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RESEARCH ARTICLE

ECOLOGICAL AND MORPHOLOGICAL ASPECTS RELATING TO PHYSIOLOGY.

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Abstract

Vivipary is a characteristic feature of mangrove plants. Seeds in these plants germinate within the fruit wall while still attached to the parent tree. Phenolic acids and their derivatives are abundant in *Burquiela* and *Avicennia* seedlings. These phenolic acids protect seedling. They also play an important role in regulation of the development of the viviparous plant. Vivipary permits the assimilation of substantial food reserves within the seedling. The development of the seedling provides resistance to unfavourable conditions even after detachment from parent tree. Hypocotyls function as assimilatory organ in the developing plants. Exposure of seedling to the water delays establishment. Seedling in mangrove provides capacity to tolerate a complete or partial anaerobic conditions for varying periods and to grow successfully after such exposure.

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Introduction:-

In any plant the initial germination and subsequent development of the seedling are stages which are most susceptible to unfavourable environmental conditions. Many of the higher plant swamp species known collectively as "mangroves" are characterized by vivipary, i.e. by the possession of seeds which germinate within the fruit wall while still attached to the parent tree. The germination stage is not directly exposed to the environment. While not all mangroves possess such seeds, "vivipary of such intricate designs is not found in any other vegetation type" (Ding Hou, 1958). Both *Avicennia* and *Bruguiera* are viviparous genera.

The growing *Avicennia* embryo ruptures the testa and fills the pericarp (fruit wall) which then starts to enlarge in proportion to the growth of the embryo (Ding Hou, 1958). The seedling at this stage consists of a larger cotyledon ensheathing a smaller, and a short incurved hypocotyl up to 1 cm. long covered by a felt of upward directed hairs (Chapman, 1962). The thick, fleshy cotyledons which constitute the chief storage organs, are made up of tightly packed mesophyll cells containing numerous starch grains, a small proportion of air spaces, and a row of vascular strands. The *Avicennia* seedling at maturity is not seedling at maturity is not considerably more advanced in growth or structure than may seeds of dicotyledonous mesophytes, e.g. legumes, although it has a very different physiology (Hill, 1966). The hypocotyl develops to a very limited extent compared to the great development attained by the same organ in *Bruguiera* where vivipary is a much more advanced type.

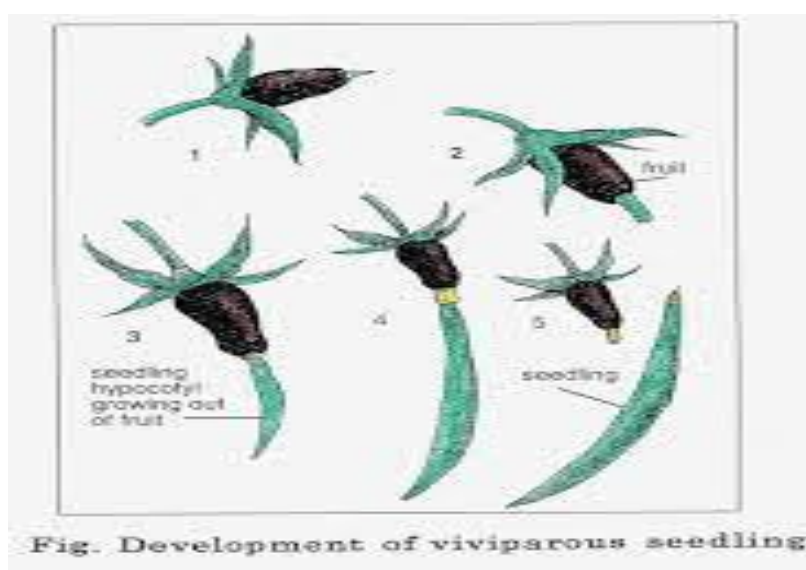
In *Bruguiera* the apex of the hypocotyl pierces the fruit wall and grows cigar-like from it. The much reduced cotyledons "serve, by their glandular epidermal nature, for assimilating nutrients from the pericarp and feeding the hypocotyl" (Ding Hou, 1958). The hypocotyl is made up of an inner and an outer cortex and a pith, the whole consisting of small starch-packed cells with few air spaces. It has a thick cuticle and a ridged surface with lenticular openings on the ridges.

Phenolic acids and their tannin derivatives are abundant in both *Bruguiera* and *Avicennia* seedlings (Carson, 1907; Chapman, 1962). Ridley (1930) considered it possible that the "strong tannin" in *Bruguiera* seedlings "protects them from injury from some marine mollusks", for instance, during dispersal. It is extremely rare to find *Avicennia*

seedlings which show signs of animal damage; however, many of the *Bruguiera* seedlings had been attacked both by caterpillars and by 'boring beetles.

Panier and del Pinar Rodrigues (1967), in their work on the phenolic B-inhibitor complex and its relation to vivipary in *Rhizophora mangle* seedlings (which are very similar to those of *Bruguiera*) came to the conclusion that: "The identified phenolic acids present in the extracts..... could have an important role in the regulation of the development of the viviparous plant." They identified the cinnamic acid derivatives *c*-coumaric acid, *p*-coumaric acid, ferulic acid and caffeic acid. Ferulic, caffeic and *p*-coumaric acids are known to be present in the bark of *A. marina* (Cheesman, 1964) and it is probable that the same phenolic compounds occur in the seedlings. It is possible that these compounds could have significance in both *Bruguiera* and *Avicennia* similar to that postulated for *Rhizophora*.

Vivipary allows for the formation of substantial food reserves within the seedling. The development of the seedling proceeds to stage where it can better withstand the many unfavorable conditions of the swamp habitat which it encounters when detached from the parent tree, and still make active growth. Nevertheless it is liberated at a stage of development when possible adverse factors of the environment can still have deleterious effects.



Mangrove Swamp Environment:-

From the solubility coefficient of oxygen in water, Williams and Barber (1961) have calculated that "water in equilibrium with air contains only 0.69 m/s. Oxygen per 100 m/s. Water" at 25° c. The presence of salts lowers this value to approximately 0.5 m/s. In sea -water (Richards, 1957). These are maximum values for dissolved oxygen at or near the surface. The oxygen content of deeper water depends on the diffusion coefficient of oxygen which is only 2×10^{-5} cm.Sec.⁻¹ (Williams & Barber, 1961). This rate of oxygen diffusion through water is of the order of 10^4 times slower than its rate of gaseous diffusion (James, 1953 a). The degree of saturation further depends upon the balance between oxygen consuming factors in the water (including the respiratory demands of the organisms present) and the addition for oxygen in many aquatic environments (Beadle, 1961). This may be particularly so under the commonly stagnant conditions found in swamps. Standing water often produces a markedly anaerobic environment and many of the oxygen values recorded have been well below the maxima (e.g. Conway, 1937; van Ralte, 1940). Oxygen depletion of water can be brought about, for example, by an abundance of organic material providing a substrate for micro-organisms, by a rise in temperature lowering the percentage of dissolved gases (Leonard, 1939), or by shading causing an inhibition of photosynthesis. All may lower the oxidation-reduction potential drastically and lead to an accumulation of carbon dioxide, hydrogen sulphide, ferrous iron, and end-products of anaerobic metabolism (Beadle, 1961). Troll and Dragendorff (1931) report an entire lack of oxygen from the water-table of African mangrove swamps and Champman (1944) taking samples from both the surface water and the soil water table of Jamaican swamps found areas with apparently no oxygen in the water.

Moving water is better aerated than still water. Harvey, in 1945 (See Raymont, 1963), found that under quiescent conditions in the laboratory the rate of invasion by oxygen could be one hundred times less than if the water was kept moving by air currents above it. It is well known that tides oxygenate the surface water of a mangrove swamp (Ding Hou, 1958). In estuarine areas of East Africa the oxygen Concentration of a flood tide may be near the maximum value, but at the end of the flood period when stagnation sets in the value may fall by 60. %. Of its former level (Toll & Dragedorff, 1931).

Although oxygen is not necessarily wholly absent from mangrove area, its concentration is sufficiently low, in terms of higher plant metabolism, to be an important limiting factor of the environment.

Carbon dioxide is approximately thirty-five times as soluble as oxygen at 0°C (Leonard, 1939). Sea-water contains 45m/s. carbon dioxide per 100 m/s., but at the pH of sea-water (pH 7.04-8.2) most of this is bound as carbonate or bicarbonate so that the actual amount of free carbon dioxide is approximately equal in amount to that in the atmosphere (Raymont, 1963). Leonard (1939) records that water at 25°C contains only .024%. Carbondioxide. Beadle (1961), however, speaks of very high levels of free carbon dioxide produced in tropical swamp waters protected from circulation.

The mud of a mangrove swamp is often clinging, black and evil-smelling. The gaseous content of such mud has been analyzed by Troll and Dragedorff (1955). Their results point to its predominantly anaerobic or even reducing nature. This may be alleviated to some extent by crab and worm holes which riddle the mud (Cockaye, 1921; Baylist, 1935), but nevertheless, the results emphasize the importance of the aerating function of pneumatophores. It is interesting to note that in *Avicennia* pneumatophores develop only where there is constant water –logging. None develop in glass-house plants or in those not in the permanent water-table (Chapman, 1944).

Seedlings Dispersal and Establishment:-

Ecologically, mangroves differ “so much from ordinary land plants (Bharucha & Shirke, 1947). The seedlings fall from the parent tree on to wet or drying mud or into standing or moving salt or brackish water whence they may be dispersed by ocean currents (Egler, 1948). The pericarp of *A. marina* ruptures as the seedling drops or soon afterwards. Chapman (1944) found that immersion of *Avicennia nitida* seedlings in water brings about a release from the fruit wall, an immediate unfolding of the seedling and an elongation of the hypocotyl outside the cotyledons. Establishment of the *Avicennia* seedling may be almost immediate. Haberlandt (1914) observed that anchoring hairs on the hypocotyls of *Avicennia officinalis* serve to fix these seedlings in the mud when they first fall from the parent tree. *Avicennia* seedling of appropriate age generally quickly become anchored by the formation of four or five adventitious roots (Laing & Blackwell, 1957). When a mass drop of seedlings occurs, such as at the end of the fruiting season, only the larger ones seem to become established. The smaller seedlings develop feeble, mechanically ineffective roots and eventually die.

When the *Bruguiera* seedling is mature the food supply fails and the pressure of the fruit wall slackens. The seedling drops out of the receptacle leaving the four cotyledons behind. The hypocotyl then acts as an assimilatory organ in the developing plant (Carson, 1907), assuming the function of both photosynthetic stem and storage organ.

If the seedlings fall into water establishment may be delayed. Observations on natural regeneration in Malayan mangrove swamps (Watson, 1928) indicate that here new *Bruguiera* plants grow from seedlings from nearby trees, whereas *Avicennia* may grow from “seed that has been waterborne for a considerable distance. “However, both seedlings have separation from the parent tree and of establishment.

Guppy (1906) observed that *A. nitida* seedlings may drift in the sea for over four months and still retain their vitality, i.e. their ability to grow when stranded. Similar ability to grow when stranded. Similar observations have been made with *A. marina* (Laing & Blackwell, 1957). Guppy found that after 117 days in sea-water *B. gymnorhiza* seedlings were still healthy. Davis (1940) studying *Rhizophora mangle* (*Rhizophoraceae*) seedlings, which are very similar to those *Bruguiera*, concluded that the maximum time the seedling may remain floating or submerged under normal conditions must be a year or more. Of the several hundred seedlings he tested many did this without apparent harm. Hill (1966) has shown that the actively growing tips of the hypocotyls of mangrove seedlings are very susceptible to damage caused by exposure to anaerobic conditions. *Bruguiera* seedlings have “a perfect adjustment of specific gravity” which causes the lower end of the hypocotyl to sink. In general the seedling floats vertically with the leaf bud just projecting from the water (Crossland, 1903). Guppy (1917), however, observed that many seedlings floated

horizontally or even sank. *Avicennia* seedlings are in general very buoyant in salt water, although a small proportion of cotyledons removed from their pericarps sink. *Avicennia* float with no particular orientation.

Whether the seedling falls on to mud or into water, it will at some stage, be exposed to oxygen concentrations which are low in terms of higher plant metabolism. Bharucha and Shirke (1947) found that the "respiratory index" of *A. officinalis* seedling under submerged conditions, and attributed this to the "limiting influence of oxygen." It is possible that adaptation to an aquatic environment may require a species to develop tolerance towards low oxygen and high carbon dioxide conditions (Boulter, Coult & Henshaw, 1963).

It has been suggested that the presence of aerenchyma in the tissues of floating seedlings would prevent, through photosynthesis, the build-up of an oxygen-deficient gas atmosphere in such seedlings (Chapman, 1962). There is no data on the photosynthetic rate of floating seedling. However, the seedling tissues are compact with few air-spaces. Only 8.5% of the *Avicennia* cotyledon and 5.7% of the *Bruguiera* hypocotyl is air-space (outer, 1966). In *Avicennia* this is evenly distributed through the mesophyll tissue, while in *Bruguiera* 84% of the total air-space is in the inner cortex. Analyses of the internal gas atmospheres of mangrove seedlings (Outred, 1966) have shown it to be unlikely that photosynthesis would release enough oxygen into the intercellular spaces to build up an aerobic internal atmosphere. In an anaerobic acid and ethanol there is no clear evidence that floating seedling do experience anaerobiosis.

Indications are that growing tissues may face seriously adverse conditions if they are submerged. La rue and Musik (1954) found that embryos of which were completely immersed in water produced roots two months after planting and shoots in four months. They concluded, "the ability to grow even when immersed in water months demonstrates a remarkable capacity in the seedling for anaerobic respiration".

Hill (1966) found that both *Avicennia* and *Rhizophora* seedling were capable of active growth after being subjected to both exposed and submerged anaerobic conditions, and that *Rhizophora* displayed the greatest tolerance. Taking as the criterion of survival the healthy growth of a seedling one month after its exposure to anaerobic conditions, Hill obtained the following figures for limits of tolerance of the seedling could survive 5-6 days in nitrogen; 40% survived 5 days in sea water. Survival in fresh water was poor and limited to 2 days. Of the *Rhizophora* seedling, 100% survived 7 days in nitrogen and 50% survived 5 days in either sea or fresh water.

It seems possible that mangrove seedling have the capacity to tolerate a complete or partial anaerobic environment for varying periods and to grow successfully after such exposures. But although Chapman (1962) has noted that a capacity for anaerobic respiration "may well be of ecological significance" any capacity for tissue anaerobiosis is not necessarily related to the conditions of the environment. Mangrove seedling, immersed will have a greatly reduced oxygen supply and although this may be adequate for normal reduced oxygen supply and although this may be adequate for normal respiration purposes it is more likely that until the seedling has become rooted, produced its first leaves and developed a stem aerenchyma it is very largely dependent upon anaerobic respiration. While it is rare in higher plants for anaerobic respiration to account for any great proportion of the total respiration, slow initial growth may mean that the energy available is adequate. Rice, for example, is known to have a very functional fermentation system which is replaced by the first leaf stage.

In the *Rhizophoraceae* roots may appear while the hypocotyl is still floating. *Bruguiera* hypocotyls often develop roots while lying on the laboratory bench and *Rhizophora mucronata* seedlings have been observed to grow small roots in gaseous anaerobic atmospheres. *A. merikana* seedlings with primary roots form a conspicuous element of the drift-line debris along Auckland beaches. Although upon stranding on a suitable (usually muddy) substratum, the seedling are in a condition for immediate establishment and growth, subsequent growth may not be particularly fast. For example, in *A. mitida* it is not until 7 days after liberation from the pericarp that the first primary roots act as an anchor. After 9 days there are 5 primary roots and at 20 days the plumule is appearing above the cotyledons. The growth of *A. officinalis* seems to be somewhat faster. Bharucha and Shirke (1947) found that after eight days of growth the cotyledons had expanded, there was a well-developed ring of roots and a shoot just producing its first leaves.

A. maritima seedling are found abundantly over swamps for several months after the maximum ripening period but generally they do not survive longer unless rooted with rapidly growing tops. Davis (1940) observed that if the top growth of *Avicennia* is two inches or over, it can survive nearly constant submergence but if less than this, it cannot. Plants with four to six leaves failed to develop or very frequently submerged. Chaman (1944) found that *A. mitida*

seedlings can become established where the tide reaches to six inches above the growing tops, but they cannot survive persistent submersion.

Hill (1966) found that the survival of young *Avicennia* and *Rhizophora* seedling depends on the length of time the meristematic regions can withstand anaerobic conditions. His results showed that both seedlings can tolerate, as a maximum, 8-10 days in pure nitrogen before damage occurs. The *Avicennia* hypocotyls then turn brown and the cotyledons, returned to air, are unable to regenerate new leaf and root primordia. The apical and basal meristems of the *Rhizophora* hypocotyls also show irreversible damage.

The possibilities for exposure to an anaerobic environment may occur either on the parent tree, or during the early stages of development after release from the parent tree. Once the seedlings have become established, aerobiosis, accompanied by the development of an extensive aerenchymatous system, is likely to replace anaerobiosis.

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2. **Chapman (1962)**, the thick, fleshy cotyledons which constitute the chief storage organs, are made up of tightly packed mesophyll cells containing numerous starch grains, a small proportion of air spaces, and a row of vascular strands.
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4. **Williams and Barber (1961)** have calculated that "water in equilibrium with air contains only 0.69 m/s. Oxygen per 100 m/s. Water" at 25° c.
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