Heterophylly in *Proserpinaca palustris*, L.

BY

GEORGE P. BURNS,

University of Michigan.

With Plate XXXVIII.

INDIVIDUALS of the same species growing under different conditions often show great variation in form and structure of their organs. These variations are, in some cases, very slight, but in others so marked that plants showing them have been taken for new species or at least varieties. Not only do we find great variety in form and structure of organs on separate individuals, but the same individual may form organs of very different structure at various stages of its development. These variations are in part caused by external conditions. Goebel (1) says: 'We know that external conditions may act as stimuli, but the influence of these depends upon the capacity of reaction of the individual plant.' The reactions of plants due to morphogenic stimuli have been studied for the most part on the leaves of amphibious plants. These vary in form and structure of the leaf. The leaf formed in and remaining in water is quite different from the leaf known as the 'land-type.' Many land plants also develop two kinds of leaves, and offer a very promising field for experiment, but so far very little has been done. Only in a few cases do we have any experimental knowledge of the stimuli causing the variations.

In working experimentally along this line two important points must be kept in mind. First, 'the capacity of reaction of the individual plant' toward external stimuli is not always the same. Goebel (2) cites numerous examples in which the same individual reacts differently in its juvenile and adult forms. Secondly, a given reaction is not necessarily the result of a single stimulus, but the same reaction may be produced by two or more stimuli. However desirable it may be to give a detailed analysis of all the possible factors which determine form, and to determine the influence of each component upon the protoplasm of the primordial cells, it seems that there is little possibility of accomplishing such an end.

Two of the questions which arise in a study of variations in plant-organs are, in how far are they determined in form and structure by external stimuli? and, do these show a direct adaptation to the environment? This paper deals largely with the first question.

Most of the literature upon this subject deals primarily with the effect of external stimuli on the anatomical structure of the organs of amphibious plants. This side of the question is omitted in the present paper, although it is of great importance, because McCallum (3) promises a detailed account of the results of his experiments in the near future. For this reason the results of the work along this line will be briefly given.

Mer (4) refers the differences in structure to weakened illumination and poor nutrition. Constantin (5) finds that the aquatic form is due to poor vegetative conditions. Schenck (6) agrees on the whole with Mer.

On the other side of the question must be noted first the work of Goebel (7). In several cases he has shown that the form of the leaf is determined by external stimuli. This is true of *Sagittaria*, *Campanula rotundifolia*, and the Cacti. In these plants it depends upon the intensity of the light. In other cases, as *Ranunculus multifidus*, the form of leaf is dependent upon the water-environment to the extent, at least, that the leaves formed in water are more finely divided than those formed in air. However, in some cases, notably in the case of *Limnophylla heterophylla*, he could prove no direct relationship between the form of leaf and external stimuli. He thinks, however, that a direct causal relationship may have formerly existed even though it cannot now be proven (Org. p. 546).

McCallum (3) attempted to analyze more carefully the morphogenic factors working upon water-plants. From experimental work on *Proserpinaca palustris*, he concludes that the stimulus to the development of the water-form of leaf in this plant is not involved in the light-relations, in the nutritive conditions, temperature, the gaseous content of the water, nor contact-stimulus, but is due to the 'checking of transpiration and consequent increased amount of water in the protoplasm.' He continues, 'When the protoplasm of the primordial cells is in that condition of dilution which accompanies the absorption of a large amount of water, the nature of the growth and the orientation of the cell-division is such as to produce the water-form, while those physical and chemical conditions resulting from a partial withdrawal of water by evaporation (i.e. an increased density of protoplasm) result in that sort of cell-behaviour which produces the air-form of leaf.'

One other paper is that of Familler (8) on *Campanula rotundifolia*. He found that cuttings from stems of this plant, which were producing linear leaves, returned to the formation of round leaves. As we have seen, Goebel got the same reaction on this plant by decreasing the amount of light. Thus not only light, but a disturbance of vegetative activity—such

a disturbance is certainly made in the case of cuttings—may cause the same reaction in the plant named.

While engaged in an ecological study of certain parts of the Huron Valley, in the vicinity of Ann Arbor, my attention was repeatedly called to the great variations in the form of the leaves of the plants growing in the margins of the river, and especially to those of *Proserpinaca palustris*, *Ranunculus multifidus*, and *Ranunculus aquatilis*. The last two are familiar through the work of Goebel and others. *Proserpinaca* was first described by McCallum, who gives us a very satisfactory account of this plant, illustrated with some good photographs and drawings.

Proserpinaca palustris grows in great abundance in the vicinity of Ann Arbor, usually in water about 30 cm. deep. It may, however, grow in water one metre deep. At Dead Lake it grows in great abundance near the shore, and some plants are out of water during a large part of the summer. It is very easy of culture both on land and in water. The 'land-type' of leaf is lanceolate, from 3 to 5 cm. in length and 6 to 8 mm. broad. The margins are serrated (Pl. XXXVIII, Figs. 1 and 5). The 'water-type' of leaf is very different. It is finely divided, with a central rib and from three to five filamentous divisions on each side (Figs. 2 and 4). These divisions are almost round in cross-section.

A comparison of the development of the two types of leaves shows that they are exactly alike in form in the primordium, and that they continue to develop along the same lines for a comparatively long time, independent of external conditions. Thus, whatever factor or factors determine the type of leaf to be developed from a given primordium must come into play relatively late. Each type of leaf begins as a small protuberance on the side of the vegetation-point. Lobes soon appear on the margins in basipetal order. The leaf and each of the lobes ends in a peculiar gland-like structure which very soon reaches its full development. Thus far all leaves have the same history of development (Fig. 6). The final type of leaf formed depends upon the later growth of this primordium. If the growth is confined to the central portion, a broad leaf with serrated margins is the result (Fig. 5). On the other hand, if the growth is confined mostly to the ribs, a finely dissected leaf is produced (Fig. 4).

DEVELOPMENT OF THE SEEDLING.

A large number of the seeds were gathered in October and divided into four lots of twenty seeds each. Those in lot 'a' were placed in a damp chamber between filter paper; those in lot 'b' were placed in soil under eight inches of water; those in lot 'c' were placed in two-inch pots; those in lot 'd' were planted in two-inch pots and then placed in a pail of water. The first three were left in the greenhouse under good conditions for

germination, the fourth was allowed to freeze and remain frozen during the winter.

In March of the following year seedlings began to develop in all four lots. Those in 'a' were transplanted to two-inch pots and kept in as saturated an atmosphere as it was possible to obtain. Lot 'd' was removed to the greenhouse. We have now seedlings growing in water, in air—under the same conditions as *Geraniums*—and in a saturated atmosphere. In every case, after the entire cotyledons, there appeared the 'water-type' of leaf. I cannot say how long this would continue, as my seedlings died when they had from eight to twelve leaves.

These experiments show that the young plant will produce a divided leaf regardless of external conditions as such.

CUTTINGS.

Reference has been made to the work of Familler on *Campanula rotundifolia*. Cuttings made from stems of this plant, which were producing linear leaves, reverted to the round form of leaf. To test this on *Proserpinaca* a large number of cuttings were made from that part of the plant growing in air and producing entire leaves. These cuttings were made on May 28, rooted in sand, and finally transplanted to two-inch pots. They were kept in the greenhouse in comparatively dry air. They all grew luxuriantly, producing entire leaves on the main stem, blossomed, and ripened fruit (Fig. 1). It would thus seem that this plant differed from *Campanula rotundifolia*. However, on August 12, these plants were divided into three groups. One was left in the same condition as before and served as a control, another set was placed in an aquarium under water, and cuttings were made from the third which were planted in earth in air. The control plants continued to produce entire leaves. Those in the aquarium did not all act alike. In some the vegetation-point of the main stem stopped producing leaves and side-branches developed, always with the 'water-type' of leaf. In other cases the plant on its main stem reverted to the production of the 'water-type' of leaf. But most interesting was the behaviour of the cuttings. These were left under exactly the same conditions of light, heat, &c., as the control plants, and yet they began immediately to produce the 'water-type' of leaf. Thus there is a stage in the development of *Proserpinaca* during which a reversion may be caused by propagating by cuttings.

A second set of cuttings was made from plants growing in water and producing the 'water-type' of leaf. These were started exactly as those in the first set. These cuttings were made in September. After transplanting to two-inch pots they were divided into three sets. One set was placed in an aquarium under water; another set was placed in 5 cm. of water, thus immersing the root-system only; the third set was placed

on the bench in ordinary conditions. All three sets were kept in the greenhouse. During the entire winter all of these plants produced the 'water-form' of leaf. None of them grew luxuriantly. The lobes on the leaves of the submerged plants were longer than those of the other two, but the type of leaf was the same. One fact observed was very interesting. The plants in the air did not grow erect, and those in the water seemed to grow aimlessly round, never projecting their vegetation-points above the surface, although the growth in length was more than sufficient.

Early in the spring the plants behaved quite differently. Those in the water projected above its surface and produced entire leaves; those not in water grew erect and they too produced the entire or 'land-type' of leaf (Fig. 2). In the late spring of the present year this change in behaviour took place about four weeks later than it did in the year previous, when we had an early spring. Had I been able to improve the vegetative conditions under which my plants were growing, I am confident the plants would have produced their entire leaves much earlier.

Cuttings made early in May, from stems producing the 'water-type' of leaf in water, begin to produce the 'land-type' of leaf when grown in air much earlier than the control plants left in water.

A number of cuttings were made from the water-form of *Ranunculus aquatilis*. These were rooted in sand and potted, the pots being out of water. They grew two years in the greenhouse, never growing erect, but forming a dense tuft on the earth in the flower-pot and rooting at every node. The water-form, on account of weakened illumination, stretches its internodes. None of the plants produced the three-cleft leaf 'opposite or in the immediate vicinity of the blossom.' The same finely divided 'water-leaf' was formed for two years in air, only differing from the leaf developed in water in the length of the lobes. None of my plants blossomed, but I found one plant growing in the air near the water's edge, which was producing flowers. This plant produced only the 'water-type' of leaf.

A comparison of the cross-sections of lobes from leaves developed in water and those developed in air shows marked differences in anatomical structure. The leaf of the latter is dorsiventral. The epidermal system is well developed both in regard to the thickness of the cuticula and the absence of chlorophyll-bodies in the epidermal cells. The mesophyll is differentiated into palisade and spongy parenchyma. The fibro-vascular bundle contains from six to ten well-developed vessels. Stomata are present. The leaf of the water-form is finely divided into cylindrical lobes whose tissues are little differentiated. The cuticula is very thin, and the epidermal cells contain fully as much chlorophyll as any cell in the mesophyll. The cells of the mesophyll are not differentiated. There is a marked reduction in the number of vessels found in the bundles. Only a few stomata are found, and these were not fully developed.

Returning to the cuttings (p. 582) which were made in May from *Proserpinaca* plants producing entire leaves, it will be remembered that they continued to produce entire leaves, blossomed, and in many cases produced fruit (Fig. 1). Early in September it was noticed that the main stem did not grow so rapidly and that several side-shoots developed at the surface of the pot. Here we meet a most interesting picture in leaf-formation. The main stem is orthotropic and produces the 'land-type' of leaf, while the side-stems are plagiotropic and produce the 'water-type' of leaf. Both vegetation-points are under the same external conditions, as far as they could be controlled, and yet what a marked difference in the leaf formed! Again a little later the main stem undergoes a change. It ceases growing erect and grows horizontally, and the vegetation-point, which since May has been producing the 'land-type' of leaf, begins to produce, in air, the 'water-type' of leaf (Fig. 5). This experiment finds its exact reproduction in nature and is of the greatest biological importance. As has been pointed out, *Proserpinaca*, during the summer, sends its branches out of water, producing entire leaves, flowers, and fruit. In the fall the main stem becomes plagiotropic, produces divided leaves, and finally sinks into the water. Here it passes the winter protected by the water, and in the late fall and early spring multiplies rapidly by the growth of axillary buds. It must be noted that this return to the water-form is not caused by the water-stimulus. I have fastened many plants so that the vegetation-point could not possibly be closer than 30 cm. to the water, and yet these plants returned to the formation of the 'water-type' of leaf.

In June of the present year the vegetation-point was removed from a number of plants producing entire leaves. This caused the lateral branches to develop. In many cases the leaves on these were more or less divided, although the plant grew in air under the same conditions as many other *Proserpinaca* plants, all of which were producing entire leaves (Fig. 3).

Thus we see that the presence of water is not necessary for the development of the 'water-leaf.'

On the other hand, *Proserpinaca palustris* may produce entire leaves in spite of a water-environment. In the spring I always found a number of plants producing the 'land-type' of leaf under 24 to 30 cm. of water. This I found only on rapidly growing branches. In June of the present year, in a large area at Dead Lake, I found that almost every plant was producing the 'land-type' of leaf, although dozens of them were growing under as much as 30 cm. of water (Fig. 4). This certainly points to other factors than water or checked transpiration as the cause of the division.

In Fig. 4 attention is called to the two leaves *a* and *b*. This tip was growing under 26 cm. of water. These two leaves show a transition from the one type to the other; they are 'water-leaves' at the tip and 'land-

leaves' at the base. A similar example is pictured by Goebel (9) in the case of *Ranunculus aquatilis*.

I will not give in detail a description of my experiments with such factors as light, temperature, nutrition, gaseous content of the water, &c., but only refer the reader to the work of McCallum, whose results are essentially the same as my own, especially agreeing with the results I obtained from experiments conducted in the winter.

I repeated the experiments cited by McCallum on p. 107 of his paper. In the fall of 1902 I set up the following: Cuttings were made from plants producing the divided leaf. They were divided into four sets; one set of plants was placed in a nutrient solution not quite strong enough to plasmolyze them; the second set was placed in a weak solution of potassium chloride; the third was placed in pots and cultivated as land plants; the fourth was placed in battery jars under about 18 cm. of water. In every case the leaf-form which developed was divided, although I allowed the solutions to become stronger by evaporation. In the early spring I repeated the experiments not only on *Proserpinaca*, but also on other plants, and my results were different. This time the plants in solution of potassium chloride and the nutrient solution showed a tendency to produce more entire leaves, at least on some stems. However, about the same time my control plants, growing in tap water, also began to show the same tendency, as did also the plants growing in air. As the control plants as well as those in the solutions showed the same tendency, it hardly seems possible that these salts either directly or indirectly could be the cause of the production of the entire leaf.

This phenomenon was explained by McCallum (p. 108) thus: 'It would seem here as if some of the plants after a time become accustomed to the stimulus and refuse to respond. Or it may be that as only the air-form is capable of fruiting, in the effort to produce flowers the plant has the ability of self-adjustment to its conditions and develops the air-form in spite of its environments.' . . . 'It is possible also that the protoplasm is able to adjust itself, perhaps by the expulsion of water, into that condition in which it exists when in air.'

Reference has been made to the biological importance of the change in the direction of growth of the stem which was observed in the fall. An effort was made to find the cause of this change. Why are all stems orthotropic in summer and plagiotropic in winter? Is it a different response on the part of the plant at different stages of its development; or, is it due to a change in external conditions? The facts observed in the field-work point to temperature as a controlling factor, but the work in the greenhouse excludes it as such. A solution of the question was finally reached in some experiments set up to study the effect of weakened illumination on leaf-formation. Two plants, both plagiotropic, one growing in air and

the other in water, were placed in the dark room. Within a few hours all the side-branches as well as the main stem were growing erect. The vegetation-point of stems growing in water soon appeared above the surface. This experiment was repeated with a large number of plants, and it was found that light was the determining factor. When light was removed the stems responded to the geotropic stimulus and turned up. When the plants were returned to the light the curves were straightened and the branches continued to grow horizontally.

The answer to our question seems clear. At one stage of its development *Proserpinaca* is positively heliotropic and at another it is diaheliotropic. That is, this plant changes its relation to light at different stages of its development. Furthermore, we find that the production of the 'water-type' of leaf is intimately connected with that stage when it is diaheliotropic; the 'land-type' of leaf with that stage when it is positively heliotropic.

Finally, we find that the primitive form of leaf is always the 'water-type'; that side-branches developing in the air from a plant whose main stem is producing entire leaves develop the 'water-type'; that all stems, regardless of all external conditions which I could control, produce the 'water-type' in the fall; that stems whose vegetation-points were removed in June threw out side-branches with the 'water-type' when other plants under the same external conditions were forming the 'land-type.' On the other hand, we find that at the time of flowering only entire leaves are formed; that in summer almost every plant, whether in water or in air, produces the 'land-type' of leaf; that the change from 'water-' to 'land-type' takes place earlier on strongly growing than on weak stems, and is dependent to a certain degree on external stimuli; that the plant in its positive heliotropic stage forms the 'land-type' of leaf, and in its diaheliotropic stage the 'water-type.'

These results do not point to one or more definite factors which will explain the form of the leaf in *Proserpinaca palustris*. It is evident the water-environment is not the cause of the division of the leaf. Nor does it depend upon light, temperature, gaseous content of the water, or contact-stimulus as such. The only conclusion that seems justified by my experiments seems to be that *Proserpinaca palustris* has two forms—an adult form and a juvenile form (10). Under good vegetative conditions it has a tendency to produce the adult form with the entire leaf, blossom, and fruit; under poor vegetative conditions it has a tendency to produce the juvenile form with the divided leaf. And furthermore, a reversion to the primitive form may be caused by unfavourably influencing the vegetative conditions.

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EXPLANATION OF FIGURES IN PLATE XXXVIII.

Illustrating Dr. Burns's paper on *Proserpinaca palustris*.

- Fig. 1. Typical land plant, bearing fruit.
- Fig. 2. This plant produced divided leaves in air during the winter, and is beginning to become orthotropic and to produce entire leaves. May 10, 1903.
- Fig. 3. Explanation in text.
- Fig. 4. Tip of stem found growing under 26 cm. of water. Leaves of 'a' and 'b' show transition forms. Collected in June, 1903.
- Fig. 5. Photograph of plant started in the spring from a cutting. Taken November, 1902.
- Fig. 6. Figure showing oldest stage in the development which is common to all 'types' of leaves. Magnified 65 times.

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