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On the ecology of the mangrove vegetation

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On the ecology of the mangrove vegetation

by

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Trees and shrubs that enter the composition of the mangrove flora are so very diverse that they attrected the attention of the investigators very long ago. THEOPHRASTUS and other ancient authors had written about the mangroves. The presence of the vivipary in the mangroves had been mentioned by the botanist RAY in the XVII century (DAVIS, 1940). However, a more systematic study of these peculiar trees both from the morphological and physiological aspects was startet in the second half of the XIX-th century. The works of KARSTEN (1891), HABERLANDT (1893), SCHIMPER (1898) and other investigators have revealed several ecological and biological peculiarities of the mangroves and of their geographical distribution. One of the most interesting adaptations of the mangroves, the family Rhizophoraceae in particular, is their vivipary. The seeds, or better to say, the sole seed of their fruit germinates on the maternal plant. Its strongly elongated hypocotyl reaches in some representatives up to 50 — 60 cm.

The occurrence of the mangroves in the tidal zone was explained by almost all the authors as an adaptation for the establishment of their seedlings in the silty ground.

Having got personally acquainted with the mangrove flora at the end of 1957 on the Hainan island I rather doubt this interpretation. The point is that the mangroves dwell not only on the silty but on the sandy ground as well. Several representatives, the genus *Bruguiera* in particular, possess relatively small seedlings with obtuse ending that are unable to stick. Only *Kandelia* candel has a very acutely ending seedling and grows on a silty ground. On a sandy substrate we succeeded in noticing most of the shoots to lie horizontally at the surface of the ground during ebb = tide; only some of them have already become rooted. The observations of SCHIMPER made in Indonesia where the mangroves are represented especially abundant show the same.

The bulk of the authors refer the mangroves to halophytes and it seems that there are no especial grounds to think that their germination and growth encounter difficulties in the case of a high salinity.

However, if we regard the resistance to salinity not as a permanent character but as a property developed during the ontogenesis on the basis of the whole preceding evolutionary history of this species then it can be understood that even the extreme halophytes pass adaptation to salinization in their individual development.

All terrestrial halophytes, without exception, are secondary halophytes having certainly originated from glycophytes. In this connection the seeds

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formed at the onset of the new ontogenesis and the seedlings developing from these latter are non-resistant to salinity and acquire this property in the process of adaptation to salinization during their own individual development. The higher was the salt resistence of the maternal plant, the easier and the more rapid is realized the adaptation of the young plant to salinization. That is the great advantage of the halophytes compared to glycophytes. In the light of these concepts it is clear that mangrove seeds when dropped into the marine water find themselves under severe conditions of salinization. Salinity of the marine water in the South China Sea is 3,4 — 3,5 % which corresponds to 24 — 25 atmospheres of osmotic pressure. In our opinion, vivipary of the mangroves is an adjustment to the development of high salt resistance in the young plant. While *Salicornia* and other annual terrestrial halophytes pass the process of adaptation in the spring, when saline soil is being washed from the salts by autumnal-winter precipitation, the mangroves adapt to high salt content directly on their maternal plant. Getting salts and assimilates from the maternal plant and partially producing them independently (the shoots of green coloration), they adapt to a high salt concentration, i. e. become salt resistant.

This was found with the use of a comparative microscopical method of diagnostics of salt resistance suggested earlier by the author (HENCKEL, 1950). The sections of plant leaves are immersed into the molar solution of sodium chloride for several hours and then the number of surviving cells (plasmolysed) is being counted. This method is not always applicable to halophytes since the elasticity of their protoplasm is low and they hardly sustain mechanical injury from the plasmolysis of cells (HENCKEL, 1954). In the experiments carried out in Central Asia such a halophyte as *Statice Gmelini* perished in several minutes when exposed to plasmolysis with salts.

Our fears that this method will be inapplicable for the representatives of the family Rhizophoraceae were not justified. This circumstance stresses the xeric nature of the mangroves. As shown by the works of HENCKEL (1954, 1956), some groups of xerophytes and drought resistant mesophytes are distinguished by the elastic protoplasm. In the work of PANNIER (1959) is showed that *Rhizophora Mangle* L. develops better in the added sea water and the author considers on this bases that mangroves originated from the terrestrial glycophytes.

SCHIMPER (1898) thought the mangroves to be xerophytes and ascribed them low transpiration intensity. As shown by special investigations of FABER (1923), the mangroves show a somewhat more intensive transpiration than the bulk of the plants in evergreening tropical forest. However, FABER stressed the xeric nature of the mangroves and regarded them as relatively high transpiring xerophytes. From our viewpoint, they have to be regarded not as xerophytes which only show features of their xerophytic origin.

WALTER and STEINER (1936) showed the mangroves to be distinguished by a relatively low transpiration. According to a personal communication of FABER made to WALTER, his transpiration values were ten times increased, due to a misprint.

In FABER'S opinion, the mangroves are not distinguished by the xeromorphic structure making in this respect no exception to typical plants of a tropical forest. The mangrove leaves are somewhat succulent at the expense of several layers of relatively large cells in water storing tissue.

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LÖTSCHERT (1960) thinks the pilous cover on the lower epidermis in *Avicennia* leaves to be an adjustment for a decrease in water losses. The mangroves seem to encounter some difficulty in water supply during the ebb = tide. Taking into consideration high salt concentration in their tissues, it is very likely that water storing tissue serves to the levelling of water deficit during the ebb = tide thus protecting the plant against an exceeding salt concentration in its tissues.

Returning to the determination of the relative degree of salt resistance of the mangrove, it should be mentioned that the above described procedure was somewhat modified by the present author. In order to determine salt resistance not monomolar sodium chloride solution but one-and-a-half molar one was taken. Besides, the sections were not stained with neutral red. Cell resistance to salts was determined on the epidermis of leaves, flower parts and seedlings. The results of some of the experiments are set out in tables 1 and 2.

Table 1

Salt resistance of epidermal cells in *Rhizophora apiculata*
(duration of the experiment 5 hours)

Leaf	—55 % surviving cells
Calyx lobe	—37 % surviving cells
Seedling on the maternal plant	—62 % surviving cells

Table 2

Salt resistance of epidermal cells in *Ceriops tagal*
(duration of the experiment 6 hours)

Leaf	—27,1 surviving cells
Calyx	— 2,3 surviving cells
Little seedling on the maternal plant	0,0 surviving cells

The data presented show salt resistance of flower parts to decrease when compared to that of the leaf, while salt resistance of seedlings greatly increases. It can be noticed the salt resistance of younger rooted seedlings is greater than that of the leaves in adult trees. After 10 hours of stay of epidermal sections in 1,5 molar sodium chloride solutions all the cells of the leaf of an adult plant were dead, while those in rooted seedlings were all surviving.

The values as follows show an increase in chlorine content in the leaves with the germination of seedlings. Chlorine content per day weight in *Rhizophora apiculata* leaf made 3,03 %, in the flower bud — 1,07 %, and in the seedling 2,79 %.

The latter data prove the results of the analyses carried out by WALTER and STEINER (1936) who found an increase in chlorine content in the cell sap of the seedling with its age. The question of what is the origin of vivipary in the mangroves is of great interest.

Under the effect of chloride salinization a delay in the formation of the separation layer and with the cast of the fruit takes place in many plants. According to the data of B. P. STROGONOV, E. F. IVANITSKAYA and I. P. CHERNYADEVA (1956), a high chloride salinization delays defoliation and a plant may even perish from the excess of salts without defoliation. A rather rapid defoliation takes place at a high sulfate salinization.

V. A. SOLOVIEV (1960) observed a strong cast of ovaries and flower buds at a high salinization by chlorine anion (0,2 %) in tomatoes, while the set fruit did not fall. Thus, the soil being salinized with chlorides, a delay not only of defoliation but also of fruit cast is observed.

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The works of Yu. V. Rakitin (1955) showed the formation on the separation layer in fruit to be promoted by ethylene excreted by these fruit and to be inhibited by auxins. It is evident that the excess of chlorine ion causes a change in the metabolism towards a decrease in ethylene production and an increase in auxin content.

The material found in literature suggests that vivipary in the mangroves is a result of the delaying effect of chlorine ion upon fruit cast. It seems that those forms in which the cast of the separation layer had been delayed under the effect of substrate salinization were the ancestors of recent viviparous forms of the mangrove vegetation. However, one more condition was required, namely, the absence of the period of rest in the seeds formed. The absence of the period of rest is being found in several tropical plants, in the mangroves in particular (Karsten, 1891; Haberlandt, 1897; Kip-Goller, 1940).

In our opinion, these are the causes of the origin of vivipary in the mangroves.

It should be mentioned that not in all the mangroves the adaptation proceeded towards the appearence of vivipary. In the representatives of other families, also entering the composition of the mangrove flora, such as *Avicennia* of the family Verbenaceae or *Xylocarpus granatum*, of the family Meliaceae, the fruit do not germinate on the maternal plant. However, all the authors accept (Gessner, 1955) that these plants have a highly developed embryo in their seed. It seems that the representatives of this group possess a hidden vivipary (cryptovivipary), the essence of which is the same as that of true vivipary of the mangroves, i. e. adaptation to the salinization on the maternal plant. In the case of cryptovivipary, chlorine ions uptaken, affect metabolism, delaying the formation of the separation layer but hypocotyl does not show intensive growth, while all the parts of the embryo grow more evenly.

Unfortunately we have had no chance to study salt resistance of these representatives of the mangrove flora due to the want of time during our short stay on the Hainan island. In several cases a transitional form, as it were, from cryptovivipary to true vivipary is being observed. Thus, Lörscher (1960) reported that a small seedling was being formed in the maternal plant in *Avicennia* and *Laguncularia racemosa.*

Conclusions

1. Vivipary of the mangroves is of a great ecological importance. During seed germination on the maternal plant the adaptation of the seedling to salinization takes place on the account of salts and assimilates entering it from the maternal plant and on those partially produced by the seedling itself.

2. Apart from vivipary characteristic of the representatives of the family Rhizophoraceae (*Rhizophora*, *Kandelia*, *Ceriops*, *Bruguiera*) cryptovivipary is also observed in *Avicennia*, *Xylocarpus*, *Agiceras* where the embryo germinates within the fruit. Cryptovivipary is of the same importance as vivipary, i. e. as an adaptation to salinization on the maternal plant.

3. In relation to the origin of halophytic mangroves from glycophytes, salt resistance of the young seedling sharply falls with the onset of the new ontogenesis (formation of the zygote and seed). High salt resistance is being acquired by the seedling on the maternal plant. This is of the greatest importance since, having detached from the maternal plant, the seedling finds

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itself under the conditions of high salinity. Due to the preceding adjustment to salinization at the onset of its ontogenesis the seedling stands high salinity very easily. The adaptation to salinity in the mangroves proceeded along two ways: vivipary and cryptovivipary.

4. The development of vivipary and cryptovivipary in the mangroves seems to be connected with the presence of a considerable amount of chlorine in the maternal plant affecting, through a change in the metabolism a delay in the rate of the formation of the separation layer, and through the absence of the period of rest in the seed formed.

5. The peculiarity of the mangroves is their origin from peculiar xeric forms of the tropical forest, while the bulk of terrestrial halophytes have originated from mesophytes or even from hygrophytes.

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