
1200-1370.....	6,000	4,233	71
Total......	14,340	6,582	46

Table IV shows the number of seedlings and plants counted on successive visits to the different plots during the 1948-49 season. On the average more than 50% of the plants which germinated survived and produced seed.

All observations support the thesis that most seeds of these desert annuals do not germinate unless the conditions for continued growth are favorable, and that most seedlings survive. Therefore, there is little selection occurring during the vegetative development of these annuals, which explains why most of them do not show special adaption in their vegetative characters to the desert habitat. Their adaptations have to be sought in their early maturation and in their germination characteristics.

SUMMARY

Twenty-three stations with rain gauges and quadrats of one square meter were set up in Joshua Tree National Monument. Over a 5 year period the germination of annuals was correlated

with precipitation and maximum-minimum temperatures.

Samples of soil were taken from each station, and placed on flats of sand in controlled climatic conditions in the Earhart Laboratory. Germinations were counted and seedlings grown to maturity and identified. Drawings of the cotyledons and first leaves of many of the species were prepared.

From the combined field and laboratory data, optimal conditions and critical extremes were determined for the species which germinated in quantity. It was found that temperatures which prevailed in a brief period following each rain, together with the amount and duration of precipitation, were the major factors that brought about germination, and that the total amount of germination was proportional to the amount of precipitation up to an optimum beyond which germination decreased. The amount of the first winter rain and the temperatures accompanying it were of especial significance. Leaching and wind were other factors of importance. Survival of the seedlings was also observed, and averaged over 50 per cent.

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NATURE OF THE PLANT COMMUNITY. I.UNIFORM GARDEN AND LIGHT PERIOD STUDIES OF FIVE GRASS TAXA IN NEBRASKA[1]

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The grassland type of vegetation approaches the ideal for an experimental analysis of the nature of the plant community. The growth form of most members of the grassland community, in contrast with those of communities in which woody members predominate, allows liberal use of transplant techniques. Readily available clones of most members at any time during the year afford ample material for an experimental study.

For an understanding of the nature of a plant community which has been geographically oriented and whose composition has been determined with respect to plant identification, the individual plant behavior within the community needs to be observed and evaluated. The present study was designed to observe individual behavior and then to compare the behavior of individuals of a number of species from one community site with individuals representing the same series of species from a different community site.

Uniform Garden Approach

While the vegetational composition varies considerably throughout Nebraska, a number of grasses occur widely in the state. When clones representing a number of these grass taxa were collected for the uniform garden study, there was an attempt to obtain samples widely throughout the state. At any particular community site, the individuals removed for transplanting represented some or all of the following taxa: *Bouteloua gracilis* (H.B.K.) Lag., *Bouteloua curtipendula* (Michx.) Torr., *Andropogon scoparius* Michx., *Andropogon gerardi* Vitman—*A. hallii* Hack. complex, and *Panicum virgatum L.* The majority of the clones were removed from the collection sites between July 24 and August 19, 1953. Certain collections of *P. virgatum* were removed on September 20. A piece of each clone was preserved as a documentation of the development under habitat conditions of 1953. The remaining part of the clone was tagged and was placed in a tub of moist Sphagnum moss. The clones were subsequently put into a spaced planting at Lincoln. At the time of planting, the cultivated soil was fairly dry and a technique of placing the clone into a pool of mud prior to covering with dry soil was used. There was no watering of the clones

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