OBSERVATIONS ON THE WATER-STORING DEVICES IN THE LEAVES OF SOME INDIAN HALOPHYTES

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While studying the xerophilous structure of the Indian halophytes some peculiarities regarding the storage of water by their leaves were observed. During the course of the investigation, it became evident that the two groups of halophytes, recognised by Warming (5) *viz.* the Littoral Swamp Forest (Mangrove) and the Psammophilous Halophytes, adopted, as a rule, distinctive methods for storing water. Furthermore, the available data showed that, in some cases, in addition to the normal methods of water storage extra water is stored up during the wet season.

The leaves of halophytes are characterised by being thicker and more succulent than those of plants growing inland. Lesage (2) has demonstrated that on watering several plants with salt dissolved in the water, their leaves show the same fleshy structure as is characteristic of maritime plants. In the course of the present investigation it was noticed that of the two groups of halophytes, the leaves of the mangroves are relatively thicker than those of the psammophilous halophytes and that the greater thickness of the former is mainly due to the presence of a well-developed aqueous tissue.

Schimper (4) has observed that the leaves of the mangroves are characterised by a distinct aqueous tissue. On examining eight plants of the mangrove formation, it was found that in seven the aqueous tissue occurs beneath the upper epidermis; while in one (*viz. Sonneratia apetala*, Ham,), it is centrally placed. The hypodermal aqueous tissue of the majority of the mangroves (Figs. 1, 6, 7, 8, 15 is very prominently developed and forms a marked feature of the leaf structure as is shown by the following table :

Name of Plant.	Thickness of Leaf.	Thickness of aqueous tissue.
Rhizophora mucronata, Lamk. ...	0.67 mm.	0.21 mm.
Ceriops Candolleana, Arn. ...	0.50 ,,	0.07 ,,
Bruguiera caryophylloides, Blume ...	0 50 ,,	0.06 ,,
Aegiceras majus, Gaertn. ...	0.50 ,,	0.13 ,,
Acanthus ilicifolius, Linn. ...	0 63 ,,	0.15 ,,
Avicennia officinalis, Linn. ...	0.50 ,,	0.13 ,,
Avicennia alba, Blume. ...	0.39 ,,	0.20 ,,

From the table it appears that, on an average, the leaves of these plants of the salt swamp are 0.52 mm. thick, while the hypodermal aqueous tissue occupies 0.13 mm. of the total thickness.

On the other hand, out of the eleven psammophilous halophytes that were examined, the leaves of only two plants, *viz. Ipomoea pes-caprae*, Sweet, and *Scaevola Lobelia*, Murr., shows a distinct centrally-placed aqueous tissue (Fig. 9); while the rest of them are altogether devoid of it. Thus, unlike the mangroves, the majority of the psammophilous halophytes are seen to be wanting in a special aqueous tissue. But a prominent feature of the leaf structure of these psammophilous halophytes is the upper epidermis which is composed of large, clear cells (Figs. 12, 13, 16, 17). These cells are, in fact, much larger than the corresponding cells of the mangroves and seem to concern themselves mainly with the function of storing water. The water-storing capacity of the upper epidermis can be gauged by its radial diameter which, as is seen from the following table, becomes considerably pronounced.

Name of Plant.	Thickness of Leaf.	Depth of upper epidermis.
Corchorus acutangulus, Lam. ...	0.15 mm.	0.04 mm.
Spermacoce hispida, Linn. ...	0.30 ,,	0.06 ,,
Spermacoce stricta, Linn. ...	0.27 ,,	0.04 ,,
Launaea pinnatifida, Cass. ...	0.45 ,,	0.03 ,,
Neuracanthus sphaerostachys, Dalz. ...	0.27 ,,	0.06 ,,
Lepidagathis cristata, Willd. ...	0.19 ,,	0.04 ,,
Clerodendron inerme, Gaertn. ...	0.48 ,,	0.03 ,,
Boerhaavia diffusa, Linn. ...	0.37 ,,	0.06 ,,
Leucas aspera, Spreng. ...	0.27 ,,	0.06 ,,

From the table it is seen that, on an average, the leaves of the psammophilous halophytes attain a thickness of 0.30 mm., the upper epidermis occupying 0.046 mm. of the total thickness.

Thus in the leaves of both the psammophilous halophytes and the mangroves there occurs a water-storing device. But while in the majority of the former group it is confined only to the enlarged upper epidermis, in the latter, the epidermal system is supplemented by a distinct, well-developed, hypodermal aqueous tissue.

Several of the plants of the two groups of halophytes are also found growing inland or were specially grown under mesophytic conditions for observation. An examination of such plants reveal the fact that the aqueous tissue shows a tendency towards reduction with the result that, under mesophytic conditions, the leaves of the halophytes become thinner. To take an example, the leaf of *Acanthus ilicifolius*, Linn. in its natural habitat is 0.63 mm. thick, with the hypodermal aqueous tissue (Fig. 1) occupying 0.15 mm. of the total thickness. When the plant is grown under mesophytic conditions, the leaf is only 0.37 mm. thick, while the aqueous tissue (Fig. 2) becomes reduced to 0.7 mm. Again, in *Corchorus acutangulus*, Lam. the leaf of the halophytic form is 0.15 mm. thick, the upper epidermis being 0.04 mm. deep (Fig. 13); while in the mesophytic form of the same plant the leaf is 0.12 mm. thick and the upper epidermis is only 0.03 mm. Thus it appears that the volume of the aqueous tissue is directly proportional to the percentage of salt in the soil, for, it is most strongly developed in plants like the mangroves which live nearest the sea and where the substratum is periodically inundated with salt water. A short distance beyond the high-water mark, e g. in most of the psammophilous halophytes, the water storage is a less pronounced feature of the leaf structure; while in inland forms of individuals belonging to both the groups of halophytes, the aqueous tissue gets markedly reduced.

Besides these normal methods of storing water, it is seen that during the monsoon, other devices are resorted to by a few plants. An examination of the leaves have disclosed the fact that, during the wet season, some of the psammophilous halophytes take recourse to special means of storing the extra water available. In those cases where there is a distinct aqueous tissue, the extra water is stored up in the tissue itself, with the result that it gets considerably enlarged during the rains. But in the cases of those individuals which are lacking in a distinct aqueous tissue, the storing of water is taken up by the old leaves, the mesophyll cells of which undergo a remarkable change for the purpose.

For instance, the leaves of *Ipomoea pes caprae*, Sweet, and *Scaevola Lobelia*, Murr. (which, as noted previously, possess an aqueous tissue) become very thick and succulent towards the end of the monsoon, while during the dry season they are not so thick. Thus in the dry season, the leaves of *Ipomoea pes-caprae* are 0.67 mm. thick, the centrally-placed aqueous tissue being 0.30 mm. Towards the end of the wet season the leaves become 1.1 mm. thick, the thickness being mainly due to the swelling of the aqueous tissue. Again, in *Scaevola Lobelia*, the lamina during the dry season measures

1.8 mm. in thickness, the medullary aqueous tissue being 0.97 mm. But towards the end of the monsoon the leaves get considerably thickened and measure 2.8 mm., the aqueous tissue occupying 2.0 mm. of the total thickness. Thus in both *Ipomoea pes caprae* and *Scaevola Lobelia*. the plant is seen to store up extra water during the wet season.

Schimper (4) has noted that in *Rhizophora mucronata*, Lamk., the old, yellow leaves are much thicker and seem to serve as water reservoirs for the younger leaves, and Haberlandt (1) has demonstrated that these old leaves do act as water reservoirs for the younger leaves. The latter authority has further noted that the old leaves were exactly thrice as thick as the leaves which had just reached the full size and that the thickness was entirely due to the enlargement of the aqueous tissue. During the present investigation it was observed that a function similar to that performed by the old leaves of *Rhizophora mucronata* seems to be taken up by the old leaves of a few of the perennial psammophilous halophytes. Since the latter are wanting in a distinct aqueous tissue, the method of storing water adopted by them is very peculiar.

For instance, in *Clerodendron inerme*, Gaertn., towards the end of the wet season, the old leaves show a tendency to grow very thick and succulent. Such leaves are quite characteristic and are of a pale yellow colour. Cross sections of these old leaves show that the thickness is mainly due to the enormous enlargement of the palisade cells. There is no starch in the palisade tissue and the chlorophyll content is very feeble, being in a state of disorganisation. The spongy tissue also gets enlarged, though not to the same extent as the palisade tissue. Owing to the enlargement, the cells of the spongy tissue arrange themselves like the palisade cells and thus reduce the inter-cellular spaces. The cells of both the palisade and the spongy tissue hold oil. a cell content which is found to be present in all the leaves of the halophytes examined. A comparison of the measurements of the different tissues of the mature leaves (Fig. 14) with the corresponding tissues of the old, yellow leaves (Fig. 10) gives a clearer idea of the enormous dilatation involved. The lamina of the normal, functional leaves is 0.48 mm. thick ; in which the upper epidermis occupies 0.03 mm. and the palisade tissue about 0.3 mm. On the other hand, the old leaves attain a thickness of 1.3 mm. : the upper epidermis occupying 0.04 mm. and the palisade tissue 0.8 mm. Thus the enlargement is seen to be mainly confined to the palisade tissue, which becomes nearly thrice as deep as that of the functional leaves.

A similar enlargement of the cells of the old leaves is also to be seen, towards the end of the monsoon, in the case of *Launaea pinnati-*

fida, Cass. These old, yellow leaves are quite characteristic of the halophytic form of the plant. The mature functional leaves of the plant are 0.45 mm. thick, while the old leaves attain a thickness of 0.9 to 1.0 mm. The thickness is seen to be more pronounced towards the margin than towards the midrib of the leaf. In short, the old leaves attain a thickness more than twice that of the mature leaves. The increase in thickness of the old leaves is again seen to be due to the enlargement of the mesophyll cells. A comparison of the cross sections of a normal leaf with that of an old leaf emphasises the great increase in size of the latter. Thus, Figs. 3 and 11 (both magnified equally) show the upper epidermis and the palisade cells of the normal and old leaves respectively. From the diagrams it is seen that the enlargement starts with the upper epidermis, the cells of which become deeper in the old leaf. The increase in size becomes much more pronounced in the case of the palisade cells and is mainly confined to their long axes. Similarly, Figs. 4 and 5 show the lower epidermis and the spongy parenchyma of the mature and old leaves respectively. In the old leaf, the cells of the spongy tissue are seen to be dilated in a direction at right angles to the surface of the leaf and are thus arranged in a manner similar to those of the palisade tissue. As in the case of *Clerodendron inerme*, there is a marked deterioration of the chlorophyll content of the old leaf which in consequence appears pale yellow.

While investigating the xerophilous structure of some epiphytes, Schimper (3) has noted the occurrence of old leaves which get excessively enlarged and which act as water reservoirs for the younger leaves. The thickness in the case of the leaves of such epiphytes was seen to be due to the enlargement of the aqueous tissue. The old leaves of *Clerodendron inerme* and *Launaea pinnatifida* seem to perform a function similar to that of the old leaves of the xerophilous epiphytes and of those of *Rhizophora mucronata* that were observed by Schimper (3, 4). But, since both the psammophilous halophytes under discussion are devoid of a distinct aqueous tissue, the storage of water in their case is taken up by the mesophyll cells which get excessively enlarged and act mainly as water reservoirs. Thus it appears that during the wet season the old leaves of *Clerodendron inerme* and *Launaea pinnatifida* concern themselves mainly with the function of storing extra water as reserve material which is drawn upon by the normal leaves during the succeeding dry seasons.

In both *Clerodendron inerme* and *Launaea pinnatifida* it is found that the old, thick leaves are quite characteristic of the halophytic forms of the plants and do not develop on the inland forms, or when the plants are grown under mesophytic conditions.

Summary.

1. Some peculiarities regarding the water-storing devices adopted by the leaves of the two groups of halophytes, *viz.* the Littoral Swamp Forest (Mangrove) and the Psammophilous Halophytes are described.

2. The leaves of the mangroves are characterised by the possession of a distinct aqueous tissue. Out of eight plants that were examined, in seven it is seen to arise beneath the upper epidermis. From the measurements of the leaves of the plants. it is seen that, on an average, the lamina gets 0.52 mm. thick, while the aqueous tissue occupies 0.13 mm. of the total thickness.

3. An examination of eleven psammophilous halophytes show that the leaves of only two plants possess a distinct aqueous tissue while the rest are wanting in it.

4. The majority of the psammophilous halophytes, though devoid of an aqueous tissue, seem to store up water in the upper epidermis which is composed of prominently enlarged, clear cells.

5. From the different measurements it is seen that, on an average, the leaves of these psammophilous halophytes attain a thickness of 0.30 mm., the upper epidermis occupying 0.046 mm. of the total thickness.

6. Several of the plants of both the groups are also found growing inland, in which case the aqueous tissue shows a tendency towards reduction and the leaves become thinner.

7. Thus the volume of the aqueous tissue seems to be directly proportional to the presence of salt in the soil : for, it is most strongly developed in the mangroves which live in a soil saturated with salt water ; less pronounced in the psammophilous halophytes which live a little away from the high-water mark ; while in inland forms of the plants of both the groups it has a tendency to get still less pronounced.

8. During the wet season it is found that the leaves of some of the psammophilous halophytes store up extra water for future use.

9. In the case of the two psammophilous halophytes which possess an aqueous tissue, the extra water is stored up in the tissue itself.

10. During the wet season owing to the expansion of the aqueous tissue the leaves of such plants (*viz. Ipomoea pes-caprae*, Sweet. and *Scaevola Lobelia*, Murr.) get twice as thick as those during the dry season.

11. In those psammophilous halophytes which are devoid of a distinct aqueous tissue, in the case of two (*viz. Clerodendron inerme*, Gaertn. and *Launaea pinnatifida*, Cass.) the storage of water is seen to be taken up by the old leaves which get excessively enlarged.

12 Such old leaves have meagre chlorophyll content and become nearly thrice as thick as the normal functional leaves of the same plant.

13. This increase in thickness of the old leaves is seen to be due to a marked enlargement of the mesophyll cells which thus get modified and act mainly as water reservoirs.

14 Such water-storing old leaves are quite characteristic of the halophytic forms of the two plants and do not develop on inland forms of the same plants or when they are grown under mesophytic conditions.

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Explanation of Plates

The initial magnification is indicated after each figure. All figures have been reduced to one-third in reproduction.

Fig. 1.—Transverse section of a leaf of *Acanthus ilicifolius*, Linn., showing the well-developed aqueous tissue (a) under halophytic conditions : e, upper epidermis ; p, palisade cells. (× 240).

Fig. 2.—Transverse section of a leaf of *Acanthus ilicifolius*, Linn., showing the reduced aqueous tissue (a) under mesophytic conditions. (× 240).

Fig. 3.—Transverse section of a leaf of *Launaea pinnatifida*, Cass. : e, upper epidermis ; p, palisade cells. (× 240).

Fig. 4.—Transverse section of a leaf of *Launaea pinnatifida*, Cass., showing the lower epidermis and the spongy tissue. (× 240).

Fig. 5.—Transverse section of an old leaf of *Launaea pinnatifida* : Cass., showing the lower epidermis and the enlarged spongy cells, (× 240).

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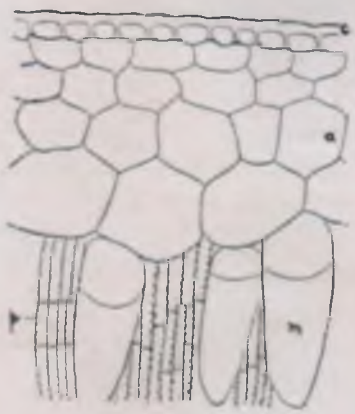

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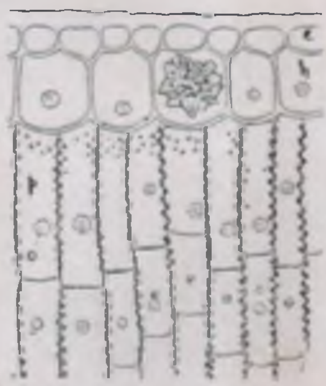

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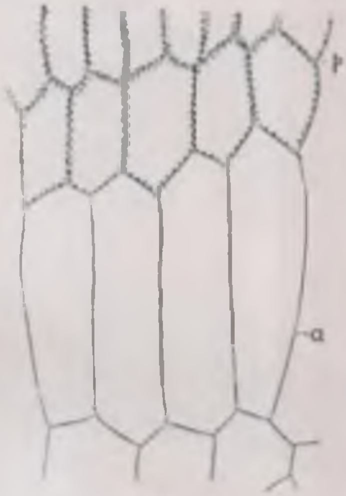

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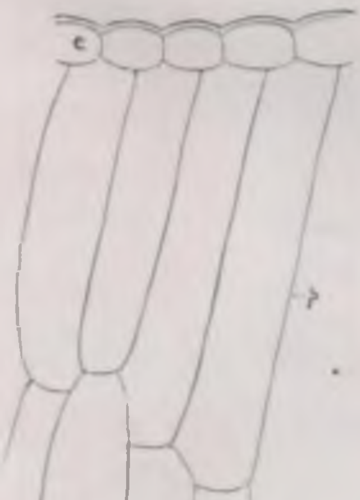

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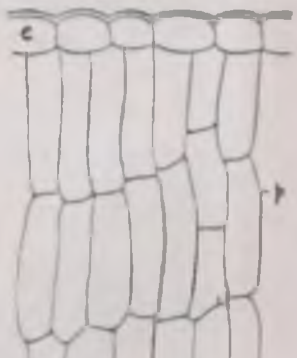

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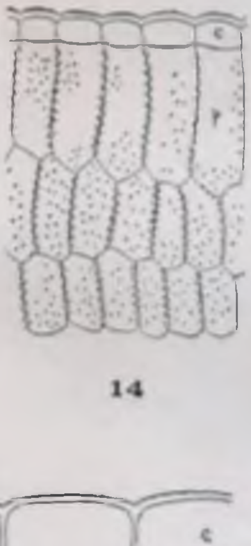

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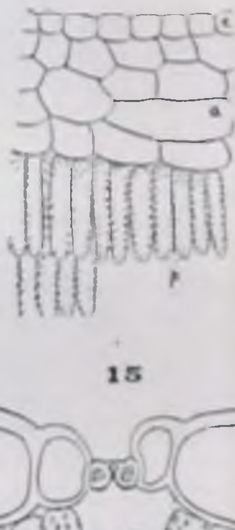

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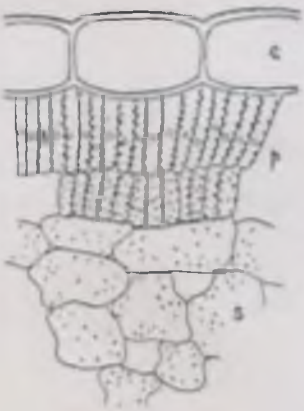

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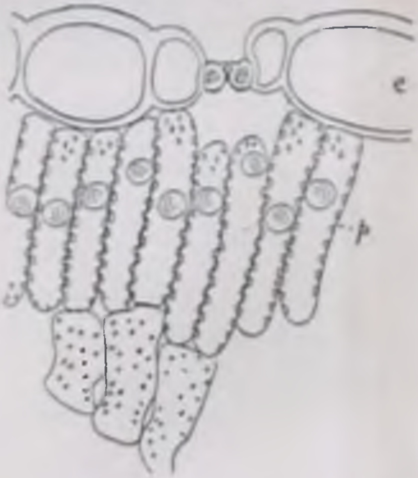

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Fig. 6.—Transverse section of a leaf of *Rhizophora mucronata*, Lamk.: c, cuticle; a, aqueous tissue; p, palisade cells; m, mucilage cell. (× 500).

Fig. 7.—Transverse section of a leaf of *Bruguiera caryophylloides*, Blume.: e, upper epidermis; h, hypodermis; p, palisade cells; o, oil globules. (× 500).

Fig. 8.—Transverse section of a leaf of *Avicennia alba*, Blume.: a, aqueous tissue beneath the upper epidermis; p. palisade cells. (× 500).

Fig. 9.—Transverse section of a leaf of *Scaevola Lobelia*, Murr., showing the medullary aqueous tissue (a); p, palisade cells. (× 240).

Fig. 10.—Transverse section of an old leaf of *Clerodendron inerme*, Gaertn., showing the enlarged palisade cells, p. (× 240).

Fig. 11.—Transverse section of an old leaf of *Launaea pinnatifida*. Cass., showing the enlarged palisade cells, p. (× 240).

Fig. 12.—Transverse section of a leaf of *Spermacoce hispida*, Linn.: e., upper epidermis; p, palisade tissue; s, spongy parenchyma, o, oil globules. (× 500).

Fig. 13.—Transverse section of a leaf of *Corchorus acutangulus*, Lam.: u, upper epidermis; l, lower epidermis; p, palisade cells: s, spongy tissue; a, sheath; k, crystal. (× 500).

Fig. 14.—Transverse section of a leaf of *Clerodendron inerme*, Gaertn.: e, upper epidermis; p, palisade cells. (× 240).

Fig. 15.—Transverse section of a leaf of *Aegiceras majus*, Gaertn. e, upper epidermis; a, aqueous tissue; p, palisade cells. (× 360).

Fig. 16.—Transverse section of a leaf of *Neuracanthus sphaerostachys*, Dalz.: e, upper epidermis; p, palisade tissue; s, spongy parenchyma. (× 240).

Fig. 17.—Transverse section of a leaf of *Leucas aspera*, Spreng.: e, upper epidermis; p, palisade cells holding oil globules. (× 500).