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Evidences of self planting propagules of *Rhizophora mangle* L.

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Abstract: The authors of the 19th century had demonstrated the viviparity of the species *Rhizophora mangle* L. with the formation of propagules in the form of spears devoid a radicle, adapted self-planting in the soil of the mangrove or to leave floating in vertical during the high tide. With low tide the propagules self-planting or remain prostrate on the soil but later become upright later. When the seedlings are unearthed, those who are self-planting are straight from end to end; those that stood erect later show a curvature at the base in the form of J (J-shaped). Authors of the last 30 years have questioned the self-planting and accurately demonstrate how the prostrate propagules rise from the ground. It has been verified that the propagule is stem from end to end and does not present radicle, that is, under the plumale there is the hypocotyls without a root. All roots are adventitious, agreeing with 19th century researchers, not lateral roots as researchers of the present century have claimed. Propagules that return to the beach in Porto Seguro (BA) probably of another flowering period show an extra growth of the lower part, but this growth remains a stem rather than a root, demonstrating that there is no root, as 19th century researchers claimed.

Key words: propagule, Rhizophore, mangrove, plant viviparity.

INTRODUCTION

The growth of the cotyledonary part of the embryo push opposite through the micropyle, the two cotyledons cease growth almost completely and the hypocotylar growth begins, pushing through the distal end of the ovary (Cook 1907). The hypocotyl carrying also the plumule separates from the cotyledons and, falls to the ground, while the ovary, containing the integuments and the cotyledons, remains hanging on the tree.

The seedling develops mainly by elongation of the hypocotyl, forming the so-called **propagules** (Tomlinson and Cox 2008). Davis (1940) noted that the hypocotyls are more frequently curved than straight, and many of them are neither sufficiently straight nor fall with sufficient force to self-plant themselves in the soil. But he does not mention how the seedling succeeds self-erecting for further growth.

Seed germination in Rhizophoraceae has been classified (Ng 1978, Juncosa and Tomlinson 1988) as “Durian-germination”, characterized by substantial hypocotylar development in contrast to the relatively static and concealed cotyledons. Juncosa and Tomlinson (1988) suggest that this is an evolutionary modification from an ancestral epigeal germination type.

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La Rue and Muzik (1951) stated that the propagules fall from the tree and plant themselves in the soil like little spears. Rabinowitz (1978) reported that the propagules could form roots in two ways, either by self-planting or after lying prostrate, although she had the opinion that the latter was more common. For this author, large propagules of *Rhizophora* could become free-floating after an initial period of embedding. Such a tendency to become free-floating, perhaps for a second time after falling, could facilitate long distance dispersal after some weeks if fixation below the mother plant was unsuccessful. Davis (1940) noted that since the propagules float in vertical, they penetrate the substrate by abrasion of their acute apex.

Observations made in Miami, Florida by Lawrence (1949) revealed that the propagules of *Rhizophora mangle* usually lie horizontally after falling and gradually become erect by means of a strong curvature of the lower region of the hypocotyl. This author searched for erect seedlings recently shed from the mother plants but found only propagules lying horizontally on the substrate. Only older seedlings were seen as established and erect, with lateral roots developing within the mud, but these seedlings showed the formation of a right angle in the lower part of the hypocotyl. Similarly, Egler (1948) suggested that the propagules land in a horizontal position, root and then become erect by their own growth. He found J-shaped propagules which indicated that they had become erect after rooting.

According to Tomlinson and Cox (2008) this explanation of how the seedling acquires a vertical position after becoming rooted in the substrate differs substantially from the frequently repeated statement that the pendent seedlings fall like little spears into the mud and thus establish themselves directly as erect. For these authors, Egler (1948) described all essential aspects of seedling establishment, including hypocotylar hook formation and development of a roughened surface, except he did not explain the mechanism for the formation of the hook. The hook is the curvature uniquely produced by self-erection.

Tomlinson and Cox (2008) considered that the conventional self-planting explanation seemed unlikely for viviparous seedlings. They verified that control seedlings, vertically planted without support and with the distal portion (which they called the radicle) buried to a depth of ca. 2.5 cm, underwent no curvature and did not form a hook. Experimental seedlings were partially buried more-or-less horizontally but at an angle of ca. 15° to the soil surface. The authors give a very clear explanation of how self-erection took place in these seedlings, by the formation of a hook and of reaction wood mechanism.

It is important to note that Tomlinson and Cox (2008) cast doubt on the notion of "self-planting" (their quotes) reported previously by a large number of authors,"championed by La Rue and Muzik (1951)" (mine quotes), i.e. the idea that the elongated viviparous seedlings of *R. mangle* are exclusively adapted to self-planting by falling vertically into the mud below the mother plant.

La Rue and Muzik (1951) studied the seedlings of *R. mangle* (N.B. they called their plant "black mangrove" but this common name usually refers to *Avicennia germinans,* while *R. mangle* is most generally known as "red mangrove") in an attempt to resolve doubts about whether the seedlings really succeed in self-planting. They counted erect self-planted seedlings in three typically muddy mangrove sites and also those seedlings which had fallen horizontally and had self-erected by curvature of the lower part of the hypocotyl. In the three sampled populations they found straight seedlings in 96 out of 100 cases (and 4 curved seedlings) in Lot A, 48 straight seedlings out of 50 cases in Lot B and 131 straight seedlings out of 138 cases in Lot C. The authors thus demonstrated a very high percentage of self-planted seedlings lacking curved lower hypocotylar regions.

Davis (1940) observed that propagules planted 12 months after falling from the fruit were still able to grow. Likewise, La Rue and Muzik (1951) showed that 68 days after falling from the fruit, the propagules had lost one third of their weight but grew when planted.

Warming (1883) hypothesized that the embryo must produce a large number of roots in order to become fixed as rapidly as possible and believed that these rootsmust develop within the hypocotyl when still attached to the mother plant. He showed the presence of two root primordia in longitudinal sections of the lower apex of the hypocotyl (Warming 1883, plate IX, X, Fig. 25); he called these **adventitious roots primordia** in the absence of the root apex, i.e. the hypocotyl should be considered entirely as a stem axis, even in the lower apex.

Casting doubt on Warming's (1883) results Gill and Tomlinson (1971), noting that he had worked with material collected six months previously in Cuba and preserved in fixative, whereas they worked only with living plants (and thus with recently collected propagules). Warming's figure shows one of the adventitious root primordia exactly located at the lower apex of the hypocotyl, at the extremity of the vascular system where the radicle's pro-meristem would be situated. The important point is that Warming defined these primordia as originating from the stem, and thus giving rise to **adventitious roots**, whilst Gill and Tomlinson (1971), Juncosa (1982), Tomlinson and Cox (2008) and others defined them as **lateral roots** and thus arising from the root.

Menezes (2006) showed that the so-called "stilt roots" or "prop roots" in *R. mangle* of previous authors are in reality stems with positive geotropism, which she called **rhizophores**. For this author, the propagule constitutes the **primary rhizophore** from which arises through its development the aerial axis which in turn gives rise to **secondary rhizophores**, termed **aerial roots** by other authors. Besides this, Menezes (2006, Fig. 6) demonstrated the presence of two adventitious roots at the extremity of the secondary rhizophore, which would not be admissible if it were in reality a root apex.

Warming (1883) stated that the development of adventitious roots preceded the development of the shoot bud in the seedling and that these roots are all terrestrial earth roots. Chapman (1976) also mentions this kind of precocious root development, citing Krause (1885, *apud* Chapman 1976).

The origin of root apical meristem, which Juncosa (1982) called the **primary root**, is an anomaly in the embryo development of *R. mangle*, since it develops in the interior of an undifferentiated embryo tissue instead of at the junction of the embryo with the suspensor. In his view, the radicular meristem appears rather more immersed in the embryo tissue than in the majority of plants he had studied up to that time. He described a region of cells at the lower apex of the embryo as the **terminal cortex** and interpreted the large cluster of stone cells which differentiated later on within its interior as protection for the meristem when the seedling falls from the tree. But this author did not call this region a **root cap**.

Furthermore, Juncosa (1982) considered the radicular apex which appeared "immersed" in the embryo to be practically inactive, but the roots that he called lateral appear early in seedling development. He cited Warming (1883) and Karsten (1891) in support for the idea that the radicle is non-functional. Tomlinson and Cox (2008) admit that the radicle has a limited development and that in *Rhizophora* it is almost always aborted. Even so, they referred to the **adventitious roots** i.e. originating from stem of Warming (1883) and Karsten (1891) as **lateral roots**, i.e. originating from roots.

The objective of the present study is to present new information on seedling development, with a focus on the characteristics of the lower region of the hypocotyls and to confirm the genuine seedlings self-plantings in *Rhizophore mangle*.

MATERIALS AND METHODS

Specimens of *Rhizophora mangle* L. were collected in mangrove vegetation at Porto de Galinhas (Pernambuco), at the Camboa beach (N.L. Menezes- 1426- SPF) and at Porto Seguro (Bahia) at the Taperapuã beach (N.L. Menezes- SPF-124080). From the specimens collected in Porto Seguro, propagules with later growth from the lower apex were fixed in FAA for paraffin embedding and serial sectioning following dehydration using a tertiary butanol series (Johansen 1940). The sections were stained with astra blue and safranin (Bukatsch 1972).

RESULTS

In Porto de Galinhas (Pernambuco, Brazil) numerous recently fallen seedlings of *Rhizophora mangle* can be observed distributed among the rhizophores (Figs. 1a and 1b) of mature plants. Most of these are self-planted as can be seen in Fig. 1b, because the majority are straight, with a few which failed to self-plant and later became erect. The propagule, when ready to fall (Fig. 2a), has the appearance of a spear, but prior to this it passes through stages in which it exhibits a curved shape (Fig. 2b). In this figure various fruits can be seen in which the propagules are beginning to appear. Those propagules which fail to embed themselves in the substrate become erect later on (Fig. 2c) as a J-shaped plant (Fig. 3a, left). The seedlings in Fig. 2d, one month after the propagules had fallen, are also evidently self-planted. Seedlings (Fig. 3a) taken from the same locality as those of Figs. 1a and 1b are also self-planted, except for the seedling on the left-hand side which failed to self-plant and

Figure 1 - (a-b): *Rhizophora mangle* in Mangrove on sandy soil at Porto de Galinhas (Pernambuco, Brazil). Aerial branches with rhizophores (solid triangles) with numerous plantlets (at the arrow head), magnified in **b**.

is curved at the base (J-shaped). The formation of adventitious roots at the lower extremity of the propagules can be seen (Fig. 3b) and these roots are formed right up to the apex of the propagule, as can be seen in Figs. 3c and 3d. Figure 3e shows a schematic longitudinal section of a propagule in which two **adventitious root primordia** can be observed, one of which is situated right at the lower extremity of the vascular system. Many of the propagules which do not succeed in establishing themselves are carried away by the tide, and when they return to the shore they can exhibit an extra growth from the lower apex (Fig. 3f) which is usually turned towards the upper tip of the propagule. The region which has undergone this later growth phase exhibits stem- anatomy from its apex to the growth point (i.e. the basal part of the

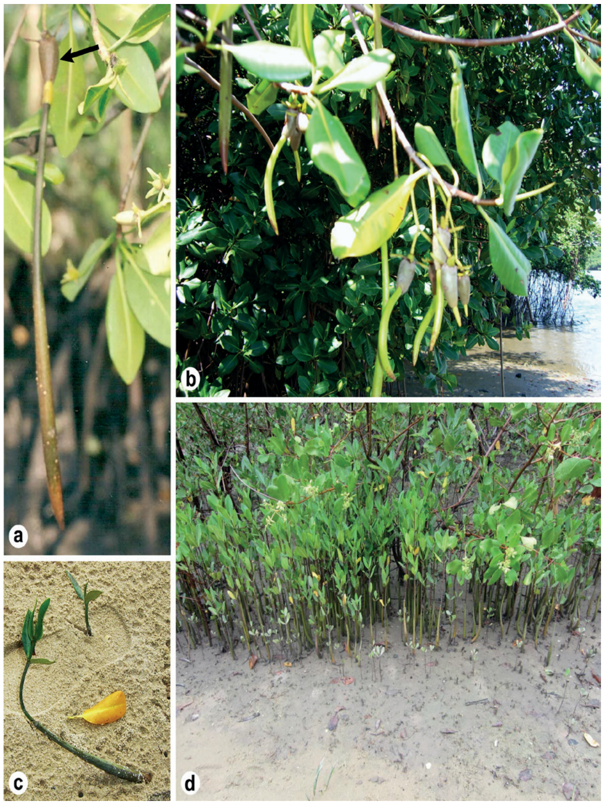

Figure 2 - (a-d): *Rhizophora mangle* at Porto de Galinhas. **a** - Mature propagule still attached to the fruit. **b** - Fruits with developing embryos at different stages. **c** - plantlet/ resulting from a prostrate propagule. **d** - plantlets one month after rooting by self- planting.

propagule) as can be seen in cross sections (Figs. 4a-d), with a wide medulla and vascular bundles with endarch protoxylem; fascicular cambium (C1) is formed within these bundles and an inter-fascicular cambium (C2) is formed between them. It is also notable that phloem strands are formed in two places, those corresponding to the bundles (Ph_1) and those formed between the bundles (Ph_2). Trichosclereids (Tr) can be observed both in the medulla and in the cortex.

DISCUSSION

The branch system responsible for the nutrition and physical stability of *Rhizophora mangle* in the muddy substrate of the mangrove habitat, rather than a system of "aerial roots", is in reality a system of cauline branches with positive geotropisim, as demonstrated by Menezes (2006). Arguing this case led the author to compare *R. mangle* to the Lepidodendrales of the Carboniferous, with its bipolar branching system: aerial branches which produce leaves and basal branches (rhizophores) which produce roots (Stewart 1983). For this reason the present author has termed as **rhizophores** the cauline basal branches of *Rhizophora* **with positive geotropism**.

Furthermore, as demonstrated by Menezes (2006), the generic name *Rhizophora* is due to the fact that the authors accepted that the root is situated at the tip of an axis (the hypocotyl of the propagule) to which they gave the name rhizophore (from Greek riz(o) = root, phoro = the bearing axis), i.e. the axis which carries the root.

Initially, Menezes (2006) accepted that the hypocotyl and the cauline branches ("aerial roots") that she called **rhizophores** were different. However, after having been unable to find a radicle at the tip of the hypocotyl, this author concluded that they are similar structures wich she termed the **primary rhizophore**.

In the present study, it was possible to confirm (or contest) the observations of other authors regarding this mangrove species.

In the first place, the work of La Rue and Muzik (1951) was completely corroborated. Their results were surprising at the time; they presented indisputable evidence of self-planting in propagules of *Rhizophora mangle*, which is also demonstrated here in the mangroves of Porto de Galinhas, Perbambuco, Brazil.

The soil of this mangrove area is sandy, such that it is possible to walk without difficulties among the plants, and self-planting is effective in the sand. Although, there are no quantitative estimates of the proportion of successfully self-planting propagules produced by a tree which. The same is true of the mangroves of the rest of northeast Brazil. In the southeast (São Paulo, for example) the mangrove

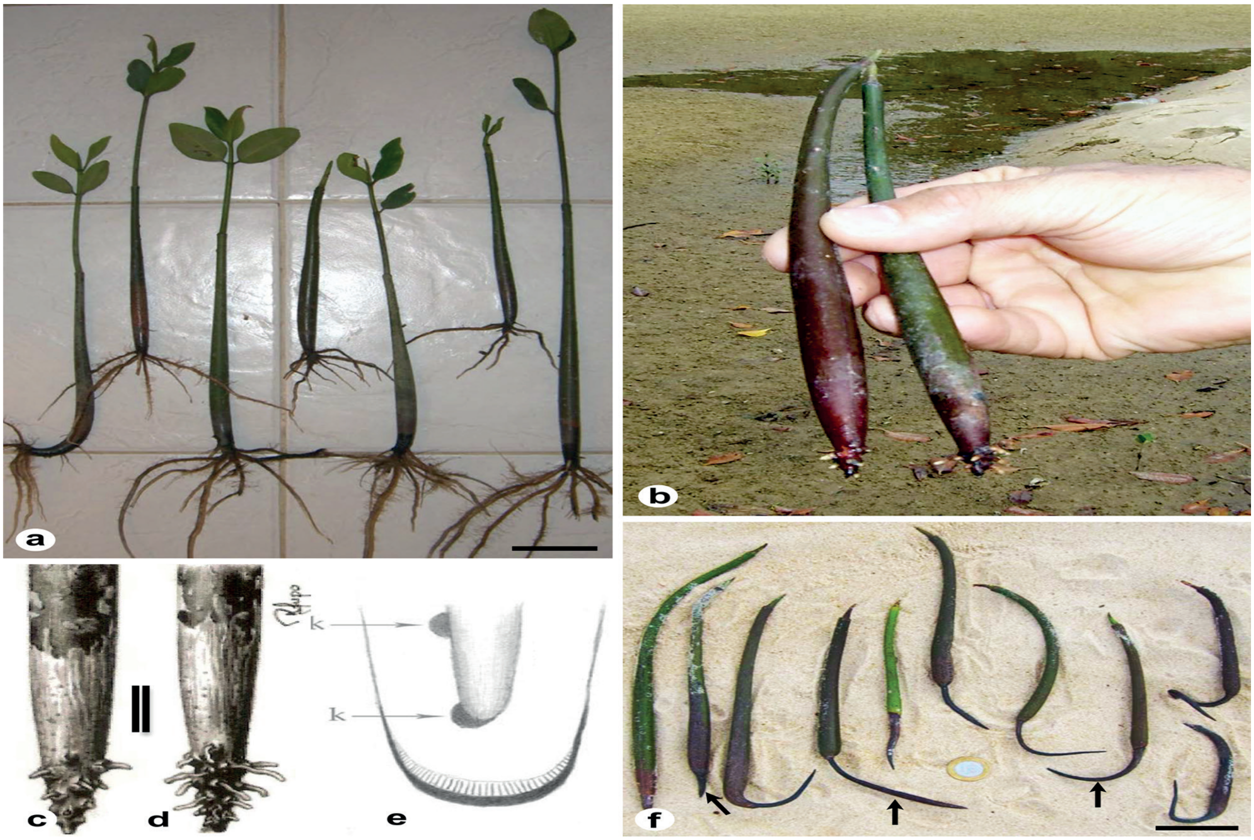

Figure 3 - (a-f): *Rhizophora mangle* at Porto de Galinhas (**a-d**) and at Porto Seguro, Bahia (**f**); - J-shaped plant (on left) and six self-planted (straight) ones. **b - d** - Self-planted propagules, with the beginning of adventitious root formation; **e** - Copy of Fig. 25 - i. Plate IX-X from Warming (1883); **f** - Propagules washed up on the beach at Taperapuã, showing later growth from the lower apex (arrows).

is extremely muddy and the difficulty of walking through it is such that it is common to lose one's rubber boots through becoming stuck fast in the deep muddy substrate.

In Porto de Galinhas, of the 20 seedlings removed from the soil, 18 were straight and two had hook formation in the lower part (J-shaped). In the mangrove of Bertioga (São Paulo) the only propagules which do not self-plant are those which fall when the tide is coming in or on the ebb. For Tomlinson and Cox (2008) to have doubted the results of La Rue and Muzik (1951) it seems almost certain that the mangrove where they made their observations must have had very different soil conditions to those of the sites we have studied in Brazil or which were studied elsewhere by the latter authors, and by Rabinowitz (1978) and Davis (1940).

In both Porto de Galinhas (Pernambuco) and Porto Seguro (Bahia), the present author observed that those propagules which did not establish themselves after falling were carried away by the tide, and may return to the shore after another flowering time with an extra growth which represents a prolongation of the lower apex. If there existed a radicle the structure of this axis would correspond to a root. However, as demonstrated here, it exhibits a wide medulla and vascular tissues (xylem and phloem) forming bundles with endarch protoxylem, characteristic of stem.

This cauline structure is exactly the same as that described by Menezes (2006) for secondary

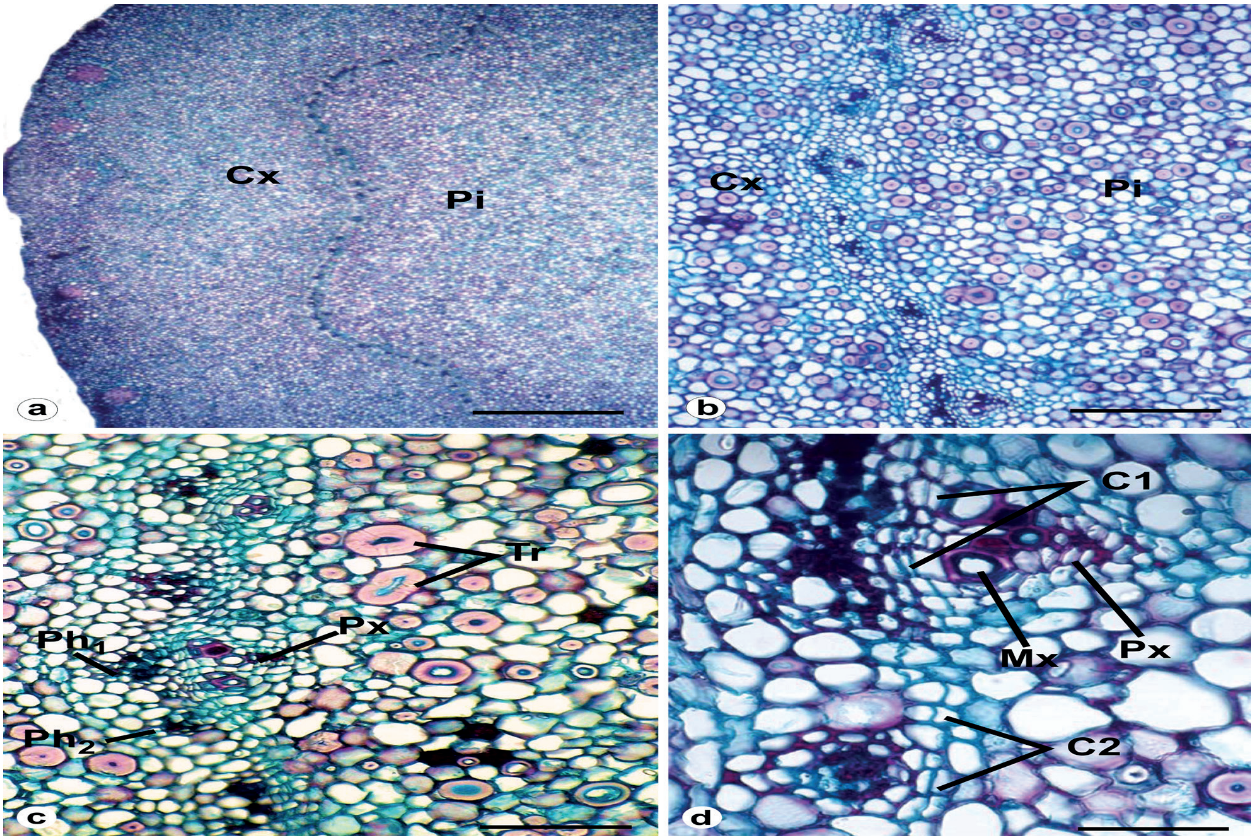

Figure 4 - (a-d): *Rhizophora mangle* - Transverse sections in the region indicated by arrows in figure **3f** - The cauline nature of the structure can be seen with a broad medulla (Pi) and a less well-developed cortex (Cx), with vascular bundles composed of phloem (Ph_1) and xylem with endarch protoxylem (Px). Phloem strands (Ph_2) can be observed between the bundles. C1 - fascicular cambium; C2 - interfascicular cambium; Mx-metaxylem; Tr-trichosclereid.

rhizophores, that is to say, it has stem bundles with intercalary phloem independent of the xylem, indicated by the author (in that publication) as Ph_2 in Figure 18, while the phloem of the vascular bundle is indicated by Ph_1, as in the hypocotylar prolongation studied here.

There is no doubt that the hypocotyl corresponds, throughout its length, with a stem, as stated by Warming (1883), and confirmed by Menezes (2006), who called that seedling hypocotyl a **primary rhizophore** and the so-called "aerial roots" **secondary rhizophores**, since both structures are stems in nature while exhibiting positive geotropic growth. This position contradicts that argued by Tomlinson and collaborators; for example Gill and Tomlinson (1971) argue that the aerial structures which stabilize the plant in the muddy substrate (Warming 1883, Karsten 1891 and Menezes 2006) are an exceptional type of root because of their **stem-like** characters.

It is noteworthy that Warming (1883) and Karsten (1891), aware of the absence of the root in the lower apex of the hypocotyl, call the roots which arise in this region **adventitious** rather than **lateral**, as termed by Juncosa (1982) and Tomlinson and Cox (2008).

Warming (1883), in his magnificent work, demonstrated the presence of an adventitious root primordium right at the lower apex of the hypocotyl, in a position that would not be possible if the apex were that of the root. It can be seen from Fig. 25 of plates IX and X in Warming's study (reproduced here) that the lower apex of the propagule is really cauline, and that the roots arising from the two primordia are adventitious, as shown by him. No root would form lateral root primordia in at the top of its meristematic region.

The primordium of a lateral or adventitious root develops exclusively from the pericycle of the root or stem respectively. Menezes (2006) demonstrated that in the secondary rhizophore apex there are only procambial strands and no promeristematic region. And there is a terminal cortex between this region and the epidermis, as demonstrated by Juncosa (1982).

In the embryo development of *R. mangle*, the origin of the apical meristem from the radicle within the undifferentiated embryo tissue, instead of at the junction of the embryo with the suspensor, was seen as an anomaly by Juncosa (1982). He considered that the radicular meristem appeared rather more immersed in the embryo tissue than in the majority of plants studied by him. In addition, he referred to the presence of a "terminal cortex" separated from the surface of the meristematic apex (which he termed radicular) by a large cluster of included stone cells.

Furthermore, Juncosa (1982) remarks that "The immersed radicle apex is practically inactive but lateral roots early appear in seedling development". For Tomlinson and Cox (2008) "the radicle shows a limited development and almost always in *Rhizophora*, and commonly in other taxa it aborts without further growth".

Juncosa's (1982) statement that the radicle meristem is "immersed" in the embryo and that there is a "terminal cortex" will be discussed in a future study on embryo development in *Rhizophora mangle* which the author will demonstrate that this "immersed" meristem is in fact cauline rather than radicular.

The apical extra growth of the propagules washed up on the shore at Taperapuam (Porto Seguro, Bahia) is a further confirmation of this position. Within the apical prolongation are found the trichosclereids that are found exclusively in the erect stem and in Menezes' secondary rhizophores.

In the roots the thickening of the the cortical cells, termed Warming Cells by Menezes (2006) after Warming's (1883) first description of them, are completely different from trichosclereids.

Evans et al. (2005), in a study of the movement of air within the root of *Rhizophora mangle*, demonstrated notable characteristics in the anatomy of the "aerial root" which distinguish it from the roots that develop within the muddy substrate. They state that the "stilt roots" of mangrove plants do not exhibit a typical dicot root anatomy. For example, roots do not have a central triarch or tetrarch arrangement of vascular tissues but resemble more the structure of a stem. The centrally located inner aerenchyma area resembles pith of stems".

Groff and Kaplan (1988) considered that researchers and teachers of botany were unduly influenced by the prevailing paradigm that the dicotyledonous embryo is always bipolar, with the root and shoot systems meeting only in the hypocotyl. According to these authors, Goebel (1905) criticized this model in 1930 as a generalization for all plants and proposed in its place the concepts of **allorrhizy** (referring to the bipolar embryo model) and **homorrhizy**, referring to plants lacking bipolar embryos in which all the roots develop from stems, as in ferns, and are therefore all adventitious.

Troll (1949) referred to allorrhizic plants as **allorrhizophytes**, describing them as capable of forming a root system consisting of a primary root (derived from the radicle of the embryo) and its lateral branches. On the other hand in a typical **homorrhizophyte** (homorrhizic of Goebel) as for example *Lycopodium* and the ferns, all roots excluding the first root of the embryo arise on the sporophyte stem and are therefore adventitious.

As shown by Menezes (2006), there is a very exact correspondence between the habit of *R. mangle* and the Lepidodendrales of the Carboniferous, i.e.

a bipolar cauline axis: aerial branches from which leaves develop and basal branches from which roots are formed (Stewart 1983). The basal branches are **rhizophores** and both taxa, *Rhizophora mangle* and the Lepidodendrales, fit within the categories of Goebel (1905) and Troll (1949) as homorrhizic or homorrhizophytes respectively. All the roots are **adventitious**.

The results of the present study make it possible to show that Warming (1883) and Karsten (1891) were correct when they defined as **adventitious** the roots that arise on the lower apex of the propagule of *Rhizophora mangle*. It therefore follows, as argued here, that the propagule of *R. mangle* is entirely cauline in nature.

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