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Seedling Morphology of Three Mangrove Species and Its Taxonomic Implications

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Seedling establishment is an important part of the life cycle of mangroves. Very early in the juvenile stage, they face adverse situations such as a variable and unstable substrate as well as a high-saline environment. Therefore, the propagules should have some ability to float in saline water. Seedlings differ morphologically from the adult plants. Here, I examined the seedling growth stages in three species of mangrove: *Aegialitis rotundifolia* Roxb., *Aegiceras corniculatum* (L.) Blanco, and *Avicennia marina* (Forsk.) Vierh. that grow in the Sundarbans swamps of West Bengal. In all cases, fruits were the propagating units; seeds were inseparable from those fruits. Germination was rapid and required no dormancy period. The hypocotyl pierced the seed coat rather than emerging from the pericarp -- a variation on the traditional viviparous type of germination. Seedlings then became exposed prior to abscission from parent plants. Based on germination patterns and differences in seedling morphology observed here, these species should be classified in a more relevant taxonomic group than was done previously.

Keywords: cryptovivipary, Mangrove, seed germination, seedling morphology

Seedling establishment and propagation are the most important stages in the mangrove life cycle. In particular, the young plant must be protected as it begins to develop in an unstable, variable substrate with a saline environment that is regularly influenced by the tides.

In addition to its several other morphological peculiarities, the seed germination pattern of the mangrove taxa differs remarkably from other mesophytes. The particular pattern found in *Aegialitis rotundifolia, Aegiceras corniculatum*, and *Avicennia marina* is an adaptive feature for avoiding high salinity during germination (McMillan, 1971; De Vogel, 1980). Although the traditional pattern of seed germination may occur sometimes, a unique morphological feature of most mangroves is a germinating hypocotyl that either 1) pierces the seed coat and, ultimately, the fruit wall before dispersal (i.e., vivipary, as in Rhizophoraceae), or 2) grows out of the seed coat rather than from the fruit wall, before abscission (i.e., cryptovivipary, as in *Aegialitis*, *Aegiceras*, and *Avicennia*). These mechanisms are interpreted as serving to 'protect' the juvenile embryo from the deleterious effects of high saline concentrations until maturity. This is necessary because most propagules spend some time in seawater before becoming established, and must gradually adjust to their saline environment.

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Because some distinct morphological changes occur between the seedling and adult stages, they are very relevant for determining seedling taxonomy. The majority of mangrove seedling research has dealt with aspects of their development, physiology (Pannier and Pannier, 1975; Juncosa, 1982; Werner and Stelzer, 1990) and ecology (Rabinowitz, 1978a, 1978b; Clarke and Myerscough, 1991, 1993). Early morphological studies, though providing mostly accurate structural features, were not comprehensive. De Vogel (1980) published an elaborate work on seedling morphology, making classifications based on germination patterns and seedling characters, and emphasizing the degree of specialization in the family Rhizophoraceae. However, those classifications were not adequate for the taxa studied here. Likewise, Tomlinson (1986) provided an overview of the mangrove seedling morphology, commenting that basic biological features were not well appreciated.

Although various aspects of mangrove seedlings have been investigated, as mentioned above, the present work is an attempt to provide a few missing morphological details, and to clarify certain disputed points of more appropriate taxonomic consideration.

MATERIALS AND METHODS

Mangrove seedlings of three species, *A. rotundifolia*

Roxb. (Plumbagenaceae), *A. corniculatum* (L.) Blanco (Myrsinaceae), and *A. marina* (Forsk.) Vierh. (Avicenniaceae), were collected from the mangrove swamps of Sundarbans, West Bengal. Their respective mature fruits also were gathered and grown in-vitro to ensure correct species identification and to observe gradual morphological changes during different stages of development. Descriptions of the seedlings were made according to Duke (1965), Bokdam (1977), and De Vogel (1980). Because their morphology may change at relatively short intervals, the seedlings taken from both the laboratory and the natural habitats were observed. Relative growth of individual seedling parts was expressed as "slightly elongating", "elongating", and "strongly elongating" for lengths that were <2 cm, 5 cm, and >5 cm, respectively. Illustrations were made of particular anatomical characters during seedling development, and measurements were taken of various parts of each seedling.

RESULTS

For all the investigated taxa, the propagule is defined as a fruit with a germinated hypocotyl. The seedling is described as the most juvenile plant, whose morphological characters usually differ from the adult. Detailed morphological descriptions for the various growth stages follow:

A. rotundifolia Roxb. (Figs. 1, A-F and 2, A and B).

Seedling cryptocotylar, geal (cryptoviviparous). Taproot emerges from tip of hypocotyl after dehiscence from capsule (fruit), length 1.0 to 1.5 cm, greenish-white, slender. Hypocotyl elongating from fertilized ovule without resting phase, primarily greenish-brown, terete, but at maturity dark brown and having longitudinal ridges; 4.0 to 4.5 cm long after emergence from fruit, but strongly elongating (7.2 to 7.8 cm) till emergence of plumular leaves. Cotyledons

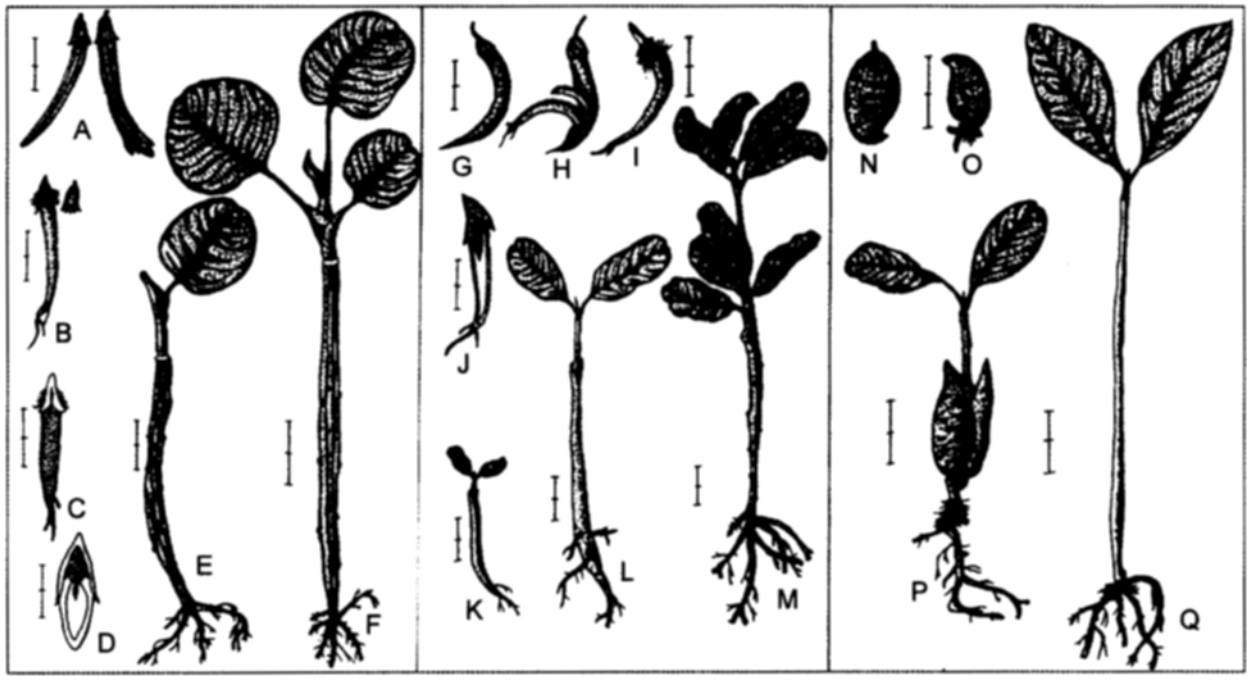

Figure 1. Illustrations of the developmental stages in mangrove seedlings. (Each division on the scale represents 1 cm.) **A-F.** *A. rotundifolia*. **A,** mature fruit and rupturing of fruit wall; hypocotyl emerges; **B,** roots emerging from tip of hypocotyl and calyx pushed off by plumule; hairy placental remains are shown; **C,** L. S. of hypocotyl; **D,** L. S. of young fruit, hypocotyl piercing seed, but not fruit; plumular leaf primordia enclosed by seed coat, a cap-like fibrous zone encircling seed; **E,** young seedling with strongly ridged elongated hypocotyls; **F,** mature seedling. **G-M.** *A. corniculatum*. **G,** mature fruit; **H,** hypocotyl emerging from fruit wall, with roots at proximal end and plumule at distal end; **I,** hypocotyl free from fruit wall, hairy placental remains encircling leaf bud; **J,** L. S. of young fruit, plumular leaf primordia enclosed within seed coat, hypocotyl emerging from seed coat rather than from fruit; **K,** young seedling with long hypocotyl and two young leaves; **L,** seedling with elongating first internode; **M,** mature seedling. **N-Q.** *A. marina*. **N,** mature fruit; **O,** fruit without fruit wall, rupturing fruit wall, taproots emerging through a two-folded cotyledon; **P,** young seedling at two-leaf stage with hypocotyl, and two-folded cotyledon still attached to hypocotyls; **Q,** seedling at two-leaf stage.

undifferentiated externally, short, bluntly pointed, enclosing plumular leaves, during fruit dehiscence the placenta remains attached to seed coat externally; at maturity, cotyledons pushed off by plumular leaf primordia. Internode very much reduced till the 3-leaf stage. First two leaves alternate, exstipulate, petiolate, petiole grooved adaxially, and extended basally into tubular leaf sheath with complete encircling insertion, blade broadly ovate (3.5 to 4 cm × 3.0 to 3.7 cm), herbaceous, glabrous, base and apex rounded, margin entire, one primary vein abaxially raised; subsequent leaves same as that of the first two, except for measurements.

A. corniculatum (L.) Blanco (Figs. 1, G-M and 2, C-E).

Seedling cryptocotylar, geal (cryptoviviparous). Taproot formation takes place only after hypocotyl emerges via rupture of fruit wall, shortly elongating (1.2 to 1.5 cm), creamy white, slender with few side roots. Hypocotyl develops following fertilization, emerges from fruit by rupturing pericarp longitudinally; embryo placed at distal end of pedicel, strongly elongating at time of dispersal (5.0 to 6.0 cm), terete, greenish-brown, glabrous, apex bluntly pointed. Cotyledons undifferentiated externally, elongated hypocotyl along with cotyledons on its tip enclosed within testa with few hairy placental remains; longitudinal section shows rudimentary plumular leaves growing at axil of cotyledons and hypocotyl piercing the seed coat proximally. Internode elongating (2.0 to 2.5 cm) at 2-leaf stage, terete, greenish-brown, glabrous; subsequent internodes elongating (1.0 to 1.2 cm) but not as much as the previous one, characters same as that of first. First two leaves alternate, exstipulate, petiolate, coriaceous, blade elliptic (3.8 to 4.2 cm × 1.7 to 1.5 cm), base cuneate, apex blunt to rounded, margin entire, one primary vein; subsequent leaves spirally arranged, other characters same as that of the first two leaves except for measurements.

A. marina (Forsk.) Vierh. (Figs. 1, N-Q and 2, F-I).

Seedling phanerocotylar, epigeal (cryptoviviparous).

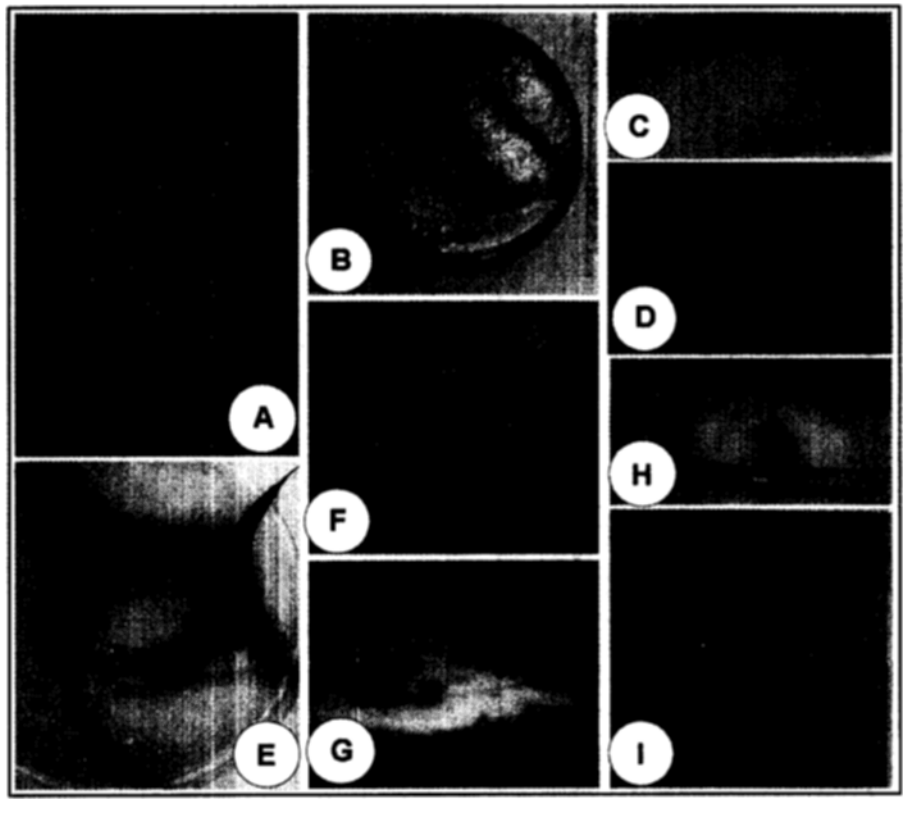

Figure 2. Photographs of the developmental stages in mangrove seedlings. **A-B.** *A. rotundifolia*. **A,** mature fruit (x 0.9); **B,** germinating capsule (x 0.25). **C-E.** *A. corniculatum*. **C,** mature fruit (x 0.8); **D,** germinating fruits (x 2); **E,** roots initiating from tip of hypocotyl (x 0.8). **F-I.** *A. marina*. **F,** mature fruits (x 0.33); **G,** radical emerging from fruit wall, with rootlets (x 0.38); **H,** slightly elongated hypocotyl with two eophylls (x 0.45); **I,** young seedling with strongly elongated first internode, attached to cotyledons (x 0.8).

Taproot elongating (2.2- to 2.5 cm), white, slender with few side roots, tuft of scale-like delicate roots at transitional zone below cotyledons. Hypocotyl slightly elongated (1.5 to 1.7 cm), terete, green, glabrous. Cotyledons folded, length 3.0 to 3.5 cm, width 1.0 to 1.5 cm, erect, sessile, blackish-green, glabrous, apex tapered, succulent, persistent till emergence of 2 or 3 pairs of eophylls. First internode strongly elongating (5.5 to 6.0 cm) at 2-leaf stage, terete, green, glabrous; second one also elongating (3.7 to 4.2 cm) at 8-leaf stage, other characters same as that of first one. First two leaves opposite, simple, exstipulate, petiolate, herbaceous, glabrous, blade narrow, long, lanceolate (7.1 to 7.4 cm × 0.5 to 0.7 cm), base cuneate, apex acute, margin entire, one primary vein; subsequent leaves same as the first two except for measurements.

DISCUSSION

Table 1 presents a comparison of major morphological characters for the taxa studied here. Because the propagating units of all mangroves are dispersed by seawater, the propagules have some ability to float, at least for a limited time. In all the investigated taxa, fruits are capsule or capsule-like, one-seeded, with seeds inseparable from the fruits. Rapid seed germination (with little or no dormancy period) occurs with elongated hypocotyl inside the pericarp. This results in exposure of the seedling before it abscises from the mother plant. Ng (1978) and De Vogel (1980) confirmed that in the tropical rain forest, rapid germination is common and the life span of the seed is usually short (i.e., a few weeks).

In the phanerocotylar-epigeal seedling type inherent to *A. marina*, the cotyledons are exposed from the seed coat and emerge from the soil surface. In the typical cryptocotylar and phanerocotylar seedlings, their cotyledons either remain inside or emerge during germination, respectively. During germination of *A. rotundifolia* and *A. corniculatum*, the seeds remain neither under nor above the soil surface but, rather, at the soil surface - a situation defined as 'geal' (Smith, 1981). In those two taxa seed dispersal occurs by the germinating embryo along with extending the hypocotyl enclosed within the pericarp. In *Avicennia*, germination is evident by the protruding radical within the pericarp.

In *Aegialitis* and *Aegiceras*, the cotyledons are undifferentiated in the early stages of seed germination, but at maturity, the sectional view reveals plumular leaf primordia growing at the axil of the cotyledons as well as endosperms present at the periphery of the cotyledons and totally consumed by the developing embryo (Fig. 1, C, D, and J). In both species the extended hypocotyl grows out of the seed coat, but not from the fruit, before dispersal. After detachment from the mother plant, the fruit wall ruptures longitudinally and the hypocotyl emerges, having plumular leaves enclosed within the testa being placed on its tip. The hairy placenta remains attached with the seed coat. Though the seed germinates epigially, it differs from the traditional way in that the cotyledons do not emerge during germination. This phenomenon is termed 'cryptovivipary' (Tomlinson, 1986).

In *Avicennia*, the cotyledons are two-fold: one adaxially, the other abaxially placed to the plumular axis. The radical, with a tuft of hairy roots, extends on the hypocotyl beyond the cotyledons within the pericarp. This serves as anchorage to prevent the seedling being washed away.

In all three taxa, germination is rapid, with the hypocotyls emerging from the seed coat. These seedlings become exposed before dispersal, and the embryo emerges only from the seed coat, but not the fruit wall, before abscission (Carey, 1934). This differs from the other typical viviparous type of germination (e.g., in Rhizophoraceae). Therefore, these three species are typical examples of 'incipient vivipary'. In contrast, 'true vivipary' is defined as the condition in which an embryo, following sexual reproduction, normally grows out of both the seed coat and the fruit, rather than remaining attached to the parent plant (Juncosa, 1982).

Table 1. Comparison of the major characters among the investigated taxa.

Characters	*A. rotundifolia*	*A. corniculatum*	*A. marina*
Fruit type	Capsule	Capsule	Capsule
Seedling	Cryptocotylar	Cryptocotylar	Phanerocotylar
Germination	Geal	Geal	Epigeal
Cotyledons	Undifferentiated	Undifferentiated	Two-folded
Hypocotyl	Strongly elongated	Strongly elongated	Slightly elongated
First internode	Reduced	Elongated	Strongly elongated
First leaf	Ovate	Elliptic	Lanceolate

Ng (1978) described four seedling types based on morphological characters, and considered Rhizophoraceae to be of the 'Durian type', in which the hypocotyl is extended and the cotyledons rise above ground level. However, this phenomenon is not accurate in the case of Rhizophoraceae. In fact, de Vogel (1980) classified it as a separate group, "Rhizophora type", which included *Aegiceras*. Nevertheless, *Aegiceras* showed many differences from Rhizophora in the current investigation, and should not be placed in same group.

Likewise, *Avicennia* has historically been placed under 'Sloanea type/subtype 2a', which includes a strongly elongating hypocotyl (de Vogel, 1980). However, the morphological 'missing link' here is that the hypocotyl always emerges from the seed coat, but not from the fruit, during the early stage of seed germination, thus very much resembling the cryptoviviparous type found in *Aegialitis* and *Aegiceras*. Because the type of seed germination found in *Aegialitis*, *Aegiceras*, and *Avicennia* differs greatly from that described by de Vogel (1980), and because these three taxa share great similarities, one should place them in a separate group whose germination is considered 'incipient viviparous'. Tomlinson (1986) also has agreed that it is more appropriate to consider them as "cryptoviviparous".

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