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# Studies on the Growth of Red Mangrove (*Rhizophora mangle* L.)

## 4. The Adult Root System

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### ABSTRACT

Aerial roots in *Rhizophora* arise from stems, branches, and secondarily thickened, anchored, aerial roots, but only after injury from unanchored aerial roots. Lateral subterranean roots are abundantly developed upon penetration of a mud substrate whereupon the histology of the root undergoes marked and abrupt changes so that chlorophyll is no longer developed, trichosclereids no longer differentiate, tannin cells become few, the cortex becomes markedly lacunose, and the sequence of protoxylem differentiation changes. Root systems developed in contrasting environments like water, sand, or mud provide evidence as to the relative importance of light and air in affecting anatomical differentiation. The overall morphology of the root system is discussed in relation to its likely function in aeration of subterranean parts.

WE HAVE OUTLINED briefly the general features of the root system of *Rhizophora mangle* (Gill and Tomlinson 1969), and we now amplify that preliminary statement. In another article in this same series (Gill and Tomlinson 1971a) the distinctive method of growth of aerial roots of red mangrove, which leads to distinctive anatomical features, was described. This present article completes the account of the development of the root system by describing distal anchorage of aerial roots, the overall establishment of the characteristic looping, above-ground root system, changes in the anatomy of roots as they penetrate the substrate, and also discusses the likely physiology of roots in relation to the distribution of gas space within them. An attempt is made to relate these features to the general ecology of the *Rhizophora* root system in differing environments.

Since the aerial roots of *Rhizophora* are one of the most striking features of the genus, they have occasioned frequent comment, as early as 305 B.C. by Theophrastus (Bowman 1917). Scientific investigations in more recent times have included those of Warming (1883), Karsten (1891), Schenck (1889), and Boergesen and Paulsen (1900). Most interest has centered on the likely function of aerial roots in the aeration of the attached subterranean roots which are typically anchored in anaerobic soils (Jost 1887, Karsten 1891). Direct demonstration of this role in aeration remains to be done, as indeed it does with the root systems of most trees. In fact, the aerating

function has remained difficult to demonstrate convincingly (e.g., Kramer *et al.* 1952 for *Taxodium*). Evidence is largely circumstantial, but the most recent comprehensive investigation by Scholander *et al.* (1955), using *Rhizophora* and *Avicennia*, seems conclusive. Mention should be made, however, of the interpretation by Troll and Dragendorff (1931) of the root system of *Sonneratia caseolaris* as a mechanism for adjusting to soil accretion and not as an aerating system.

In our present study we are concerned more with the dynamic morphology of the root system than with its function, but we emphasize that a detailed knowledge of structure must precede any discussion of physiology. Further, the root system of *Rhizophora* provides one among many examples of aerial root systems in tropical plants in which there are striking morphogenetic responses to abruptly changing environments (Gill and Tomlinson 1975). Our present study includes little experimental work; we have largely relied upon natural variation of roots in different substrates to provide evidence for causal responses. This information has provided insight into the ecological adaptability of the *Rhizophora* root system, since so much previous description has referred to an invariable root environment which is tide-washed and has a soft, anaerobic substrate. In South Florida, at least, *Rhizophora* habitats are often varied, and the response of root systems to this variation must be considered along with aeration.

## METHODS

Investigations were conducted largely in the vicinity of Fairchild Tropical Garden, Miami, Florida, during the period 1968-1971, the locality already reported on in earlier papers of this series (Gill and Tomlinson 1969, 1971a, 1971b). Additional observations were made on a wider variety of root habitats elsewhere on the shores of Biscayne Bay and in the Everglades National Park. Roots were mostly observed and measured after excavation. In the main area of observation there was about 1.3 m of mineral soil over oolitic bedrock.

Measurements of the gas space of roots were made on thoroughly washed portions of the detached roots cut into 10 cm lengths, surface dried with paper towels and weighed to determine fresh weight. The pieces were then submersed in water to determine volume by displacement, completely infiltrated with water under vacuum, reweighed again after surface drying, and the volume again redetermined by water displacement. From the difference in weight between normal (air-occupied) and artificially waterlogged roots the percentage of the root volume occupied by gas space could be determined, corrected for by changes in volume as a result of infiltration.

## ROOT HABITATS

Variation in root environment is important in appreciating root function and is described here in some detail. It should be understood that none of these environments is necessarily peculiar to South Florida. Red mangrove habitats are subjected to variation in salinity, soil type, and local topography. The circumstances under which mangrove communities in South Florida are flooded by salt or fresh water have been described by Craighead (1971: 88-117). Near the shoreline, flooding by seawater is periodic and based on the rhythm of the tides. In contrast, flooding in inland localities is seasonal and by fresh water, typically as a result of high summer rainfall. In yet other, perhaps intermediate, localities an interchange between salt and fresh water is a consequence of spring tides alternating with fresh-water run off. Salinities then fluctuate most widely and irregularly. A common situation is for fresh water to form a layer above salt, the layers rising and falling with the tides. Variation in substrate salinity, however, has no obvious direct effect on root expression.

Soil composition varies. That of inland areas is largely mineral, either quartz sand or marl. Quartz-sand soils are often well-drained when well above mean high water, dunes and beaches providing typi-

cal examples. Marl soils are usually poorly drained. In contrast, peaty soils are equally common, and *Rhizophora* trees may be restricted to shallow pockets of peat or mud within otherwise continuous areas of a contrasted substrate. Elsewhere peat deposits may be up to 3 m deep and form extensive and continuous deposits (Spackman *et al.* 1969, Craighead 1971: 111). Otherwise *Rhizophora* can develop on coral rock, the roots finding support in shallow pockets of shell sand or marl.

Mangrove shorelines in South Florida seem frequently to be eroding, and this situation may be consequent upon shifting current patterns. In some areas a low sandy bank above high-tide level is formed landward of the erosive edge and provides another habitat for mangroves. Fringing mangroves form another characteristic community in which the habitat is provided by the margins of natural drainage channels, or, more recently and quite extensively, by canals and other man-made channels. Under these circumstances aerial roots will penetrate water for some considerable distance before reaching a substrate. Continuously waterlogged substrate may be regarded as anaerobic, with considerable evidence of chemical reduction (Ponneramperuma 1972).

In general one can say that the root system of *Rhizophora* is established by units which are initiated aerially and therefore in high oxygen levels and completed in a substrate which is anaerobic. This contrast between dry aerobic and wet anaerobic environments conditions the development of the system.

## PATTERNS OF ROOT DEVELOPMENT IN THE ADULT PLANT

Seedling root systems have been described briefly in Gill and Tomlinson (1969) but are not dealt with in this paper, although this information is clearly vital to an understanding of establishment of individuals. The seedling root system plays a negligible role in the adult by virtue of it being by-passed by the development of aerial roots. This result is seen in the mature trunk, which is obconical near ground level and supported by aerial roots which resemble flying buttresses and which are progressively larger in the distal direction. The seedling root system usually disappears from the adult plant.

ORIGIN AND BRANCHING OF AERIAL ROOTS.—Aerial roots to a diameter of between 5 and 10 mm arise from trunk, branches, and other aerial roots; they never arise from subterranean roots. However, the delayed branching of anchored aerial roots occurs such that branches often originate on the upper surface of the parent root. Aerial roots, in the first instance,

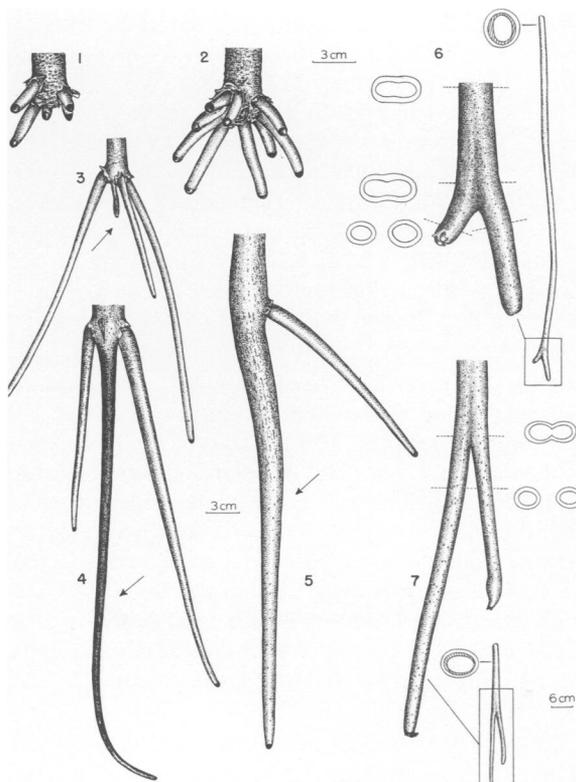
branch only on injury. Otherwise an aerial root will remain unbranched until it reaches the substrate.

Injured roots produce up to five new laterals in normal circumstances as illustrated in figure 1. Figure 2 shows an unusually high number. The time for these new roots to develop has been measured by cutting either 1 cm or 20 cm from the end of roots, one set of experiments being initiated in December 1968. When 1 cm was removed, elongation of the root continued for a short time. Removal of 20 cm stopped root elongation immediately. This difference is evidently due to the long zone of extension (up to a maximum of 23 cm) which we have demonstrated (Gill and Tomlinson 1971a). Development of lateral roots was similar in both treatments. Swelling close to the cut surface was observed five months after cutting; within a further month half of the 20 roots treated had evident new laterals. When the experiment was repeated in summer, commencing 5 August 1969, the recovery response was quicker; swelling response was evident as early as two months after injury, and nine of twelve roots had developed evident new laterals after four months. This difference in time of response between winter and summer reflects the generally more favorable climate for growth in summer (Gill and Tomlinson 1971b).

Injury to root systems of *Rhizophora* is common, as in all trees, and may be due to both biological and physical agents. The major biological agents are the beetle *Poecilips rhizophorae* (Woodruff 1970) and a scale insect (*Pseudococcus* sp.). The beetle tunnels into and along roots while the scale insects are surface feeders. Destruction of aerial roots has been reported by Docters van Leeuwen (1911) also as a result of attacks by scolytid beetles, with resultant induced branching. The epidemic proportions of incidence of the isopod *Sphaeroma* in parts of South Florida have been commented upon by Rehm and Humm (1973). Isopods are very destructive of aerial roots.

Physically, roots are damaged by abrasion and possibly also by desiccation. Death of the root apex by drying out is assumed to have occurred when the root appears undamaged but shrivels, as in figures 3 and 4 where the arrow indicates the original apex, now dead.

Various patterns of response to injury are illustrated in figures 1-7. Figures 1 and 2 show early stages in root branching immediately behind the aborted main root apex. Figures 3 and 4 show the effect of branching at varying distances behind apices which have apparently aborted by desiccation. Figure 5 shows the only example of branching observed without apparent injury but probably occurring after



FIGURES 1-7. *Rhizophora mangle*. Aerial roots responding to natural damage by branching. Figures 1 and 2. Roots branching immediately behind an apex which has been physically damaged. The large number of branch roots in figure 2 is exceptional. Figures 3 and 4. Roots branching behind an apex which has aborted, presumably by drying out, the main axis (now dead) is shown by the arrow. Figure 5. Apparent monopodial branching due to a prolonged quiescence of the main root apex. Figures 6 and 7. Apparent dichotomy of the aerial root, presumably by incipient damage to the apex. Usually such roots die shortly beyond the level of bifurcation. The inset diagrams show the transverse outline of the roots at the levels indicated and illustrate the bifurcation of the stele.

prolonged quiescence of the apex. The dichotomous branching of roots, illustrated in figures 6 and 7, may represent a response to minor injury, comparable to that reported by Wilson (1970) in subterranean roots. However, no evidence of injury was found in these examples. Anatomically in such roots there is a gradual bifurcation of the stele, indicated by the diagrammatic cross sections in figures 6 and 7. One or both axes produced in this way usually die shortly after bifurcation.

**ANCHORAGE AND DEVELOPMENT OF THE SUBTERRANEAN ROOT SYSTEM.**—On reaching a firm substrate, roots become anchored, and since anchorage seems to be accompanied initially by continued elon-

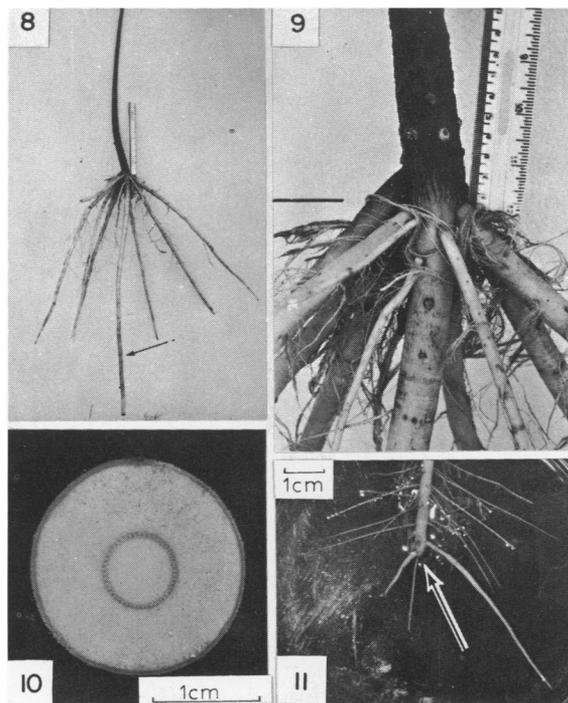
gation, the root bends slightly just above the level of rooting. Remarkable internal changes in root organization occur, to be described below. We will consider first the superficial changes as penetration proceeds. The appearance of an aerial root after it has undergone ramification in mud is shown in figure 8 with details in figure 9. The contrast between the unbranched dark aerial part and the white subterranean part with several orders of branching is obvious. The distal underground part of the continuing main axis is not shown since it was broken in excavation; the total length must have been over 1 m.

The most obvious feature of this transition is the presence of several wide lateral roots (about 7) near the soil surface. The aerial axis itself becomes swollen at the soil surface, by aerenchymatous growth (fig. 25), and numerous conspicuous white lenticels are developed. In figure 9 there is shown an evident zone of abrupt narrowing of the parent root at the level of penetration, and it is at this level that the wide laterals are inserted. This tapering zone is produced entirely as a result of primary growth and indicates a change in the developmental potential of the root apical meristem.

Beyond the zone of taper and level of insertion of wide first-order laterals the main root continues to branch, but the laterals produced are much narrower. In figure 9 they are represented only by scars since they have been stripped off in excavation. Distally, laterals continue to be initiated but extend relatively late so that the distal part of the growing root is always branch-free. Branches of up to three orders are produced, the ultimate branches being the fine capillary rootlets less than 0.1 mm diameter which have been described by Attims and Cremers (1967). Capillary rootlets may be of the second or third order, depending on the diameter of the first-order branch. Second-order laterals are sometimes quite wide (up to 5 mm).

In relatively firm substrates the most profuse development of fine lateral roots is just below the substrate surface, and this circumstance typically leads to the establishment of a mat of capillary rootlets intimately mixed with the soil (fig. 15).

The pattern of underground branching of the main root and wide first-order laterals, which normally produce narrow laterals, is modified by injury. Under this circumstance a lateral root of larger diameter than normal is formed, as shown in figure 11. This replacement root then continues to develop and shows properties similar to those of roots with the same diameter elsewhere in the system. This process of replacement corresponds to that described by Lyford and Wilson (1964) in *Acer rubrum*.



FIGURES 8-11. *Rhizophora mangle*. Aerial and underground roots. Figure 8. Anchored aerial root, with underground branching; arrow indicates original root axis, the distal end of which has been broken off in excavation. Figure 9. Details of figure 8 at substrate level to show difference in root texture between aerial and underground parts. Many of smaller laterals have been broken off in excavation and are represented by their scars. Solid line indicates surface of solid substrate. Figure 10. Cut surface of underground root to show wide cortex and medulla, polyarch stele and lacunose cortex, periderm scarcely developed. Figure 11. Distal part of an underground first-order lateral root whose apex has been destroyed (arrow). The response has been to produce two distal laterals which are wider than otherwise would be developed.

**FURTHER EXTENSION OF THE AERIAL SYSTEM.**—We have already indicated that underground roots never produce aerial roots so that further development of the aerial system is not possible from a given root once it is anchored. How then does the aerial system become elaborated? In contrast to the normally unbranched state of aerial roots *before* anchorage, *after* anchorage they may form new above-ground laterals even in the absence of injury. Usually the first lateral to form is on the upper, curved, aerial part of the existing root a little above soil level (10-20 cm) and aligned with the parent root. This contributes to the outward extension of the aerial root system. Other belated branch aerial roots may arise not necessarily aligned with the parent root system, and these, apart from proliferating the whole system, also permit lateral spread. All belated branch roots

have the properties typical of aerial roots, and consequently a series of successive loops is built up. A complete segment of the root system is plotted in profile and plan view in figure 12, with the direction of extension from A (stem attachment) to B. Points of anchorage are shown by open circles in the plan view. Levels at which the root system has branched as a result of injury can be recognized by the dead snags of injured roots and are shown in two places in figure 12, profile; remaining branches represent belated laterals produced post-anchorage. From the profile diagram of figure 12 it is evident that the root system forms a series of loops, each of which may be subdivided into an arch and a column. The arches represent the upper part of the root system between the levels of branching and in which secondary thickening is most extensive. The columns represent the connections between the arches and the underground system, and relatively little secondary thickening occurs in them. Abundant lenticels are developed on their surface. Very little secondary

thickening occurs in subterranean roots. For example, at a level 3 cm above the soil surface the width of the secondary system was 2 mm in one root, but less than 0.3 mm at a level 3 cm below the soil surface (see figs. 10 and 23).

This method of construction involving a series of secondarily thickened root arches supported by less-thickened columns seems essential to the continuing function of the root system, as is discussed later.

Injury to the arches is rare, the most common abnormality is the development of woody galls on older parts, comparable to those often found on trunks and which are apparently pathological. Galls rarely cause either death of the root or further proliferation of branch roots. Lateral roots can be induced in the arches by cutting into them. In two samples so treated it took 14 months for new laterals to be formed. This process may be compared to that taking place on the stem and branches.

A few examples of root penetration followed by

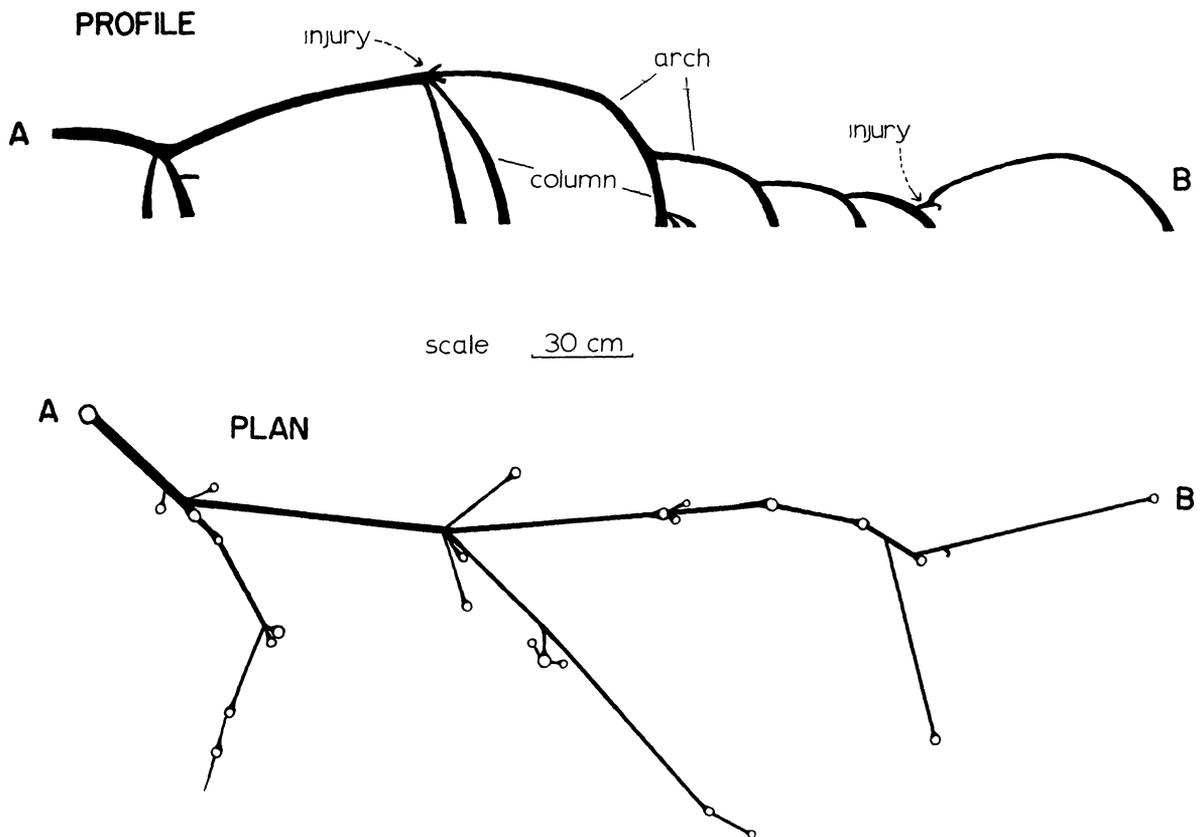


FIGURE 12. *Rhizophora mangle*. Example of one sector of the aerial root system, plotted in profile (above) and plan (below). The attachment to the trunks is at A; the most distal, as yet unbranched, unit is at B. Open circles in the plan view represent levels of insertion of roots into the substrate. Two levels of aerial branching induced by injury are shown in the profile view, which also illustrates the distinction which can be made between column and arch.

the development of belated, root-borne aerial roots have been observed throughout the development of a complete arch. In the area of study this takes a minimum of 12 months. In this respect the ease with which underground roots can penetrate the substrate may influence the period of the cycle.

**ANATOMICAL CHANGES ON ANCHORAGE.**—The pattern of histological differentiation within the root changes completely as it penetrates the substrate. External changes previously noted are in color and in diameter. Internal changes are quite dramatic. It may be recalled that the growth of the aerial root of *R. mangle*, as we have already described (Gill and Tomlinson 1971a), involves the following features:

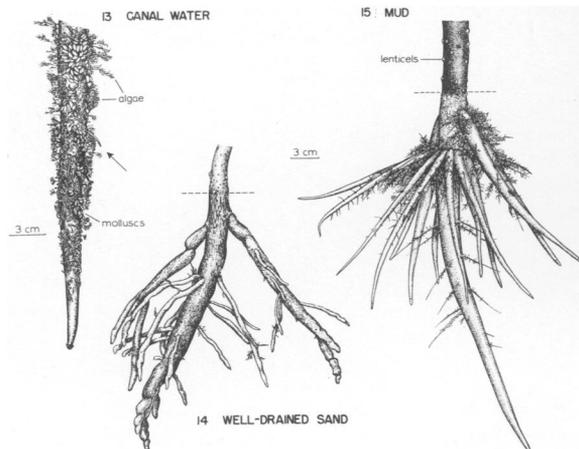
1) A long zone of extension and relatively rapid rates of growth.

2) A polyarch stele (fig. 17) with a wide medulla and development of initially endarch but subsequently exarch metaxylem. The root therefore has only typically exarch protoxylem close to the apical meristem, most development of protoxylem occurring within the zone of elongation so that at maturity, an endarch, superficially stem-like arrangement is presented.

3) Abundant development of H-shaped trichocleoids and tannin cells within the ground parenchyma which has relatively small intercellular spaces (figs. 16, 17).

4) Evidence of active transverse cell division of the ground parenchyma throughout the elongation zone.

5) A superficial phellogen, with lenticels in the



FIGURES 13-15. *Rhizophora mangle*, root response in different substrates, illustrated by parts of underground roots submerged in canal water (fig. 13), well-drained sand (fig. 14), and mud (fig. 15). Further explanation in the text.

older parts. This condition produces a cork which is continually sloughed from extending parts.

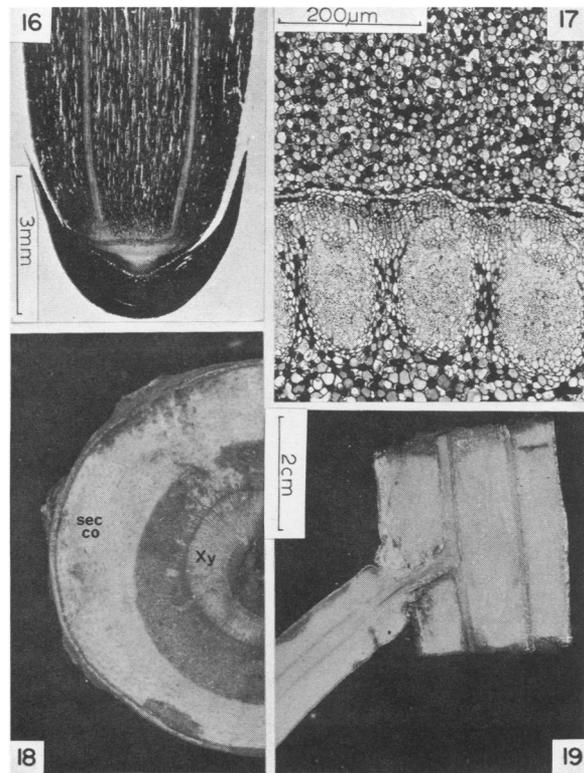
6) Secondary vascular development from a cambium in older roots.

7) Chloroplasts present in the surface layers below the phellogen.

The following changes in the pattern of development occur as the root apex penetrates the substrate such that the subterranean roots are characterized by the following features:

1) A short zone of elongation. This is a matter of inference, rather than observation, but there is circumstantial evidence to support it (cf. 2 and 4 below). It would seem impossible for a subterranean root to grow effectively with a long zone of elongation.

2) A decline in the number of protoxylem poles,



FIGURES 16-19. *Rhizophora mangle*, root anatomy. Figure 16. L.S. apex of aerial root with well developed rigid root cap and abundant tannin (cf. fig. 20). Figure 17. T.S. aerial root in region of vascular tissue (cf. fig. 22) (for detailed description see Gill and Tomlinson 1971a). Figure 18. Cut transverse surface of a column to show well-developed secondary xylem (xy) and wide zone of secondary cortex (sec co). Figure 19. Cut longitudinal surface of underground root showing insertion of a first-order lateral with cortical constriction which, however, does not inhibit gas exchange.

although a large number of protoxylem poles remains (fig. 10). There is no centrifugal metaxylem so that the protoxylem remains obviously exarch in position (fig. 22).

3) Absence of trichosclereids (except occasionally in the inner cortex) and infrequency of tannin cells but development of a very wide system of air-filled lacunae (figs. 21-23). The cortex consists of a mixture of long and short cells (fig. 24), and these form a reticulum enclosing the lacunar system. The difference in anatomy of ground tissues is strikingly revealed in longitudinal sections of root tips, or may be seen by comparing figure 16 (aerial root) and figure 20 (subterranean root). The difference in texture of the root caps is here evident.

4) No evidence of extensive late transverse cell division in the ground parenchyma.

5) Lack of a superficial phellogen. The surface layers consist of a small-celled epidermis without root hairs and a layer of 2-3 hypodermal cells. No phellogen is developed, and there are no lenticels.

6) Little or no secondary thickening (fig. 23).

7) Absence of chloroplasts; subterranean roots are always white.

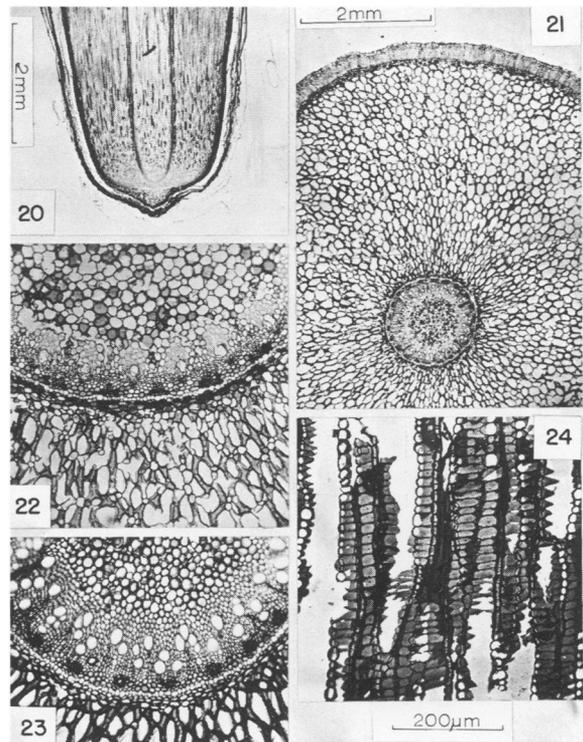
These histological features are essentially repeated in roots of successively smaller diameter and in branches of successively higher order. The number of protoxylem poles is directly but only broadly correlated with root diameter so that smaller roots have fewer poles; the capillary rootlets, as described by Attims and Cremers 1967), are usually diarch and always lack root-hairs.

## EFFECT OF SUBSTRATE ON ROOT DEVELOPMENT

We have emphasized earlier the variability of root environment, and it is possible to see the effect of different media on the development of the root simply by comparing roots found naturally in contrasted environments. The main effects may be categorized as follows:

1) Roots in air (high light intensity and oxygen concentration). This could result in the unbranched aerial root whose properties we have described (Gill and Tomlinson 1971a).

2) Roots in standing canal water (relatively high light intensity, low oxygen concentration). The appearance of such a root is illustrated in figure 13. Lateral roots are mostly absent, chlorophyll is developed, but no or few sclereids are differentiated. Such roots rapidly become festooned with algae, molluscs, and



FIGURES 20-24. *Rhizophora mangle*. Anatomy of underground roots. Figure 20. L.S. root apex, with delicate root cap and relatively little tannin (cf. fig. 16). Figure 21. T.S. root to show narrow, polyarch stele and lacunose cortex without sclereids. Surface periderm developed. Figure 22. T.S. root in stelar region. Figure 23. T.S. old root in stelar region to show limited secondary activity. Figure 24. L.S. root cortex to show differentiation between long and short cells (cf. fig. 22).

worm casts. Shadowing by these epiphytes could account for the occasionally developed narrow laterals (arrow).

3) Roots in well-drained beach sand (low light intensity, relatively high oxygen content). An example is provided by the root illustrated in figure 14. First- and second-order laterals are developed, but there is no well-developed system of capillary rootlets. Neither sclereids nor chlorophyll pigments are developed. Such roots appear to be distorted, and this condition may reflect a reduced growth rate.

4) Roots in waterlogged mud (low light intensity, low oxygen concentration). This situation represents the most common substrate, and the normal root system, described above, is developed; for comparative purposes such a system is illustrated in figure 15. The histology of this kind of root has already been described and illustrated (see above and figs. 20-23).

## GAS SPACE AND ROOT AERATION

The measurements of gas-space volumes as percentages of the total volume of the root are given as ranges for the number of samples measured in the bottom line of table 1. These show that gas is highest in roots anchored in mud, with as much as 50 percent of the root being gas space, but lowest in the aerial roots where less than 6 percent of the root volume represents gas space. The intercellular spaces of the subterranean root system are readily seen even with the naked eye (fig. 10, cf. fig. 21). Longitudinal continuity throughout the root can be demonstrated simply by blowing through the roots into water as if through a straw. This can be done over lengths of at least 60 cm. Continuity of the gas-space system from the main axis into lateral roots can be shown in the same way, despite the constriction apparent at their junction (fig. 19) which is a consequence of the method of cortical development of the newly emerged lateral root. In discussing the control of gas flow later, it is necessary to be aware of the overall dimensions of the system. The deepest axis excavated was only 1.3 m (cf. fig. 8), and it is reasonable to suppose that roots may penetrate to at least 2 m,

where the substrate allows, as in peaty soils. There are obvious difficulties in excavating root systems where water tables are high.

With the aeration of the subterranean root system dependent on the primary intercellular spaces of the pith and particularly the wide cortex, it is no surprise to find that the cortex is remarkably persistent as compared with the roots of most trees (see table 2). Limited activity of the vascular cambium, such that there is little secondary increase in root diameter, chiefly permits this. However, in older columns there is the development of an extensive tissue which is derived from a well-developed phellogen. This tissue is evident in figure 18 as a thick white zone internal to the phellogen. It originates mainly from internal derivatives of the phellogen and includes numerous lenses of sclereids, which are visible in figure 18. In contrast, the primary cortex, while retaining trichosclereids, becomes quite spongy. It must be remembered that the aerial root at the time it makes contact with the substrate is provided with an extended growing zone. Clearly the distal part of each column is anatomically specialized and is being examined by us in further detail.

TABLE 1. *Rhizophora mangle*. Root properties in various root environments. (— = more or less completely absent. + = present).

Property	Environment				
	Air	Mud	Water		Sand (Drained)
			Light	Dark <sup>a</sup>	
Lateral roots	—	+	—	+	+
Chlorophyll	+	—	+	—	—
Trichosclereids	+	—	—	—	—
Lenticels	+	—	—	—	—
Percent volume of gas space <sup>b</sup>	0-6 (10)	42-51 (9)	22-29 (7)	35-40 (4)	22-28 (10)

<sup>a</sup> Induced experimentally by allowing roots to grow into "Alfoil" screened buckets filled with water.

<sup>b</sup> Figures in parentheses refer to number of samples measured.

TABLE 2. Comparison of the properties of the mature root system of *Rhizophora mangle* with that of *Acer rubrum*, a temperate terrestrial tree.

Property	<i>Rhizophora mangle</i>	<i>Acer rubrum</i>
Root crown (at trunk base)	absent	very large
Major horizontal roots	aerial	subterranean
Method of spread	sympodial	monopodial
Orientation of major subterranean roots	vertical	horizontal
Maximum size of root tips	7-8 mm	2-3 mm
Maximum length of root elongation zone	23 cm	1 cm
Cortex	persistent	not persistent
Gas capacity (maximum)	very high	very low
Plasticity of lateral root development to environment	marked	slight
Mycorrhizae	absent	very common

## DISCUSSION

**MORPHOGENETIC RESPONSES.**—Our previous description of the root system of *Rhizophora* has indicated that its overall construction, pattern of branching, and histology all vary according to the environment. Our observations may be summarized in the form of table 1 and the effects of light and oxygen levels discussed. In the presence of light, lateral roots are absent, chlorophyll is present, and trichosclereids are present. In the absence of light, lateral roots are abundant, and both chloroplasts and trichosclereids are absent. Lenticels develop only in the presence of air. The formation of abundant intercellular spaces may be influenced by the oxygen concentration near the root surface as well as by the lack of light. Where light is available, chlorophyll is developed, and the oxygen produced through photosynthesis may partly offset the effects of a low oxygen concentration, as in canal water. In well-drained sand, oxygen concentrations are higher than those in water but are not likely to be as high as those in air; the gas contents of such roots reflect this circumstance, since they are lower than might be expected. It is suggested, therefore, that external oxygen concentration primarily determines the degree of development of the internal gas-space system.

**AERATING SYSTEM.**—Where subterranean roots are in an anaerobic substrate, as is most commonly the case, oxygen for root growth must come from the aerial portions. We have seen that the aerial portion is built up of a series of secondarily thickened arches supported by columns which must be the site of most gas exchange. There are several reasons for this. First, this is the zone closest to the underground roots, and the pathway for gas transport is thus at a minimum. Second, the columns have an abundant development of intercellular space, this gas space declining with distance above the substrate (which is more consistently exposed at low tide). The contrast between gas-space system in column and arch is indicated in figure 25. Third, there is a concentration of lenticels, the "portholes" of gas exchange, within the columns, their numbers declining rapidly with height above the substrate. In contrast, the secondarily thickened arches have low percentages of gas space (0.6%), few lenticels, and are farther from subterranean roots. We can reasonably conclude that the columns represent localized sites of gas exchange between air and root. The well-developed gas space of the underground system provides an effective pathway for redistribution of gas within the roots, independent of the anaerobic substrate.

Changes in the gas volume within the root due to

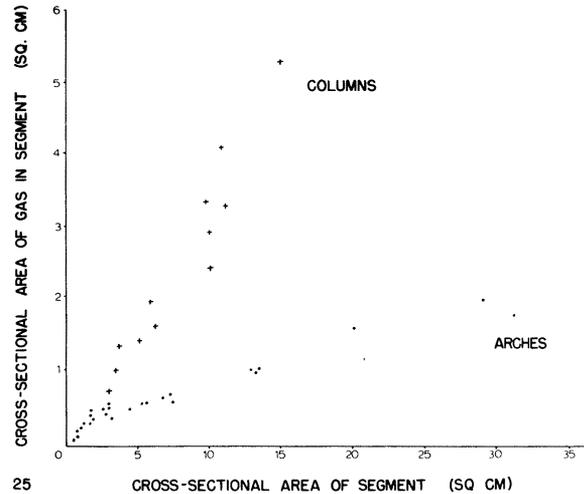


FIGURE 25. *Rhizophora mangle*. Gas-space volume in columns and arches compared; each value represented a measurement on a different segment. The method of obtaining these values is described in the text.

environment are now seen to be important. We have suggested that oxygen status is the environmental trigger in determining aerenchyma development and the bottle-shaped nature of the root columns, reflecting their gas space at different levels. This response is the most significant effect of the trigger on the anatomy of the column.

In *Rhizophora*, we have no cause to question the significance of the intercellular space system as a medium for gas transport, although this has been done in aquatic plants generally both by Williams and Barber (1961) and Crawford (1969), chiefly because it is observed that lacunae are segmented by diaphragms with a low conductivity to gases. The experiments and observations of Scholander *et al.* (1955) have, however, verified the gas-transport role of aerial roots in *Rhizophora*. These authors found that a rising tide blocked the lenticels and that oxygen content and gas pressure in the root dropped until the lenticels were again exposed to air as the tide fell. Air was sucked into the root on re-exposure by virtue of the pressure difference between the outside and inside of the root.

A mechanism based on fluctuating conditions as described by Scholander *et al.* (1955) is neither ubiquitous nor essential for gas exchange. Not all mangrove roots are tide-washed. However, it is likely that oxygen consumption in roots at some depth will enhance longitudinal diffusion. It remains to be seen if a pathway longer than 2 m (the apparent maximum depth of rooting) is too long to maintain adequate exchange.

It is noteworthy that the root system of *Rhizophora* is effectively the same as that of many other mangroves in which part of the root system projects upward from a subterranean system. This situation is illustrated diagrammatically in figure 26 with functionally equivalent parts shaded in the same way. In mangroves with pneumatophores of various types, these are connected by an underground horizontal system (lower diagram in fig. 26), and therefore only indirectly attached to the absorbing system. In *Rhizophora* the arching aerial system (upper diagram in fig. 26) links the columns (= pneumatophores) which are in turn directly attached to the absorbing system.

The distinctive property of unattached aerial roots to become branched only when injured but to proliferate numerous lateral roots when attached is peculiar. This phenomenon is not isolated, however; it has been observed in dicotyledonous trees of the Puerto Rican rainforest (Gill 1969).

Cambial activity of aerial roots at their level of attachment to the trunk largely determines trunk shape. We have seen that secondary thickening is pronounced on the upper surface of old aerial roots, such that they become ellipsoidal. Cambial activity is preferentially accentuated in favor of the upper (younger) roots at the expense of the lower (older) roots. The older part of the trunk is then thinnest, and the obconical outline of the base of the trunk is explained. Also mangrove roots which grow underground have little secondary thickening, a fact which is very evident when one examines *Rhizophora* peat which is largely made up of a primary root system. For these reasons a *Rhizophora* forest can be cleared relatively easily by a bulldozer, since the root system is easily sheared by a direct push. Storms which exert leverage to the crown are less destructive by toppling, but may be destructive by erosion (Craighead 1964).

**RHIZOPHORA IN COMPARISON WITH ACER.**—It is instructive to compare the root system of *Rhizophora* with that of a more typical dicotyledonous tree. This is done in table 2, by making a point-by-point comparison of *Rhizophora* with *Acer rubrum*, investigated in some detail by Lyford and Wilson (1964) and Wilson (1964), in such a way that contrasts are seen in each of the criteria selected. These serve to emphasize the biological uniqueness of *Rhizophora*. Many of the features shown by *Rhizophora*, however, relate to the special properties of aerial roots, as we

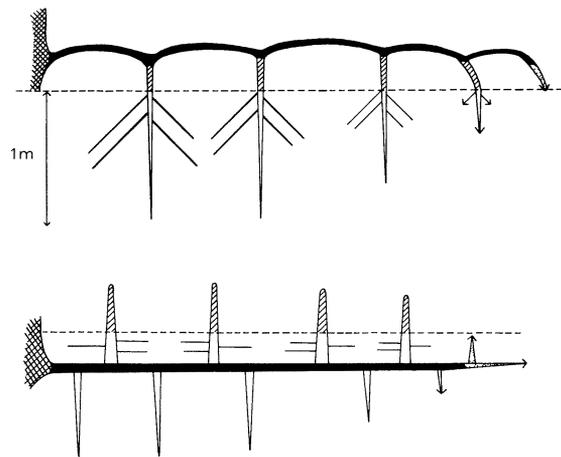


FIGURE 26. Mangrove root systems contrasted. In each the part with the same physiological function is represented by similar shading. Cross-hatched=trunk; solid black=horizontal conducting system; hatched=region of gas exchange; solid lines=feeding roots; outlined=anchoring system and support for feeding roots; stippled=growing and extending parts. Above, *Rhizophora*, conducting system is above ground, gas-space zones are columns. Below, e.g., *Avicennia*, conducting system is below ground, gas-space zones are pneumatophores.

have pointed out elsewhere (Gill and Tomlinson 1975).

The important conclusions arising out of our observations which we wish to emphasize are that the *Rhizophora* root system has a high degree of plasticity which renders it capable of adapting to changing environments. Further, the physiological roles of roots have to be understood in dynamic terms, i.e., root development is an important parameter in understanding the adaptive functions of gas exchange. Finally the control of various aspects of root expression, both morphological and anatomical, deserve more detailed and experimental investigation.

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