STUDIES ON THE ECOLOGICAL AND PHYSIOLOGICAL SIGNIFICANCE OF AMPHICARPY IN GYMNARRHENA MICRANTHA (COMPOSITAE)1

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ABSTRACT

The 2 types of fruit (aerial and subterranean) borne by the dwarf desert annual Gymnarrhena micrantha were compared with regard to their responses to factors affecting their formation, dispersal, germination and seedling mortality. The 2 types of fruit differed markedly in several respects. In comparison with the subterranean fruits, the aerial ones are much smaller and more numerous, but the formation of the inflorescence in which they develop is more dependent on a favorable supply of soil moisture. The aerial fruits are dispersed by wind, after becoming detached by a complex series of hygroscopic movements which involve several organs and tissues, while the subterranean fruits do not leave the dead parent plant, germinating right through its tissues. Germination of the subterranean fruits starts after a shorter incubation period and is less temperature-dependent in both light and dark. Light stimulated germination of both types of fruit, increasing their germination rates and final percentages, but not affecting the duration of the incubation period. In the subterranean fruits, the rate of germination was equally stimulated by light over the entire temperature range, with a well-defined optimum at 15°C in both light and dark. In the aerial fruits, the same optimum was found only in the light, rates in darkness increasing with decreasing temperatures. In the aerial fruits, alternations of light and dark were more favorable to germination than either continuous light or dark, the full effect being obtained with a single 8-hr or 16-hr light period, provided it was preceded by 16 or 8 hr of darkness, respectively. Similar reactions to combinations of light and dark were not observed in the subterranean fruits. Seedlings developing from the subterranean fruits were much larger, but grew at a relatively much slower rate than those from aerial fruits. The former were distinctly more tolerant of unfavorable soil-moisture regimes, such as low moisture supply and drought. It was concluded that the 2 types of fruit serve 2 distinct functions in the biology of the plant. The aerial fruits are adapted to the function of increasing the distribution of the species within suitable habitats, while the subterranean fruits are adapted to increasing the probability of the survival of the species.

The phenomenon of amphicarp, where the same plant bears both aerial and subterranean fruits, is known in quite a few species. There have been several suggestions regarding the ecological significance of this phenomenon. One suggestion is that seedlings germinating from the subterranean fruits are provided with a better chance for subsequent survival, since their micro-habitat is that which provided the parent with conditions adequate for completion of the life cycle (Zohary, 1937). Another suggestion is that the subterranean fruits are better protected from the extremes of the climate and from foraging animals than are the aerial fruits (Engler, 1895; Warburg and Eig, 1926), but this suggestion is opposed by Zohary (1937). Yet another suggestion is that the very fact that the subterranean fruits are already in the soil provides them with a better chance for germination and, therefore, presumably with a better chance for survival of the plants to which they give rise (Engler, 1895). All these suggestions are based mostly on observations, and much less on direct experimental evidence.

The studies described below were aimed at a more detailed investigation of the physiology of the seeds and seedlings of a typical amphicarpic plant, in order to determine any possible differences which might be related to the value of this particular adaptation to the survival of the species. Gymnarrhena micrantha was selected because it has aerial and subterranean fruits which are very distinct from each other and because intermediate forms of fruit are lacking.

Gymnarrhena micrantha Desf. is a dwarf composite, belonging to the Saharo-Sindian phytogeographic element (Eig, 1931–32). The plant is a winter-growing annual of wide occurrence in the steppe and desert regions of the Negev (Israel). In this region it is conspicuous by having habitat requirements far less strict than the majority of other winter annuals, since its distri-

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bution is as abundant on slopes, plains and "ham-
mada" (gravel pavement) as in gullies, dry water-
courses, depressions, etc., which receive additional
runoff water.

Materials and methods—Germination tests
were carried out in Petri dishes, on a single layer of
Whatman’s No. 1 filter paper, moistened with
5 ml deionized predistilled water. Incubators
operating within ±0.5 C of the preset tempera-
tures were used. These incubators were illuminated
with a mixture of incandescent and fluorescent
white light. Temperature stratification was pre-
vented by a forced air circulation. Dark germi-
nation tests were carried out in light-proof tins.
The course of germination was followed by fre-
cquent counts, at which time the germinated
seedlings were removed. Dark germination was
counted at the same time, by use of a dim green
light (green fluorescent lamp wrapped with several
layers of green and blue cellophane), which was
found to have no effect on dark-germination of
this species.

Soil for tests of survival was loess from the
natural habitat of this species. Before use, the
soil was cleaned of stones and plant debris. These
tests were carried out in an exposed location in
Be’er Sheva. Detailed climatological data for this
area are available from the Meteorological Service,
Israel Ministry of Transport.

Results—Morphology and biology—A detailed
description of the plant is given by Zohary (1937).
The following description is based on our own
observations, which were made over a period of
several years, on the morphology of the plant and
on its behavior in the field.

Gymnarrhena micrantha has a compressed stem,
bearing a rosette of leaves. The aerial inflores-
cences produce numerous, small achenes in a
compact capitulum, and each is borne at the end
of a short branch. The subterranean inflorescences
are sessile, borne in leaf axils which are situated
10–15 mm below the soil surface. Each inflores-
cence produces only 1–2 large achenes. The
number of aerial inflorescences may vary between
none and several (see below), while the number of
the subterranean inflorescences is usually between
1 and 3. The corolla tubes of the subterranean
florets open on the soil surface. The achenes
formed in the aerial inflorescences are small and
are equipped with a well-developed pappus,
whereas those formed in the subterranean inflores-
cences are much larger and lack a pappus, or
bear only a vestigial one. During the summer, the
dead plants are sometimes grazed by animals,
which pull the plants out of the ground in their
search for the subterranean achenes, which they
remove by chewing the entire plant. Zohary’s
findings (1937) that the formation of the sub-
terranean inflorescences precedes that of the
aerial ones were confirmed. It was further noted
that in years with low rainfall, the plant can
wither and die without altogether forming the
aerial inflorescences. This behavior occurred also
in experiments with controlled water supply,
either as flood irrigation, or as simulated rainfall.

Dispersal—The achenes formed in the subter-
ranean inflorescences remain enclosed within the
dead lignified tissues of the mother plant, and
when they germinate, the radicle penetrates the
surrounding tissues and the seedling becomes
established in the identical position of the parent
plant. This may repeat itself in successive gener-
ations, leading to the formation of a dense colony
of live and dead plants (Fig. 1a, b).

The achenes formed in the aerial inflorescences
are dispersed most commonly all at the same time,
leaving the receptacle bare. The mechanism of
dispersal was studied under both field and con-
trolled conditions. These studies have shown that
dispersal is operated by a form of hygrochastic
mechanism, responding to repeated cycles of
moistening and drying. The responses were the
same whether the moistening agent was liquid
water, dew, or saturated water vapor. Details of
the mechanism were studied by dissecting the
inflorescence, as well as by microscopic exami-
nation of median sections through the receptacle.

Dry sections were mounted in paraffin oil. The
following organs and tissues were found to par-
ticipate in the mechanism of dispersal, by per-
forming hygroscopic movements, or by under-
going other changes, upon being moistened or
dried. (1) The uppermost layers of the dome-
shaped receptacle form a thin tissue, composed of
collenchymatous cells, which becomes nearly
transparent when wet. The mechanical strength
bonding the cells together is apparently weakened
thereby, since the tissue is easily disrupted in this
condition. (2) A second collenchymatous tissue,
which underlies the above-mentioned surface
layer of the receptacle, swells very rapidly upon
being moistened. (3) The dry bract subtending
the achene is elongated and lanceolate, with the
edges slightly rolled inwards. When it is first
moistened, it straightens, but its edges roll further
inwards. When it is subsequently redried, it coils
and becomes hook-shaped, and this coiling be-
comes more pronounced upon further drying.
(4) The pappus of the dry achene is in the form of
a paint-brush and the entire achene is enclosed
within the rolled edges of the subtending bract.
When it is moistened, the hairs bend outwards at
their base and the pappus opens up as the ribs of
an umbrella. This movement is not reversible by
drying. These features are shown in Fig. 2–5.

Some simple histochemical tests were made, in
order to obtain more detailed information on the
nature of the receptacle. Freeland median sec-
tions were cut through the receptacle and stained
with Genevois Reagent and CI-Zn-I Reagent,
respectively. These stains showed that whereas

\[ \text{Genevois Reagent} = 2.5\% \text{ Chrysoidin} + 2\% \text{ Congo Red}, \text{ in ammoniated aqueous solution.} \]
Fig. 1–3.—Fig. 1a. Colony of dead plants of Gymnarrhena micrantha, with seedlings of subterranean fruits germinating through their tissues.—Fig. 1b. Single dead plant, with 2 of its subterranean fruits germinating through its tissues.—Fig. 2. Median section through dry receptacle of the inflorescence, mounted in paraffin oil.—Fig. 3. Median section through moistened receptacle.
both the uppermost layer of the receptacle and
the underlying swelling layer are both composed of
collenchymatous cells, cell walls of the former
layer do not stain as cellulose, while those of the
latter layer do. The presence of hemicelluloses
in the cell walls of the uppermost layer was
indicated by the fact that this tissue was com-
pletely macerated in 3% HCl, during 12-hr soak-
ing of the inflorescence, by dissolution of the
primary walls. The achenes were thereby de-
tached. A similar soaking in water caused none of
these changes. The suspected presence of hemi-
celluloses in this tissue was further confirmed by
the pink stain obtained in the cell walls after
treatment with Phloroglucinol-HCl, according to
Johansen (1940).

The dispersal mechanism apparently involves
the participation of all the above mentioned
tissues and organs (Fig. 7). The ripe, dry infor-
escence is compact and strawberry-shaped. When
it is wet, the expansion of the receptacle and the
straightening of the bracts bring about a dis-
tending of the entire capitulum into the form of a
hedgehog. The pappus opens up. At this stage
none of the achenes is released. When the head is
redried the receptacle contracts and the capitulum
regains more or less its original shape. However,
the irreversible opening of the pappus is evident
by the protrusion of its hairs between the bracts.
Further cycles of moistening and drying bring
about the curling of the bracts, and they are thus
extracted from their insertion in the receptacle,
which by this time the moistening had weakened.
This movement of the bracts pulls out the achenes
which they subtend. Very frequently all the
chenes are thus loosened at the same time, and
are easily dispersed by wind. The pappus is
permanent (at least up to germination) and serves
as an aid to dispersal. Achenes from aerial in-
florescences have been observed to come to rest in
crevices in the soil and at the bases of stones and
rocks.

Germination—The germination behavior of the
2 types of achene was investigated by studying
the effects of light and temperature on their
germination responses. Material of different ages

Fig. 4-7.—Fig. 4. Disintegration of top layer of receptacle in moistened capitulum (median section).—Fig. 5. Top:
Moistened floral bract. Bottom: Bracts coiling at different stages of re-drying.—Fig. 6. The 2 types of fruit of G. micrantha
and 6-day old seedlings produced from them. At top, 2 subterranean achenes and 2 of their seedlings. At bottom, 2 aerial
achenes and 2 of their seedlings. Dry achenes on left, moistened and redried achenes on right. Note absence of pappus on
subterranean achenes, unopened pappus in unmoistened aerial achene, and irreversible opening of the pappus in moist-
ened, redried aerial achene.—Fig. 7. Fruiting heads of G. micrantha. Dry—on left, moist—on right, and after dispersal—in
center. Divisions at bottom of Fig. are 1 mm apart.
(from ripening) and from collections of different years was compared. Only minor quantitative differences were observed and qualitative responses were the same, so that when an experiment was repeated at different times the results could be treated as replications and combined.

The responses of the 2 types of achene to the experimental conditions were complex. In order to facilitate an analysis, the results were plotted graphically. The germination curves were almost perfectly sigmoidal. The values “P” (final percentages), “S” (time in days until germination reached P/6) and “R” (rate of germination in percent per day, between P/6 and 5P/6) were computed from the germination curves (Koller, 1957). The relationship between these values and temperature, in light and in darkness, respectively, are presented in Fig. 8. These results were combined from 4 separate experiments, with 3 replicates of 25–50 achenes in each.

The results in Fig. 8 show that the 2 types of achene behaved similarly in the following respects: In continuous light, final percentages were consistently higher than those in continuous darkness, at all temperatures. The depressing effects of high temperatures on final percentages were stronger in continuous darkness than in continuous light, the decline in darkness setting in already at 15°C, while in light the decline set in only at 25°C. Start of germination was the most rapid between 15 and 20°C, in both light and darkness, and was not affected by continuous presence or absence of light. Rate of germination was increased by light, but the interaction between temperature and light or dark was different in the 2 types, as will be described below.

Except for these 2 similarities, the types of achene differed markedly in several important respects. Final germination percentages of the aerial achenes were much more temperature-dependent than those of the subterranean ones. This difference in sensitivity was apparent in both light and dark. Thus in darkness, “P” of the aerial achenes was reduced almost linearly by 78% (from 82 to 4%) as the temperature was increased from 10 to 25°C, while that of the subterranean achenes was reduced only by 44% (from 74 to 30%) under the same conditions. In light, this temperature sensitivity is evident only at the higher temperatures (between 20 and 25°C), causing the reduction of “P” by 8% (from 95 to 87%) in the subterranean achenes, and by 50% (from 88 to 38%) in the aerial ones. Start of germination of the subterranean achenes was more rapid than that of the aerial ones. The differences are small, but consistent at all temperatures in both light and darkness. Rate of germination presents a complex interaction between light and temperature effects. In the subterranean achenes, a clear optimum is evident at 15°C in both light and darkness, and light is nearly equally effective in increasing germination at all temperatures. In the aerial achenes, the rate of dark germination decreases almost linearly with increase of tem-

Fig. 8. Effects of light and temperature on start “S”, rate “R” and final percentages “P” of germination of aerial and subterranean fruits of Gymnarrhena micrantha. Description and details in text. (Results at all temps., except 5°C, are means of 4 separate experiments, with 3 replicates of 25–50 fruits in each. Results at 5°C are of only 1 such experiment.)
temperature\(^1\), while in light a clear peak is evident at 15 C. At temperatures above this optimum, light seems to stimulate germination equally, since \(R_{dark}\) is parallel to \(R_{light}\).

Under natural conditions, the seeds are not exposed to continuous light, but to alternations of light and dark. The stimulating effects of light on germination were, therefore, studied with reference to such alternations. However, scarcity of subterranean achenes permitted extensive experimentation only with aerial achenes, and rather limited ones with subterranean achenes. Germination of the aerial achenes was tested several times at 20 and at 25 C, in continuous light, continuous dark, diurnal alternations of 8 hr light with 16 hr dark, and darkness interrupted after 16 hr incubation by a single 8-hr light period. The course of germination was plotted graphically and analyzed as described above. The results in Table 1 are typical.

The results in Table 1 showed that combinations of light and darkness were more favorable for germination than either uninterrupted light or dark. Work with *Plantago coronopus* showed that the sequence of light and dark was of importance in the control of germination (Koller and Roth, unpublished data; see Koller, 1962). It was therefore decided to extend these experiments by testing the effects of such sequences on germination of *G. micrantha*. The results in Table 2 show the responses of the aerial achenes.

1 It must, however, be remembered that the values for 5 C are based on a single experiment.

The results summarized in Tables 1 and 2 show that treatments which incorporated L were invariably more favorable for germination than those carried out in continuous D. At the same time, it is clear that treatments in which a period of L was preceded by D were more favorable even than those carried out in continuous L, or in D which was preceded by an initial L-period.

These stimulatory effects manifest themselves in different ways, in the temperatures tested. At 15 C, "P" and "S" are the same in all treatments, but "R" is increased in all treatments incorporating both L and D, irrespective of sequence. At 20 C, the optimal treatments in all respects were those in which a period of L was preceded by an initial D period. However, "P" in continuous L was as high. Highest "S" values (slowest start) were obtained in continuous L and in continuous D. At 25 C, the values of "S" and "R" do not differ significantly between the various treatments, but "P" values are highest in treatments where a period in light is preceded by an initial dark-period.

Scarcity of subterranean achenes prevented extensive comparisons with the aerial achenes, on the effects of light-dark sequences and combinations upon germination. Material was available for only 1 sufficiently detailed experiment. The results of this experiment are presented in Table 3.

For a variety of technical reasons, experiments with the 2 types of achene were carried out at different times. Direct comparisons are, therefore, not justified. However, the data in Table 3 show that in the subterranean achenes there were

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**Table 1.** The effects of light (L)/dark (D) regime on start "S" (days), rate "R" (percent per day) and final percent "P" of germination (on 8th day) of aerial achenes of *G. micrantha* at 20 C and 25 C, respectively. Three replicates of 50 achenes each. Explanation in text.

<table>
<thead>
<tr>
<th>Light regime</th>
<th>20 C</th>
<th></th>
<th></th>
<th>25 C</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>S</td>
<td>R</td>
<td>P</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>Continuous D</td>
<td>12</td>
<td>5.0</td>
<td>3</td>
<td>3</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Continuous L</td>
<td>85</td>
<td>4.2</td>
<td>18</td>
<td>31</td>
<td>5.0</td>
<td>6</td>
</tr>
<tr>
<td>16 hr D → 8 hr L alternation</td>
<td>99</td>
<td>3.2</td>
<td>19</td>
<td>52</td>
<td>5.1</td>
<td>14</td>
</tr>
<tr>
<td>16 hr D → 8 hr L → cont. D</td>
<td>98</td>
<td>2.6</td>
<td>28</td>
<td>43</td>
<td>4.3</td>
<td>11</td>
</tr>
</tbody>
</table>

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**Table 2.** The effects of light (L)/dark (D) sequences on start "S" (days), rate "R" (percent per day) and final percent "P" of germination (on 14th day) of aerial achenes of *G. micrantha* at 15 C, 20 C and 25 C. (Expt. at 15 C not simultaneous with others.) Three replicates of 50 achenes each. Explanation in text.

<table>
<thead>
<tr>
<th>Light regime</th>
<th>15 C</th>
<th>20 C</th>
<th>25 C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>Continuous D</td>
<td>83</td>
<td>1.9</td>
<td>35</td>
</tr>
<tr>
<td>Continuous L</td>
<td>85</td>
<td>1.9</td>
<td>24</td>
</tr>
<tr>
<td>16 hr D → 8 hr L → cont. D</td>
<td>87</td>
<td>1.8</td>
<td>65</td>
</tr>
<tr>
<td>8 hr D → 16 hr L → cont. D</td>
<td>91</td>
<td>1.9</td>
<td>61</td>
</tr>
<tr>
<td>8 hr L → cont. D</td>
<td>78</td>
<td>1.7</td>
<td>65</td>
</tr>
<tr>
<td>16 hr L → cont. D</td>
<td>92</td>
<td>1.7</td>
<td>62</td>
</tr>
<tr>
<td>24 hr L → cont. D</td>
<td>92</td>
<td>2.0</td>
<td>77</td>
</tr>
</tbody>
</table>
Table 3. The effects of light (L)/dark (D) sequences on start “S” (days), rate “R” (percent per day) and final percent “P” of germination (on 5th day) of subterranean achenes of G. micrantha at 20 C and 25 C, respectively. Three replicates of 25—30 achenes. Explanation in text

<table>
<thead>
<tr>
<th>Light regime</th>
<th>20 C</th>
<th></th>
<th>25 C</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>S</td>
<td>R</td>
<td>P</td>
</tr>
<tr>
<td>Continuous D</td>
<td>76</td>
<td>1.2</td>
<td>38</td>
<td>42</td>
</tr>
<tr>
<td>Continuous L</td>
<td>79</td>
<td>0.9</td>
<td>49</td>
<td>69</td>
</tr>
<tr>
<td>16 hr D → 8 hr L, alternation</td>
<td>91</td>
<td>1.0</td>
<td>37</td>
<td>84</td>
</tr>
<tr>
<td>16 hr D → 8 hr L → cont. D</td>
<td>90</td>
<td>1.0</td>
<td>56</td>
<td>83</td>
</tr>
<tr>
<td>8 hr D → 16 hr L → cont. D</td>
<td>88</td>
<td>0.7</td>
<td>50</td>
<td>79</td>
</tr>
<tr>
<td>8 hr L → cont. D</td>
<td>86</td>
<td>1.1</td>
<td>62</td>
<td>81</td>
</tr>
<tr>
<td>16 hr L → cont. D</td>
<td>89</td>
<td>1.1</td>
<td>84</td>
<td>72</td>
</tr>
<tr>
<td>24 hr L → cont. D</td>
<td>83</td>
<td>1.0</td>
<td>65</td>
<td>88</td>
</tr>
</tbody>
</table>

no striking effects to treatments incorporating both light and darkness, over those carried out in continuous light. It must, however, be remembered that subterranean achenes are not as light-sensitive as the aerial ones, at the temperatures tested, which would make it more difficult to pick out small effects with such a limited experiment.

Seedling development—Size and weight differences between the 2 types of achene were paralleled by differences between the seedlings to which they gave rise (Fig. 6). Air-dry weight of achenes of the 2 types was determined by averaging the weight of 10 individual achenes of each type. Growth of the seedlings was compared in the following manner. Achenes of both types were incubated at 15 C in the dark. After 3 days, 10 achenes of each type were selected, in which the radicle of the seedling was just protruding. These seedlings were left to grow at 15 C in the dark for an additional 3 days, after which the total fresh weight, and the fresh weight of the shoots and roots was determined. The results are given in Table 4.

The results in Table 4 show that although seedlings from aerial achenes were much smaller than those from the subterranean achenes, the “growth” of the former was several times more rapid. Actual growth rates were not determined, since these would have to be related to initial imbibed embryo weight. The relationship between this weight and the weight of the achene is different in the 2 types of achene, since the aerial ones include floral parts of considerable size which are absent (or vestigial) in the subterranean ones. Endosperm is absent in both. It is thus clear that the weight ratio of embryo to entire achene is lower in the aerial achenes than in the subterranean ones. These considerations indicate that the difference in actual growth rate between the seedlings from the 2 types of achene are much larger than indicated by the “growth” figures in Table 4.

Table 4. Growth of G. micrantha seedlings from aerial and subterranean achenes. Seedlings germinated and grown at 15 C in the dark for 6 days. Means and S.E. of 10 seedlings or achenes. “Growth” expressed as percent increase in fresh weight from achene to seedling

<table>
<thead>
<tr>
<th>Aerial achenes</th>
<th>Subterranean achenes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fresh weight (mg)</td>
<td>Fresh weight (mg)</td>
</tr>
<tr>
<td>Achenes</td>
<td>0.37±0.05</td>
</tr>
<tr>
<td>Whole seedlings</td>
<td>4.41±0.49</td>
</tr>
<tr>
<td>Seedling roots</td>
<td>1.56±0.28</td>
</tr>
<tr>
<td>Seedling shoots</td>
<td>2.85±0.29</td>
</tr>
</tbody>
</table>

B. “Growth” (%) 1029 304

Tolerance of seedlings towards adverse soil-moisture conditions—Two methods were tried to simulate adverse soil-moisture conditions. One was by withholding irrigation for various periods, the other was by regular supply of different levels of limited irrigation.

The initial procedure was the same in both methods. Seedlings from both types of achene were grown together in drained plastic containers filled with cleaned loess soil. The water content of the soil in the containers was maintained at the same level (33 g water per 400 g soil in each) by daily addition of water to restore the original gross weight. When the seedlings appeared established (10 days), the containers were transferred to an exposed location outdoors, where the treatments were carried out. The course of seedling mortality was then followed by frequent observations. Three identical containers were used in each treatment, in each of which 8 similar seedlings from each type of fruit were grown. The experiments were repeated 3 times: in January, February, and April, 1962. The results did not differ qualitatively in the 3 experiments. During the February experiment, which is described in detail below, the minimal temperatures were between 1 and 10 C, and the maximal temperatures varied between 15 and 32 C.
TABLE 5. Seedling mortality in G. micrantha, as influenced by duration of interruption in irrigation. Explanation in text

<table>
<thead>
<tr>
<th>Duration of interruption (days)</th>
<th>1</th>
<th>3</th>
<th>5</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead seedlings from aerial achenes</td>
<td>7</td>
<td>17</td>
<td>21</td>
<td>24</td>
</tr>
<tr>
<td>Dead seedlings from subterranean achenes</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>9</td>
</tr>
</tbody>
</table>

In the first method, water was withheld from different groups of containers for various periods (1, 3, 5 and 7 days, respectively), when irrigation was resumed, as before. The effects of this treatment on seedling mortality (number of dead seedlings 24 days after planting, or 14 days from the start of interruption in irrigation) are given in Table 5.

In the second method, the treatments consisted of daily irrigations in amounts bringing the water content of the soil to 20, 25, 45 and 60 g water per 400 g soil. The effects of this treatment on seedling mortality (number of dead seedlings 30 days from planting, or 20 days from the start of the treatment) are given in Table 6.

All these experiments showed that in both methods which were used to simulate adverse soil-moisture relationships, the seedlings from subterranean achenes survived to a much larger extent than did those from the aerial achenes.

Discussion—Summarizing the observations and the experimental data, we find that the 2 types of fruit formed by G. micrantha differ from each other not only in morphology, but also in ontogeny, ecology and physiology, despite their being situated within a few mm of each other. The few subterranean fruits formed by each plant are protected by a layer of soil as well as by the tissues of the mother plant, from flower initiation until germination. The establishment of the seedlings of these fruits is offered a high degree of security by the fact that they germinate in the exact habitat where their parent plant grew successfully. The numerous aerial fruits borne by each plant are formed later in ontogeny. Their development takes place at the soil-air interface, where the environment is rather specialized (Geiger, 1959). When ripe, they become detached from the receptacle by a complex series of movements, which involve various parts of the inflorescence and require several cycles of moistening and drying for completion. The detached fruits are adapted to dispersal by wind, and become lodged in soil crevices, usually far from the parent plant. So far, no information is available on the environmental conditions which determine when the plant would cease to produce the earlier subterranean inflorescences and switch over to the production of the aerial inflorescences. However, both field observations and experimental work with controlled irrigation have shown that the production of aerial inflorescences was much more dependent on availability of soil-moisture than that of the subterranean inflorescences. This may well be due to the fact that the former are the first to be formed in ontogeny, when a relatively small part of the rain water which had caused germination had been utilized for growth. Whatever the cause, the fact is that, as a result, the subterranean fruits have a much higher probability of being formed than the aerial ones.

The data in Fig. 8 indicate that differences also exist between the germination responses of the 2 types of fruit to environmental conditions. Taking first the value of “S” as indicating the duration of the preparatory processes before the start of germination, it appears that under all conditions the subterranean fruits would germinate earlier, and their embryo will consequently establish direct contact with soil moisture sooner than the aerial fruits. Admittedly, the difference is never very large. It must, however, be remembered that under field conditions in the desert, favorable moisture relations in the soil around the fruit are ephemeral, and the advantage of even a few hours may be decisive in determining establishment. This effect is enhanced by the fact that the habitat in which the aerial fruits germinate is the soil surface, whereas the subterranean fruits are invariably situated under the soil surface, where moisture is much better protected from evaporative loss. This would account for the observation that in the field, seedlings from subterranean fruits are much more common than from aerial ones, despite their relatively small number. Final germination percentages provide an indication of the total potential of the seeds to germinate under the specific environmental complex. The results show 2 facts. One is that although “P” in both types of fruit is favorably affected by light, at all temperatures within the range tested, the promotive effect of light was relatively stronger in the aerial fruits than in the subterranean ones. The second is that the aerial fruits are more sensitive to high-temperature inhibition of “P”

TABLE 6. Seedling mortality in G. micrantha, as influenced by water content of the soil. Explanation in text

<table>
<thead>
<tr>
<th>Water content (ml per container)</th>
<th>20</th>
<th>25</th>
<th>45</th>
<th>60</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead seedlings from aerial achenes</td>
<td>13</td>
<td>10</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Dead seedlings from subterranean achenes</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
than the subterranean ones, in both light and dark. Rate of germination “R” is another parameter which indicates a difference between the 2 types of fruit. In the subterranean fruits, $R_{\text{light}}$ is equally higher than $R_{\text{dark}}$ at all temperatures, both reaching an optimum value at 15°C. In the aerial fruits, $R_{\text{light}}$ values are very similar to those of the subterranean fruits, with an optimum value at 15°C. However, $R_{\text{dark}}$ values are inversely proportional to temperature, showing no optimum within the range tested. Thus, between 15 and 25°C $R_{\text{dark}}$ parallels $R_{\text{light}}$, whereas below 15°C $R_{\text{dark}}$ increases while $R_{\text{light}}$ decreases.

The experiments reported in Tables 1–3 were designed to study the possibility whether the stimulating effects of light on germination were photoperiodic in nature. These results show clearly that at least the aerial fruits were more stimulated by some combinations of light and darkness than by continuous light. In this, their behavior resembles that of seeds of *Eragrostis ferruginea* (Isikawa, Fujii, and Yokohama, 1961) and of *Lemma perpusilla* (Posner and Hillman, 1962). This indicates the possibility that the action of light is photoperiodic in nature. The fact that a single 8-hr light period was as effective as several such periods repeated at intervals of 16 hr in no way detracts from this possibility, since the photoperiodic induction of flowering may also be satisfied with a single inductive cycle (Hamner and Bonner, 1938; Evans, 1960; Zeevart, 1962). However, the results in Table 2 raise some doubts. Thus, a single 8-hr light period is no more effective than a single 16-hr one. Secondly, it would seem that the effectiveness of the light-period depends on its being preceded by darkness, which, in photoperiodic terms, would mean that only dark processes and the second high-intensity light process are required (cf. Isikawa et al., 1961). The present results do not seem sufficient to decide whether or not the sensitivity of the aerial fruits towards light is photoperiodic in nature, and more work is in progress on this problem. For the time being it can only be said that both at 20 and 25°C some preparatory dark-requiring processes are needed for full effectiveness of light in stimulating the germination of the aerial fruits. The results summarized in Table 3 show that the subterranean fruits were also more favorably affected by combinations of light and darkness than by continuous light alone. However, the effects of such combinations were much less pronounced and no requirement for darkness to precede light is evident. This difference between the 2 types of fruit should, however, be treated with caution, since the results in Table 3 are based on a single limited experiment, which was moreover carried out at a much later date than the experiments summarized in Tables 1 and 2. It must also be remembered that the subterranean fruits are less light-sensitive at the higher temperatures than the aerial fruits. The ecological significance of the requirement for darkness to precede light must remain speculative until subjected to experimental treatment.

Seedlings produced from the 2 types of fruit also differed greatly in size, growth rate and in the ability to withstand adverse soil-moisture conditions. It must be made clear that no attempt was made to determine survival as affected by the water-potential of the soil. The 2 types of test which were performed were designed to present the seedlings with 2 variations of simulated field conditions. One of these represented a situation of a regular distribution of rainfall, of different amounts. The other represented a situation of cessation of rainfall, of different duration. Under both these experimental treatments the seedlings produced from the subterranean fruits survived much better than those from the aerial fruits. One possible explanation is that this difference is due to differences in growth-rate between the 2 types of seedling (see Table 4), rapidly growing tissues being more susceptible to drought damage than tissues which grow slowly (cf. Levitt, 1956, p. 161).

Morphological heterocarpy, which expresses itself also in physiological behavior of the seeds, has already been described in several species, e.g., *Xanthium pennsylvanicum* (Shull, 1911), *Atriplex* spp. (Beadle, 1952; Radman-Zahav, 1955; Koller, 1957), *Salsola volkensii* (Negbi and Evenari, 1961), *Aellenia autrani* (Negbi, personal communication), *Pteranthus dichotomus* (Evenari, personal communication) and several others (Becker, 1913). There does not appear to be any evidence as to whether the formation of 2 (or more) types of fruit on the same plant is determined by the physiological age of the plant or by its environment at the time of fruit development. Possibly, in species where transitional types occur, as in *Atriplex dimorphostegia* (Koller, 1957), the latter possibility might be feasible, but where transitional types are absent, as in *G. micrantha*, the former possibility seems more likely. This raises another problem. In heterocarpic plants, the various types of fruit develop at different stages in the ontogeny of the mother plant. Consequently, their ripening takes place in different seasons and thus under different environmental conditions. Differences in their physiological behavior may then be caused either by genetic pre-determination, or by environment existing at time of ripening, as has been shown to occur in *Chenopodium amaranticolor* (Lona, 1947), *Rosa* spp. (Von Abrams and Hand, 1956) and lettuce (Harrington and Thompson, 1952; Koller, 1962).

The observed differences between the 2 types of fruit may be analyzed from the viewpoint of the role which each plays in the successful existence of the species in the extreme environment of the desert. It would seem that whereas the aerial fruits function mainly in increasing the distribution of the species within its habitat, the subterranean fruits serve mainly in ensuring its survival.
The former are formed in habitats or years with favorable rainfall. Their germination is more strictly influenced by the environment, and since they germinate on the soil-surface and only after some delay, relative to the subterranean fruits, a favorable combination of environmental factors is a prerequisite for their formation as well as for their subsequent germination and establishment. This fits in well with the relatively low tolerance which their seedlings exhibit towards unfavorable soil-moisture regimes. The subterranean fruits are formed in relatively small numbers per plant, but at the same time they are a very safe investment. They are formed even with unfavorable soil-moisture supply. They start to germinate relatively soon after imbibition, and their germination is relatively less sensitive to variations in the environment. All these characteristics tend to increase the probabilities for germination and completion of the life cycle. They germinate exactly where the conditions which sufficed for their parent to complete their life-cycle are most likely to be duplicated. In addition, it has been suggested (O. Stocker and M. Evenari, personal communications) that this location is specially favored by the fact that the underground tissues of the mother plant, and the cavity left in the soil by their shrinkage, may serve as vertical conduits for deeper penetration of rain water.

LITERATURE CITED


