THE FORMATION OF LEAF-BLADDERS IN EICHHORNIA SPECIOSA, KUNTH, (WATER HYACINTH)

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General:—Bladders in plants are comparatively rare and where they occur, they are of doubtful significance in most cases. The best known instances where such structures are conspicuously seen are Sargassum, Fucus, Nereocystis among the Fucaceæ, Trapa (Onagraceæ) species of Utricularia, and Eichhornia speciosa. (Pontederiaceæ). Except in Utricularia where the bladder has been definitely proved to be an insect-catching and insect-preying organ, the functions of the bladders have been generally supposed to be either to serve as floatative or swimming organs or to serve as air reservoirs. In most of the above examples the ecological value has been better known rather than the physiological cause, and the present investigation was undertaken purely from the latter point of view. It applies only to Eichhornia speciosa, a study of which was made in the Botanical Laboratory at the Agricultural College and Research Institute, Coimbatore, where the weed attracted notice in connection with the proposed legislation for eradicating it in certain parts of the Madras Presidency.

Though Eichhornia is a water plant it thrives in such a variety of situations that observers have differed regarding its exact habitat. Kerner (7) for instance, states that the plants are not fixed in the mud beneath the water by roots but float freely on the surface of the pond. He further characterises Eichhornia as a swimming plant distinguishing it from floating plants like Trapa which are held fast to the muddy bottom beneath by means of roots. Schonland (10) on the other hand describes it more correctly as either swimming entirely and free on the water or rooting in shallow water in mud, the leaf stalks in the former case becoming strongly swollen and functioning as swimming bladders. Without seriously contradicting these authors it may be stated that plants with and without bladders are found in deep water the determining factor for bladder formation being, as will be seen below, not the depth but a plentiful supply of water that is physiologically available. The plant is also not restricted to any particular surrounding but is at home in ponds, tanks, old wells, ditches, in marshy areas and in fact in any stagnant
or slow moving fresh water of varying depths either as a free floater or rooted in the mud like a swamp plant. It is this indifference with regard to the habitat which makes it not the only troublesome weed that it is but also occasions the formation or not of bladders which are the most striking peculiarity about the plant. An examination of the plant in different surroundings will disclose four principal types, viz., (1) all the leaves of the plant with bladders; (2) all without bladders, (3) outer bladdered and inner bladderless, and (4) outer bladderless and inner bladdered.

Morphology — In its best development the bladder is a rounded or pear-shaped structure 1 to 1½ in. in diameter, representing the whole of the leaf stalk and separated from the lamina by a short neck and narrowed at the base. From ten to fifteen leaves become closely aggregated together so as to form a rosette, and from the axils of many of the leaves new shoots arise which end in similar rosettes and originate fresh shoots in their turn. In this way are formed chains of sympodes radiating in all directions and covering a wide expanse of water in a surprisingly short period. Along with these there are also plants in which the bladders attain various stages of development leading to those which show only a slight swelling in the stalk or to its complete disappearance. These do
much a large number of axillary shoots, nor do they exhibit a pronounced rapidity of growth as is seen in the other species. The transitional forms are shown in the diagram below.

In order to find out the behaviour of the plant in culture I had a bladderless plant transferred to a jar containing the solution in rain water according to Crone’s formula.

The appearance in a few days of swollen leaf stalks suggested that the chief stimulating factor was water and an examination of both bladdered and bladderless leaves would, it was thought, disclose either some difference in the water content or some sort of constitutional change brought about by the excess or deficiency of water. It is well known that stomata regulate their openings according to the amount of water present in the transpiring organs and thereby prevent too much loss of water from plants. A greater water content will thus keep them open whereas a diminished supply will tend to the closing of the aperture. A highly useful method of ascertaining the width of the stomatal opening is afforded by the work of Iljin (6) on the regulation of stomata. This author and Lloyd have shown that simultaneously with the opening of the stomata, the starch present in the guard cells disappears in some way probably by enzymic activity in the presence of a greater quantity of water and increases again when the water becomes less, as happens for instance during the day when transpiration gets more and more intense. As open stomata are sometimes found even in wetted plants, the appearance of starch does not so much indicate the closure of the stomata as a diminution of the water content in the guard cells and the leaf as a whole. By employing chloral-hydrate-iodine as a delicate test for starch, I examined the stomata of both kinds of leaves at different times during the day. The corresponding youngest leaves were chosen and the results which were confirmed by repeated observations are as follows, the drawings having been made with the help of the Zeichen Apparate.

The conclusions arrived at are:

(1) that young leaves with bladders or with a tendency to bladder showed very little starch in the guard cells of the stomata which indicates a high-water content in the leaf.

(2) that leaves without bladders always contained more starch which is doubtless a response to the low-water content of the leaf.

It thus appeared possible that the bladders could be induced to form by making the water available to its utmost capacity, and I succeeded in this by growing a plant without bladder in Crone’s solution of low concentration, viz., 1 in 1000. Plants were also grown in Sach’s solution of normal concentration and in tap-water of the laboratory which is relatively higher in salts. The latter showed no
distension of the stalk whereas the one in Crone's solution added to the medium and appeared with bladders of the intercellular type already shown above. It was also noticed that the absorption of water from the dilute solution was so enormous that a day when the temperature suddenly cooled down from 87°F at 6 P.M. to 76°F at 5 P.M. there was copious exudation of water from the apex which was not the case in the other two plants. It may, in this connection, be pointed out that the function of the apical region appears to be rather to serve as a hydathode than as an absorbing organ as maintained by Goebel (2).

Anatomy:—As an effect of this high-water content notable changes are brought about in the growth of the leaf stalk. The turgidity of the cells is maintained by a high hydrostatic pressure which leads to the dilution of the cell sap as evidenced by the fact that the cells plasmolyse readily with a 1.5 normal solution of potassium nitrate, whereas this concentration is only just enough to overcome the rigidity of the cells in the long stalked leaf. The living cells of the leaf stalk thus become so much gorged with water that a plastic stretching of the cell walls ensues due to superficial growth, and as the cells of both transverse and vertical layers are subjected to this process the stalk assumes a spherical distension comparable to an inflated bladder, and is filled with numerous polyhedral chambers bounded by layers of thin-walled cells (diaphragms) in an extremely stretched condition. Owing to this plastic stretching from the beginning the intercellular spaces in the diaphragm are considerably reduced and are practically confined to the periphery. Against this may be contrasted the structure of the bladderless stalk. This shows numerous air cavities which are partitioned by diaphragms but these are pierced by intercellular spaces from the earliest stage which points to the absence of any stretching due to turgidity. The intercellular spaces arise by the separation from each other of the walls of the diaphragms cells at several points and the air cavities communicating in this way evidently facilitate rapid diffusion of gas from the aerial organs to the root-system which is badly aerated, being fixed in mud or under other conditions referred to below. In the bladdered leaves, however, the diffusion of air contained in the chambers must be a slow process occurring only through the cell walls as the cavities do not communicate with each other. The presence of needle shaped crystals of calcium oxalate in considerable amounts also suggests the previous formation of oxalic acid which probably maintains a high osmotic pressure owing to the peculiar conditions which lead to the diminished water content. The principal changes in the anatomy are shown below:—
history of the plant should of course reveal its real nature. Unfortunately the seeds are difficult to germinate and require special conditions as shown by Crocker (1). But from the appearance of a germ shoot, *Keimpflanze*, figured by Goebel (5) it may safely be concluded that the rosettes of bladdered leaves are merely reversion shoots which are exhibited owing to an innate hereditary tendency present in the plant when the maximum facilities for growth are provided.

In conclusion, I desire to express my sincere thanks to M.R. Rai Bahadur K. Rangaiahari Avergal, for suggestive criticism and encouragement during the progress of this work and for ample facilities provided.

**Literature cited.**


**Explanation of Figures opposite.**

1. Large spaces in the leaf-stalk, bounded by diaphragms, in which lie crystals of Ca. oxalate.
2. Diaphragm cells in stalk without bladder.
   Do. without bladder—lower row.
4. Diaphragm cells in stalk with bladder.
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