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On the ontogeny of stomata and glandular hairs in some Indian mangroves

SAUREN DAS*

Agricultural Science Unit, Indian Statistical Institute, 203, B. T. Road,
Calcutta 700 108, India

Mature stomata of four mangrove taxa of different families reveal three distinct types of stomatal complex on abaxial surfaces, such as diacytic (in *Acanthus ilicifolius*), anomocytic (in *Aegialitis rotundifolia* and *Xylocarpus granatum*), and paracytic (in *Ceriops decandra*). In transverse section, there is a beak-like cuticular outgrowth overarching the stomatal pore either at the outer side or at both the outer and inner side of the stomatal pore. The guard-cell mother-cell divides once longitudinally to form two guard cells and the development of subsidiary cells is not at all concerned with the former cell. Ontogenetically it is revealed that the development of a stomatal complex in these investigated taxa is aperiginous (*X. granatum*) and periginous (*A. ilicifolius, A. rotungifolia* and *C. decandra*). Glandular hairs (salt gland) are present only at the adaxial surface of leaves in *A. ilicifolius* and *A. rotundifolia*. In *A. ilicifolius* it is pear-shaped and protrudes from the normal epidermal layer while in *A. rotundifolia* it is present within a cup-shaped crypt in the epidermal layer. In both the cases, the ontogenic pathway is similar, at least up to the three-celled stage, but at maturity, the morphology is quite different. The salt gland consists of 4–8 radiating terminal cells, two stalk cells and one basal cell.

Key words: ontogeny, stomata, glandular hair, mangroves

Introduction

The focus of interest on stomatal ontogeny and structure argues well for the application of these as systematic tools. The developmental pattern of the stomatal complex shows absolute constancy in the majority of families (VAN COTTHEN 1970). Stomatal architecture, such as the size, shape and orientation pattern of the stomatal guard cells, with the other epidermal cells (subsidiary cells), is of immense taxonomic importance (TOMLINSON 1974, STACE 1984). Some contributions from this aspect were made in different plant species (STEBBINS and KHUSH 1961, FRYNS-CLAESSENS and VAN COTTHEN 1973, BIR BAHADUR et al. 1977, NYAWUAME and GILL 1990, TERHUNE et al. 1991, DAS and PARIA 1992, KARATELA and SANGAL 1993).

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* Corresponding address: Fax: 91 033 577 6680, e-mail: saurend@hotmail.com

In mangroves, work in this direction is considerably less developed. Much has been published on the morphology of mature stomata, their orientation pattern with the subsidiary cells and the structural architecture of glandular and non-glandular leaf hairs (MULLAN 1931, BALL and DUTTA 1984, TOMLINSON 1986, SESHAVATHARAM and SRIVALLI 1989, DAS and GHOSE 1993). Very little work has yet been done on the ontogeny of stomata and the developmental pattern of glandular and non-glandular hairs in mangroves (SHIMONY et al. 1973, FAHN and SHIMONY 1977) and more attention should be paid to this area. DAS and GHOSE (1997) worked on the developmental patterns of stomata in five mangrove taxa, and the non-glandular hairs of one species among them. The present work has dealt with the ontogenetic study of stomata of four mangrove taxa and the glandular hairs of two species amongst them.

Materials and methods

Fresh leaves of four taxa of four families, viz. *Acanthus ilicifolius* L. (Acanthaceae), *Aegialitis rotundifolia* Roxb. (Plumbaginaceae), *Ceriops decandra* (Griff.) Ding. Hou. (Rhizophoraceae) and *Xylocarpus granatum* Konig. (Meliaceae) were collected from well-identified taxa from the Sundarbans mangrove forest. For ontogenetic study of stomata, young rudimentary leaves of different growth stages were fixed in FAA. Whole mounts of the rudimentary leaves were made and mounted in phenol-glycerin following 2% aceto-orcein staining. Different stages of the development of stomata were recorded by camera lucida drawings. For developmental study of glandular leaf hairs in two taxa amongst them viz. *Acanthus ilicifolius* and *Aegialitis rotundifolia*, thin hand sections and epidermal peelings were made and stained with aceto-orcein. Camera lucida drawings are provided to indicate the gradual developmental phases of glandular hairs from both the sectional and the surface view.

Results

Stomata

Stomata are present on the abaxial surface of the leaf in all the taxa investigated and are scattered over the expanded laminar surface. The diacytic type of stomata occurs in *Acanthus ilicifolius* (Fig. 1A–E), the anomocytic in *Aegialitis rotundifolia* and *Xylocarpus granatum* (Fig. 1F–I and O–R), and the paracytic type in *Ceriops decandra* (Fig. 1J–N). In sectional view, mature stomata show a distinct cuticular outgrowth overarching the stomatal guard cells, termed ledges. The ledges are present either on the outer side of the stomatal pore (*A. ilicifolius* and *X. granatum*) or on both the inner and outer side (*A. rotundifolia* and *C. decandra*) (Fig. 1E, R, I and M). In *Ceriopa* and *Xylocarpus*, the mature stomata are sunken with the substomatal chamber. These structural modifications can be explained as an adaptive tool as it provides a barrier for water loss through the stomatal pore during transpiration.

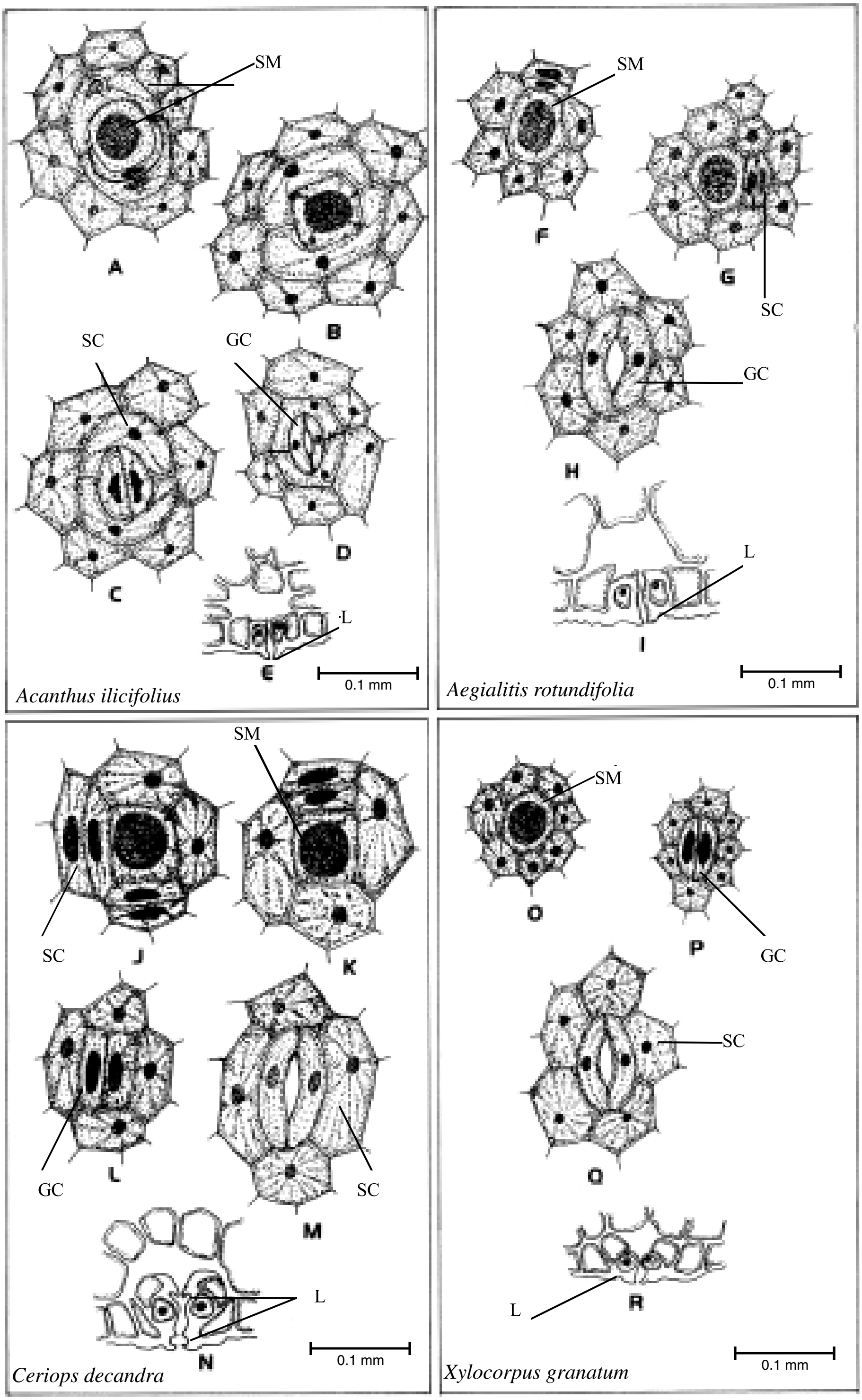
Ontogeny of Stomata

The stomatal meristemoid can be easily demarcated from the other epidermal cells, as it is quite large with a dark stained enlarged nucleus, isodiametric, tetrahedral or polygonal in shape (Fig. 1A–R). These meristemoids appear before the optimum meristematic activity of the leaf epidermis completed. Development of each stoma on a leaf does not start at once, but appears in a succession during a considerable period of growth of the leaf.

In *Acanthus*, *Aegialitis* and *Ceriops*, the surrounding epidermal cells of the guard-cell mother-cell divide tangentially before the latter undergoes division. In *Acanthus*, two polar epidermal cells divide tangentially first, while the guard-cell mother-cell remains undivided. The guard-cell mother-cell then divides once to produce two guard cells and the two polar subsidiary cells encircle the guard-cell mother-cell at right angle to the long axis of the stomatal pore; thus it is of perigenous origin and ultimately forms a diacytic type of stomatal complex. In both *Aegialitis* and *Ceriops*, the ontogenetic pathway of stomatal formation is of the periginous type. In *Aegialitis* the ultimate arrangement of the surrounding epidermal cells of the guard-cell mother-cell do not follow any definite pattern; so it is the anomocytic type of stomata, of perigenous origin. In *Ceriops*, the formation of two lateral subsidiary cells is followed by their elongation along the long axis of the guard-cell mother-cell and two comparatively smaller cells that appear in the polar region of the guard-cell mother-cell, resulting in a paracytic type of stomatal complex. After that the guard-cell mother-cell divides longitudinally to form two guard cells. The ontogeny is therefore of the perigenous type. The stomatal meristemoid is involved in the formation of the guard cell-mother cell and is not in any way concerned to the surrounding subsidiary cells in *Xylocarpus*. In this case, the surrounding epidermal cells of the guard-cell mother-cell do not divide but orient themselves without any definite pattern around the guard cells so that they can not be distinguished as subsidiary cells from the other epidermal cells, thus resulting in the anomocytic stomatal complex and the ontogeny is therefore of the aperigenous type.

Development of glandular hairs

Glandular hairs are present on the adaxial surface of the leaves only in *Acanthus ilicifolius* and *Aegialitis rotundifolia*. In *Acanthus*, mature glandular hairs are pear-shaped, while in *Aegialitis* they occurs within a cup-shaped crypt. Basically in both the cases, the mature hairs consist of four to eight radiating terminal cells, two stalk cells and one basal cell. The glandular hair primordium differs from the other epidermal cells in its large cell size with an enlarged, densely stained nucleus and vacuoles in the cytoplasm. In transverse section, the hair primordium protrudes from the epidermal layers, in the case of *Acanthus*, but in *Aegialitis* it remains within a crypt formed within the epidermal layer (Fig. 2A, I). In both these cases, the first division of the primordium occurs transversely to form a terminal and a basal cell (Fig. 2B, J). The terminal cell undergoes a second transverse division leading to one terminal and one stalk cell, while the basal cell remains undivided (Fig. 2C, K). In *Acanthus* the stalk cell divides once transversely to produce two stalk cells (Fig. 2E) but in *Aegialitis*, the third division occurs in both stalk and terminal cell, longitudinally and at right angle to each other, forming two stalk cells and two terminal cells (Fig. 2L). After this the stalk cell remains undivided and the terminal cell undergoes a series of longitudinal divisions to form eight terminal cells finally arranged radially (Fig. 2E, M). The mature glandular hair remains enclosed within the uninterrupted cuticular layer. From the surface view, in both these cases, the terminal cells appear as a radiating structure (Fig. 2F–H and N–P).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Aegialitis rotundifolia
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Ceriops decandra
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Xylocorpus granatum

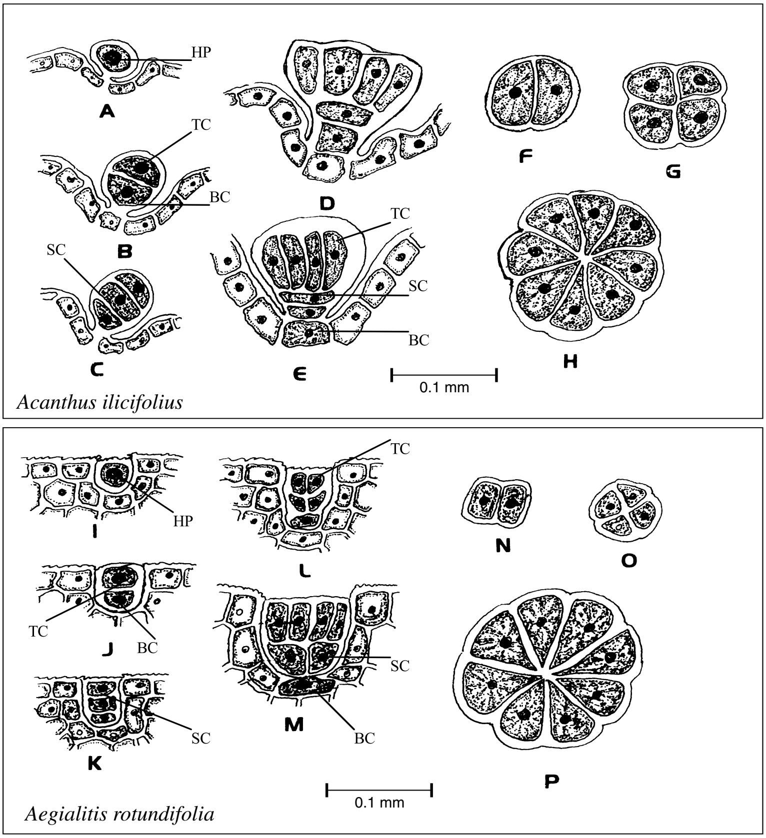

Fig. 2. A–P. Camera lucida drawings of developmental stages of glandular hairs. A–H. *Acanthus ilicifolius*; A- hair primordium. B- 2-celled stage, terminal and basal cell. C- 3-celled stage with terminal, stalk and basal cell. D- one basal cell, one stalk cell and four terminal cells. E- mature glandular hair with one basal cell, two stalk cells and eight radiating terminal cells. F–H. surface view of gradual developmental stages of terminal cells. I–P. *Aegialitis rotundifolia*; I- hair primordium within the epidermal crypt. J- dividing stages with one terminal and basal cell. K- 3-celled stage. L- undivided basal cell and longitudinal division of stalk and terminal cells. M- undivided two stalk cells and one basal cell with longitudinal division of terminal cells. N–P. surface view of gradual developmental stages of terminal cells. HM = hair primordium, BC = basal cell, SC = stalk cells, TC = terminal cells.

← **Fig. 1.** A–R. Camera lucida drawings of developmental stages of stomata. A–E. *Acanthus ilicifolius*; A- undivided guard-cell mother-cell with lower subsidiary dividing cell. B- two subsidiary cells encircling the guard-cell mother-cell. C- dividing guard-cell mother-cell. D- mature stomata (diacytic). E- sectional view of stomata showing outer ledges. F–I. *Aegialitis rotundifolia*; F, G- stomatal meristemoid with surrounding dividing subsidiary cells. H- mature stomata (anomocytic). I- sectional view of stomata showing inner and outer ledges. J–N. *Ceriops decandra*; J, K- stomatal meristemoid with lateral and polar dividing subsidiary cells. L- dividing stage of stomatal meristemoid. M- mature stomata (paracytic). N- sectional view showing inner and outer ledges. O–R. *Xylocarpus granatum*; O- stomatal meristemoid. P- dividing stage of stomatal meristemoid. Q- mature stomata. R- sectional view of stomata showing outer ledges. SM = stomatal meristemoid, GC = guard cells, SC = subsidiary cells, L = ledge

Discussion

The mature stomata of the investigated taxa reveal three distinct types, *viz.* diacytic (*Acanthus ilicifolius*), anomocytic (*Aegialitis rotundifolia* and *Xylocarpus granatum*) and paracytic (*Ceriops decandra*). In all the cases, at maturity, guard cells are placed within a substomatal chamber (sunken) in *Ceriops* and *Xylocarpus* and show a distinct beak-shaped cuticular outgrowth either at the outer side or both at the outer and inner side of the stomatal pore (ledges). This structure provides an extra preventive device against water loss through the stomatal pore during transpiration (DAS and GHOSE 1997). The two guard cells of a stoma develop from a single meristemoid by an equal division and the subsidiary cells develop from a different meristemoid, which is no way concerned with the guard-cell mother-cell. This type of development was also reported earlier in other five mangrove taxa (DAS and GHOSE 1997). In *Ceriops decandra* (Rhizophoraceae) the lateral epidermal cells of the guard-cell mother-cell divide prior to stomatal development to produce subsidiary cells, which, in turn elongate along the long axis of the stomatal pore. This type of developmental pattern was reported earlier in *Bruguiera gymnorrhiza* (Rhizophoraceae) (DAS and GHOSE 1997). TOMLINSON (1986) opined that there is no high degree of specialization of stomatal type among mangroves. The present investigation reveals that there are three distinct types of mature stomatal complex, which follows two different ontogenetic pathway for stomatal development among the four investigated taxa.

In *Acanthus* and *Aegialitis*, only glandular leaf hairs (salt secreting glands) occur on the adaxial surface of the leaf. The present investigation reveals that in both the cases, the developmental stages of the glandular hair are more or less similar, at least up to the three-celled condition, but at maturity the morphology is quite different. The salt glands in all salt-secreting mangroves show some structural similarities in having a basal or collecting cell, two stalk cells and a capitate group of terminally radiating cells. These are probably good evidence of evolutionary convergence among the taxa (DAS and GHOSE 1993). METCALFE and CHALK (1950) reported that the non-glandular hairs of *Avicennia nitida* (Avicenniaceae) consist of only three cells and proposed that the structural differences of glandular and non-glandular hairs may be due to an adaptive evolution. OSMAND et al. (1969) opined that the salt is secreted by the cytoplasm of the secretory cells of glandular hair into the large vacuoles and as the secretory cells dry out with the aging of the leaves, the salt content is left on the leaf surface as a white powdery layer. FAHN and SHIMONY (1977) reported that in *Avicennia marina* the ontogeny of glandular and non-glandular hairs follows the same pathway, at least up to the three-celled stage, and after this, the two types of hair differentiate in various ways. DAS and GHOSE (1997) observed that ontogeny of non-glandular hairs in *Heritiera fomes* (Sterculiaceae), the subsequent developmental stages from a hair primordium to three-celled structure is more or less similar to those found in *Acanthus ilicifolius* and *Aegialitis rotundifolia*, but at maturity, the morphology is quite different.

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