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PLASTICITY EXPRESSED BY ROOT GROUND TISSUES OF RHIZOPHORA MANGLE L. (RED MANGROVE)

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ABSTRACT

Roots of *Rhizophora* undergo striking changes in structure as they grow from the open air into the substrate. To test the hypothesis that darkness and oxygen deprivation are responsible for determining root form in the underground environment, above-ground roots were covered with plastic to limit gas exchange, and with foil to block out light. After 9 months growth, roots growing in darkness with restricted gas flow became swollen and branched, as did underground roots. However, in artificially covered roots, axis swelling was due to pith enlargement rather than elaboration of cortex lacunae, as occurs in underground roots. Thus, root plasticity is expressed via a different mechanism when roots are in darkness and deprived of O_2 than when they are underground. Other factors, alone or in combination, must govern development of underground *Rhizophora* roots.

Key Words: Mangrove, *Rhizophora*, root anatomy

The Red Mangrove, *Rhizophora mangle* (Rhizophoraceae) is a widely distributed tropical tree, critical to shore stability along warmer coasts, such as that of south Florida (Craighead, 1971). Its ability to stabilize coastal areas is due to the growth of conspicuous aerial roots which penetrate the substrate. Under ground, a series of striking changes occurs (Gill & Tomlinson, 1977) as roots grow from a single axis into a mass of thin, soil-building lateral roots. The underground root mass of *Rhizophora* becomes so dense that an anaerobic peat often develops.

Gill and Tomlinson (1977) review the typological literature dealing with *Rhizophra* root structure. Their studies greatly improved our understanding of mangrove roots because they stressed the changeable nature of living roots rather than treating the topic solely in terms of phenomenology. Thus, a single growing root tip of *Rhizophora* is now known to undergo drastic changes in organization and in the sort of tissue it produces during its life span.

How do field conditions induce such fundamental changes in root growth? As a root tip grows from open air into a substrate, ambient conditions important to plant growth change. Among other properties (see discussion), the subterranean environment is moist, dark, and hypoxic relative to open air. The study of root dynamics in *Rhizophora* by Gill and Tomlinson (1977) suggests that darkness and oxygen supply govern the changes in root growth which occur underground.

In this study, we test the notion that darkness and/or oxygen deprivation are responsible for the characteristic growth form of underground mangrove roots. Attempts are made to simulate underground conditions around root tips which are still above ground (aerial). Aerial tips were deprived of oxygen or light, or both, and allowed to grow 9 months before being anatomically examined. We predicted that if low O_2 or darkness was in fact responsible for the underground growth form, our simulated conditions would produce an underground growth habit in spatially aerial roots. On the other hand, if no change in root form occurred, or if a form developed which differed from that of underground roots, then some other environmental condition(s) must influence growth of *Rhizophora* roots in the substrate.

MATERIALS AND METHODS

Experiments were performed on a natural stand of *Rhizophora* (2-4 meters tall) growing in oolitic sand on the tropic of Cancer. Hummingbird (Jewfish) Cay, seven miles west of Great Exuma, Bahamas, was the study site. On trees of the study population, aerial roots grew from 1-3 mm per day from July 1981-March 1982.

In an attempt to duplicate the dark, moist, subterranean conditions, tips of aerial roots were covered. Four sets of roots were studied (3-5 roots/set). Tips (20 cm) of one set were capped by polyethylene bags which were then filled with fresh water. This set of roots grew for 9 months with a restricted gas flow (due to the plastic covering), and with natural illumination (Fig. 1). Tips of another set were likewise covered with water-filled bags but in addition, each root tip was wrapped with aluminum foil to block out sunlight. This set grew with restricted gas flow and in darkness (Fig. 1). Two other sets were untreated; one set was of aerial roots in the open air, the other was of underground roots (Fig. 1).

At the end of the 9-month growth period, root tips were collected, fixed in FAA, and sectioned for study. Only portions produced by the main root axis during these 9 months were sampled. Anatomy was studied using hand sections, stained in 0.1% toluidine blue and mounted in glycerine. Measurements were made using a calibrated ocular micrometer.

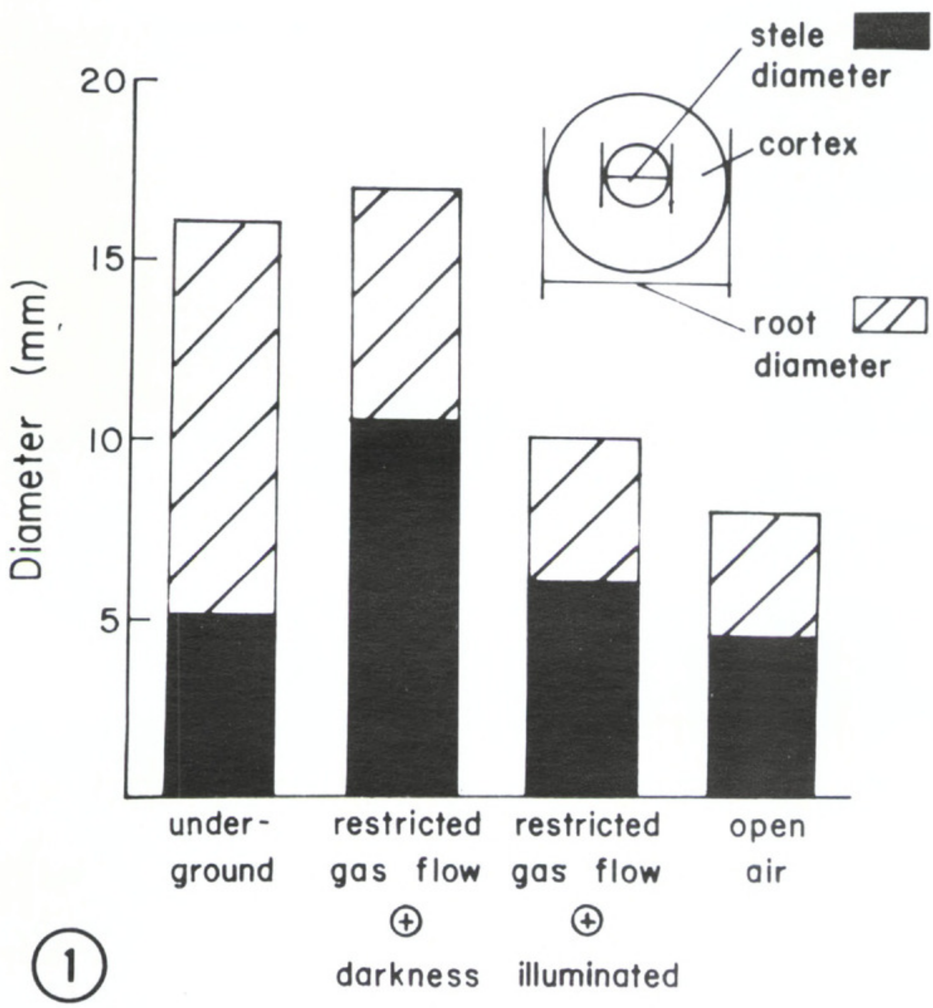


Figure 1. Cross sectional topography of *Rhizophora* roots grown 3 months under conditions indicated. Each bar represents an average derived from 3 to 5 samples. In all cases, standard error is less than 10% of the mean.

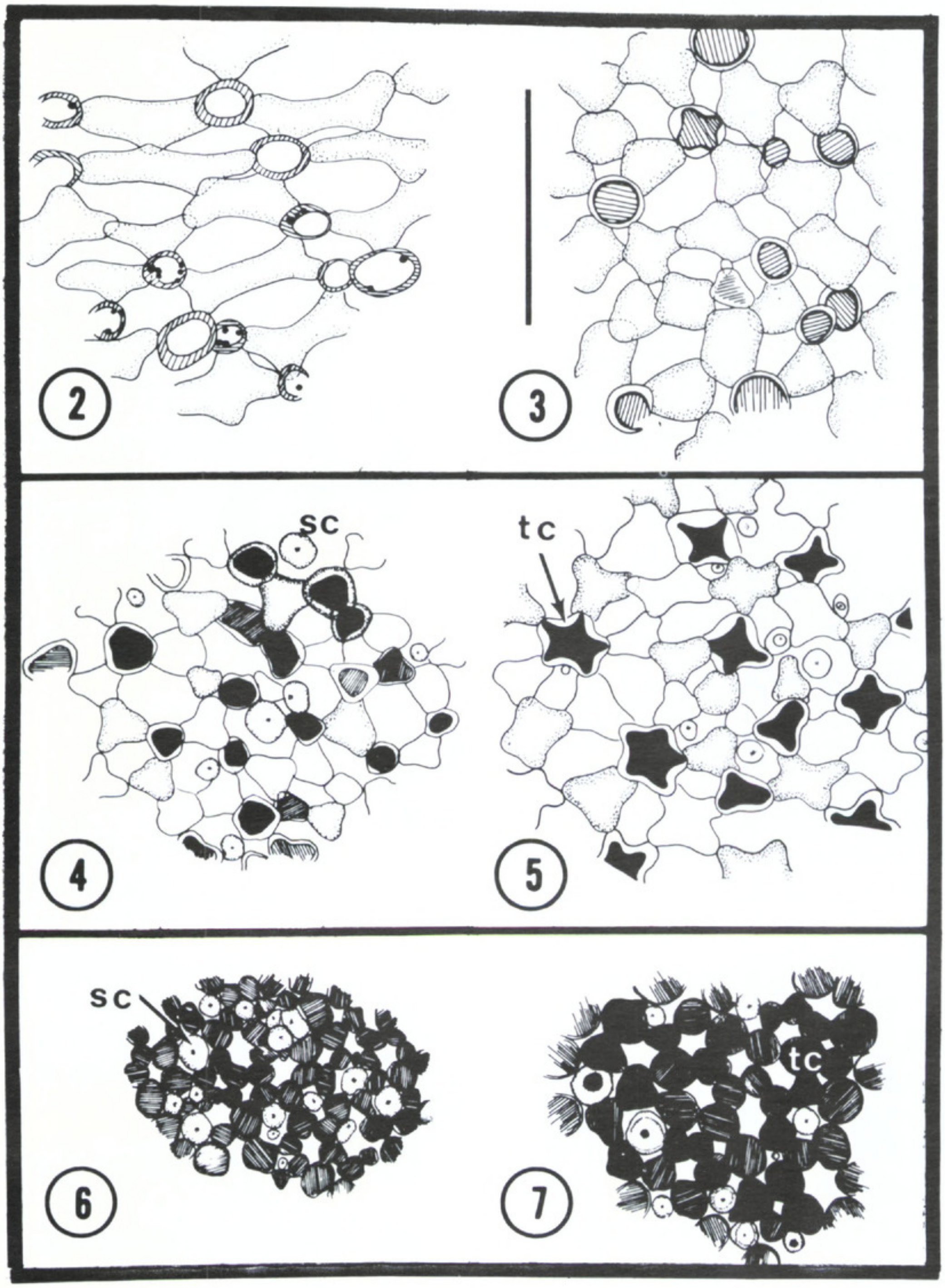
RESULTS

As previously shown by Gill and Tomlinson (1971; 1977) *Rhizophora* root structure changes dramatically as a root grows from the air into solid substrate, which at our study site is oolitic sand. Embedded in oolite, *Rhizophora* roots become twice as wide as aerial root axes (Fig. 1). Underground roots branch and show the diagnostic anatomy recently described (Gill & Tomlinson, 1977). Our attention is focused on the ground tissues (parenchyma of the cortex and pith). In the wide underground roots, 70% of the diameter is occupied by cortex, in contrast to 40% in the cortex of aerial roots (Fig. 1). Both cortex and pith are composed of vacuolate parenchyma cells (Figs. 2 and 3). Interspersed among them are cells filled with tannins and/or oil droplets. Tanniferous cells remain isodiametric, unlike the other parenchyma cells which stretch radially forming a system of intercellular spaces. In the cortex, these spaces average twice as wide (115 μm) as those in the pith (57 μm). The spaces are formed by radial elongation of cortex cells; cell-to-cell contact is maintained by conspicuous arm-like extensions of the cell wall (Fig. 2). Cells of the pith do not stretch as much as those of the cortex (Fig. 3), with the result that the gas spaces formed in the pith are smaller than those in the cortex. Trichosclereids occur only in the inner cortex.

Of the artificial growth conditions used, the combination of restricted gas flow and darkness produces roots that most resemble underground roots. Like underground roots, their diameter is over twice that of untreated (control) aerial roots (Fig. 1). However, it is the stele rather than the cortex which takes up over 60% of the root diameter (Fig. 1). In this case, intercellular spaces in the pith are on the average larger (70 μm) than those of the cortex (40 μm). Extended arms are more developed in pith parenchyma (Fig. 5) than in the cortex (Fig. 4). Trichosclereids occur in both pith and cortex. Untreated aerial roots have a narrow axis (Fig. 1). Small (19 μm) gas spaces occur in both the cortex and pith (Figs. 6 and 7). Trichosclereids are found throughout, as detailed by Gill and Tomlinson (1971).

DISCUSSION

The aim of our work was to determine the environmental cues responsbile for altering root development as the root tip grows form



Figures **2-7**. Camera lucida drawings of ground tissues in *Rhizophora* roots. **2**. Cortex of underground root. **3**. Pith of underground root. **4**. Cortex of root with restricted gas flow + darkness. **5**. Pith of root with restricted gas flow + darkness. **6**. Cortex of aerial root. **7**. Pith of aerial root. tc, tannin cell; sc, sclereid. Scale bar = 250 μm for all figures.

open air into the substrate. At first glance, roots covered for 9 months with plastic plus foil come to resemble underground axes. We were surprised to find, however, that this shift in morphology occurred via a different mechanism than any previously reported for *Rhizophora*. Like the underground root, the axis of roots wrapped in plastic and foil does swell and lateral roots develop. However, it is the *stelar* ground tissue (pith) which generates axis swelling in experimental roots (Figs. 1 and 5), unlike truly underground roots which swell via cortex enlargement (Fig. 1 and 2). This is a new example of the great plasticity of *Rhizophora* roots which allows them to contend with sudden shifts in ambient conditions. In terms of our intial hypothesis, it is clear that darkness and O_2 deprivation are not solely responsible for altering root form as apices grow under ground. If they were, roots with plastic and foil would have developed as do underground roots. Since they did not, other factors must influence development of underground roots.

Many aspects of the rhizosphere change as *Rhizophora* roots penetrate the substrate, and not all of them are obvious. Long considered have been differences in moisture, light, and O_2 levels between the aerial and underground environments. More recently, the significance to root biology of abrasion and pressure, buffered temperature regimes, soil microbes (Zuberer & Silver, 1979), and gas diffusion rates have been studied. These factors and others, such as altered nutrient availability, are known to strongly affect root development (Ellmore, 1982). For example, Drew, et al. (1979) found that a buildup in ethylene gas, rather than a depletion of oxygen, causes lacuna formation in flooded roots of *Zea*. This raises the possibility that underground *Rhizophora* roots may develop in response to increases in gases which would normally be carried away in a less confining environment. Interestingly, other aquatic plants such as *Ludwigia* (*Onagraceae*) develop lacunose tissue without producing large amounts of ethylene (Ellmore, 1981). *Rhizophora* resembles *Ludwigia* inasmuch as root lacunae develop by cell stretching rather than by the cell death seen in flooded *Zea*. Thus, it is not at all certain whether the ethylene requirement shown by *Zea* roots also applies to *Rhizophora*.

As stressed by Gill and Tomlinson (1977), the *Rhizophora* habitat is highly variable, and our results show that the stele as well as the cortex can respond to changing conditions. Knowledge of root biology (Ellmore, 1982) has advanced to the point where a quantitative assessment of factors influencing *Rhizophora* root growth is needed. Future studies should first measure morphogenetically active components of the mangrove rhizosphere, then go on to test the effects of these components on mangrove root growth under controlled conditions. Such studies may go on to pave the way to controlling the destruction of mangroves which are essential to coastal stability throughout the tropics.

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