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RESISTANCE OF DROUGHT BY LIVERWORTS

By Douglas Houghton Campbell

We are accustomed to consider the archegoniates in general as moisture-loving plants, and this is, to a certain extent, true. But it readily may be shown that there are many exceptions to the rule, even in regions of abundant moisture ; while in more arid districts it is becoming clear that many species have developed special contrivances for surviving long periods of drought.

In moister regions, like the eastern United States, many species of rock-haunting or epiphytic mosses occur which can survive a certain amount of desiccation ; and among the Hepaticae may be mentioned various foliose Jungermanniaceae which share this peculiarity with the mosses. How far this power of resisting drought is found among the eastern thallose Jungermanniaceae and Marchantiaceae, so far as the writer is aware, has not been investigated.

For a number of years the writer has been interested in the archegoniates of California, especially the hepatics, and his attention has been directed repeatedly to the power shown by nearly all the species of resisting the long dry season which regularly prevails each year. In the region around San Francisco Bay, the dry season generally lasts from about the middle of May until late September or early October. Sometimes for fully six months no rain at all falls. This was the case in 1903, when from mid-April until October there was no rain at all, and not until November was the rainfall enough to start vegetation. Nevertheless, the growth of Hepaticae during the present season has been very luxuriant, and there is no evidence of any harm having resulted from the unusually protracted drought. In the bay region, however, there is seldom the excessive summer heat

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of the great central valley of California, and the heavy ocean fogs which prevail during the whole summer undoubtedly mitigate to a very considerable degree the complete lack of rain. Nevertheless, during the dry season the liverworts remain absolutely dormant and apparently quite dried up.

The hepatic flora in the neighborhood of Stanford University is a very interesting one. There are types of most of the more important groups, and almost without exception the common species develop their reproductive organs in great numbers — indeed in most of our common species one almost never meets with sterile individuals. Besides the liverworts proper, several species of *Anthoceros* occur, two of which are extremely abundant. With the exception of the genus *Sphaerocarpus*, which seems to be annual, all of the species in this neighborhood that have been examined remain alive during the summer, and resume growth promptly with the advent of the autumn rains.

Among the most abundant liverworts of this region are several species of *Riccia*, some of which, like *R. trichocarpa*,* grow in very exposed places, subject to the full force of the sun. Of the higher Marchantiaceae, the commonest species are *Fimbriaria Californica* (*Asterella Californica*) and *Targionia hypophylla*. Less common are *Fimbriaria Bolanderi* (*Asterella Bolanderi*) and *Cryptomitrium tenerum*.

In the moist forests of the outer coast ranges, and sometimes straying down the banks of the streams, occur the cosmopolitan *Marchantia polymorpha* and *Fegatella conica* (*Conocephalum conicum*). It is doubtful, however, whether either of these species can survive such complete drying up as that which the characteristic species of the valley regularly undergo.

The number of leafy liverworts is relatively small. The commonest species are *Porella Bolanderi* and *Frullania Bolanderi*, both of which are abundant.

Two species of *Sphaerocarpus* and one of *Fossombronia* — *F. longiseta* — represent the thallose Jungermanniaceae.

The Anthocerotaceae comprise two common species of *Anthoceros*, *A. fusiformis* and *A. Pearsoni*.† Both of these species,

* This is *R. hirta* of the writer's "Mosses and Ferns."

† *A. laevis* of "Mosses and Ferns."

like the other liverworts, regularly survive the summer in a dormant state. A former erroneous statement ("Mosses and Ferns," p. 117) that they are annuals, was due to a failure to examine the plants early enough in the season.

Having observed how soon after the first rains mature reproductive organs were present, it was thought advisable to investigate the condition in which the plants pass the dry season. The matter was intrusted to one of our students, Mr. H. B. Humphrey, who has made a careful examination of *Fossombronia longiseta* and *Fimbriaria Californica* (*Asterella Californica*), as well as a less complete examination of a number of other species.

It was found that a surprisingly large amount of the thallus remains alive, and within a few hours after the dried plants are supplied with water, the forward part of the thallus has assumed its active condition and begins to grow. In both *Fossombronia* and *Fimbriaria* (*Asterella*) the first antheridia were mature in about two weeks. This early development of the reproductive organs at once raised the question whether they might not begin their development before the close of the growing period in the spring. To determine this point, dried plants were collected and placed in water and were examined as soon as they had revived. In *Fossombronia* both archegonia and antheridia were found in advanced stages of development, while in the dioecious *Fimbriaria* (*Asterella*) the male plants showed large antheridia, but the female plants had not yet formed archegonia. It is highly probable that the reproductive organs are present also in all the species of *Riccia*, and not unlikely in some of the other genera, but as yet none of these have been critically examined for this point.

That the liverworts can endure much greater desiccation than that to which they are normally subjected was shown by removing by artificial means a large part of the water held in the dried thallus. The plants so treated showed no apparent loss of vitality, and promptly revived when supplied with water.

In all the forms examined, more or less perfect devices for preventing excessive loss of water have been noted. The growing point is protected by hairs or scales, sometimes secreting mucilage, and the mucilage cells within the thallus of certain species

are probably concerned with water storage. How far the absorption of atmospheric moisture from fog takes place during the dry season has not been tested, but to judge from the behavior of the lichens of this region, shown by Professor Peirce's experiments, it may well be considerable.

The development of tubers has been observed by various students of liverworts.* A very perfect case is that of the remarkable liverwort, *Geothallus*, discovered some years ago by the writer. This liverwort comes from southern California, where the rainfall is much less than in middle California. In this species the inner tissue of the thallus becomes filled with reserve food, and the surrounding cells become dark and thick-walled, forming a sort of rind protecting the central tissue. These tubers are more or less completely buried in the earth, where they remain during the long dry season. Only a very small amount of tissue about the growing point remains alive, and no signs of the young reproductive organs are visible when the tubers begin to germinate. A similar condition, but much less pronounced, is sometimes found in *Fossombronia*, this being decidedly more marked in specimens from the southern part of the state.

Goebel† mentions the formation of tubers in several species of *Anthoceros*, and they have also been observed in some Californian species.‡ The thallus of *Anthoceros* develops an unusual amount of mucilage within its tissues, and this undoubtedly is an important factor in their survival of the dry season. Whether the association of colonies of *Nostoc*, which always are present, is of service in water storage has not been determined; but it is by no means unlikely.

Some of the Californian pteridophytes behave much as do the liverworts. Such species of *Selaginella*, as *S. Bigelovii*, and *S. lepidophylla*, dry up during the greater part of the year, but absorb water through their leaves, and resume the active condition very promptly. The latter species is the "resurrection-

* See Howe, Hepaticæ and Anthocerotes of California, Mem. Torrey Club, 7 : 69. 1899.

† Organographie der Pflanzen. Zweiter Theil. Heft. 1, p. 293.

‡ Howe, *l. c.*

plant," occasionally offered for sale as a curiosity. *S. rupestris* probably behaves in the same way.

In the neighborhood of Stanford University, a common fern is *Gymnogramme triangularis*, commonly known as "gold-back fern," from the yellow powdery secretion on the lower side of the leaf. This fern dries up in summer without the leaves dying down as they do in most ferns during the resting season. If a leaf from such a dried-up specimen is placed in water, it will in a short time absorb water through its superficial cells, and soon becomes fresh and active. That this absorption of water is by the lamina of the leaf, and not through the petiole, may be shown by placing the dry leaf in water with the cut end of the petiole completely out of water. The leaf will soon become turgescent although it is quite impossible that any water could have been taken up through the cut end of the petiole. Large prothallia of this species (and perhaps of some other ferns) are often met with in the autumn, before there possibly can have been a development of these from germinating spores. To test the ability of the prothallium to endure complete drying up, Dr. Peirce made a culture from spores of *Gymnogramme* in the laboratory, and the prothallia thus grown were allowed to remain entirely dry during the whole summer of 1903. These were given water in the fall and proved to have survived the summer perfectly, numerous young plants developing later from these prothallia of the former season.

Goebel* has recorded from an allied fern *Anogramme*, of Southern Europe, perennial prothallia which develop tuberous structures not unlike those of certain liverworts. Whether any of our native ferns develop similar structures remains to be seen.

Some years ago, the writer received from San Diego, plants of a *Selaginella* — probably *S. Bigelovii* — with the earth in which they had grown. The latter contained a good many spores that had fallen from the plants, and earth, which had been kept dry through the summer was well watered and in a very short time young plants appeared. Unfortunately, none of the ungerminated

l. c., p. 426.

spores had been kept, so that it was impossible to determine beyond doubt, whether germination had begun and the embryo had been already partially developed before growth had stopped in the spring. In view of these later observations on fern prothallia, this is by no means improbable, and if this should be the case, heterospory in *Selaginella* would be advanced one step further in the direction of seed-formation.

It is certain that further examination of the archegoniates of our arid and semi-arid regions will reveal other adaptations quite as interesting as those already recorded.

STANFORD UNIVERSITY,
March, 1904.

THE POLLEN TUBE IN THE CUCURBITACEAE AND RUBIACEAE

BY FRANCIS E. LLOYD

In a recently published paper * Longo has given us the very interesting results of his later investigations on the behavior of the pollen tube in the Cucurbitaceae. The close similarity of the facts presented by Longo to those which have been observed by myself in Rubiaceae,† and the parallelism of our conclusions, will, perhaps, warrant a brief comparative statement of our results.

According to Dr. Longo, the ovary in *Cucurbita Pepo* L. is provided with a special conductive tissue which arises, by tangential cell-division, "from the epidermis of the placental ridges and extends uninterruptedly from the style, through the three central laminae, to the ovule." The placentae, of course, fuse along their surfaces with one another, so that the layer of conductive tissue between any two of them is derived from two epi-

* Longo, B. Ricerche sulle Cucurbitaceae e il significato del percorso intercellulare (endotropico) del tubetto pollinico. R. Accad. Lincei, Va, 6 : 523–547. *pl. 1–6.* 1903. ["Presented in December, 1902." Bot. Centralb. 95 : 114. 1904.]

† Lloyd, F. E. The Comparative Embryology of the Rubiaceae. Memoirs Torrey Botanical Club, 8 : 27–112. *pl. 5–15.* 15 F 1902.