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Structure, Ontogeny and Biology of Nectaries in *Luffa acutanqqula* (L.) Roxb. var. *amara* (Lam.) Cl.

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ABSTRACT

Luffa acutanqula var. *amara* exhibits floral and extrafloral nectaries. The floral nectaries are restricted to the torus of the male flowers, while the extrafloral nectaries are observed on foliage leaves, probract, outer surface of calyx and pedicels. The floral nectaries develop from a group of epidermal and sub-epidermal initials which differentiate into secretory and subsecretory zones respectively during further divisions. The extrafloral nectary initiates from a single papillate nectary initial which gives rise to mature nectary comprising stalk layer, secretory and subsecretory tissues. Both the floral and extrafloral nectaries are vascularized. Interactions between insect-visitors and the plant with special reference to their functions are also discussed.

INTRODUCTION

Chakravarthy (1948) reported extrafloral nectaries in *Coccinia, Luffa, Lagenaria, Momordica* and *Cucurbita* of the family Cucurbitaceae. Fahn (1949) reported the presence of large nectaries in female flowers of *Cucurbits*. Metcalfe and Chalk (1950) reported seven types of extrafloral nectaries in the family Cucurbitaceae. However, detailed studies on the ontogeny, structure and functions of extrafloral and floral nectaries of *Cucurbits* are yet to be carried out. The pollination biology of this economically important plant is yet to be investigated. The paper deals with the structure, ontogeny, secretion and probable functions of extrafloral and floral nectaries of *Luffa acutangula* (L.) Roxb. var. *amara* (Lam.) Cl.

MATERIALS AND METHODS

Nectaries at different developmental stages were collected from plants raised in the University Botanical Garden and fixed in FAA (Berlyn and Miksche, 1976). Customary methods were followed for dehydration and embedding. Transverse and longitudinal sections of 6–10 μm thick were cut with Spencers AO rotary microtome and stained with combination of tannic acid, ferric chloride and Safranin 'O' and fast green F.C.F. Leaves were cleared following the methods of Rao *et al.* (1980). Bright field photomicrographs were taken with Carl Zeiss photomicroscope I. Polysaccharides were detected using periodic acid-Schiff's reagent. Frequent field visits to observe plant-insect interactions were carried out.

RESULTS

Extrafloral nectaries. The extrafloral nectaries in *Luffa acutangula* occur on four organs viz.; i) the outer surface of calyx, ii) the lower portion of pedicel, iii) probract in leaf axils, and iv) the abaxial surface of lamina.

In the leaf axils nectaries occur in groups of 5-7 as cup shaped ting structures on a small leafy organ called probract (Fig. 2A). An average of 36-43 laminar nectaries occur on the abaxial surface of leaf as small glistening dots (Fig. 1A). Pedicellar nectaries are present at the basal portion of each pedicel ranging from 1-4 in number similar to the probract nectary, while the calycine nectaries are found on the outer surface of calyx in both male and female flowers. However, they vary in their number. An average of 1-2 or 12 calycine nectaries occur on the calyx of male and female flowers respectively. It is interesting to note that the calyx is persistent in female flowers.

The extrafloral nectaries develop from single nectary initials distinguished by their papillate nature, dense cytoplasm and prominent nucleus (Fig. 1B). A nectary initial (Fig. 1B) first divides periclinally into two cells (Fig. 1C) and each daughter cell undergoes an anticlinal division giving rise to a four celled structure arranged in two tiers (Fig. 1D). The cells of the upper tier undergo a number of periclinal and anticlinal divisions giving rise to the secretory tissue (Fig. 1D, E). The cells belonging to the lower their undergo only anticlinal divisions forming stak cell layer (Fig. 1D, E).

The extrafloral nectary at maturity is clearly distinguishable into three regions viz. (i) the secretory tissue, (ii) the stalk cell layer, and (iii) the subsecretory tissue (Fig. 1F, G, H). The secretory tissue is composed of small isodiametric cells. They are darkly stained and smaller in size than neighbouring parenchymatous cells. The stalk cell layer is composed of laterally elongated cells which are lightly stained and larger in size. The stalk cell layer delineates the secretory tissue from the subsecretory tissue lying below (Fig. 2B, C, D), and is continuous with the epidermis.

The extrafloral nectaries are not vascularized. However, vascular bundle composed of both xylem and phloem are present just beneath the subsecretory zone (Fig. 2B). Observations of cleared leaves reveal that a number of veins pass just beneath the nectary (Fig. 1J).

The cuticle is seen lifted from the secretory tissue at many places during secretion(Fig. 1I). The secretory material is released as a result of breaking of the cuticle. It appears as a clear shining droplet on the nectary during early morning hours. Different types of ants were found foraging on all the extrafloral nectaries as the nectaries become functional, probably attracted by the secretory material. One of them was identified as *Camponotus* sp.

The pattern of secretion in all the four extrafloral nectary types show remarkable sequential regularity. The laminar nectary starts secreting first, followed by the probract, pedicellar and calycine nectaries in an orderly fashion. All the extrafloral nectaries start secreting even when the organ bearing them is quite young and cease to do so as they attain maturity.

Floral nectaries. The floral nectary is found on the torus of male flowers just beneath the stamens. It is absent in female flowers. The floral nectary originates from a group of epidermal and sub-epidermal cells in the torus. These cells undergo a series of periclinal and anticlinal divisions giving rise to the adult nectary structure (Fig. 2E, F). The mature floral nectary is distinguishable into two regions viz. i) the epidermal layer, and ii) the secretory tissue. The epidermal cells are barrel shaped with dense cytoplasm and prominent nuclei. The secretory tissue is composed of isodiametric parenchymatous cells (Fig. 2F). Vascular supply is mainly composed of phloem found distributed in the parenchymatous zone below the secretory tissue (Fig. 2E). The secretory cells possess abundant starch grains during secretory stage (Fig. 2G). However, during post-secretory stage the guantity of starch shows a rapid decline (Fig. 2H).

Onset of nectar secretion coincides with anthesis and the secretory activity is at its maximum during morning hours. Insect visits to flowers are found to be at its maximum after 6.30 a.m. The hymenopteran members collect nectar and pollen from open flowers.

Luffa acutangula is monoecious. Flowers are yellow colored, scented and open during early morning hours. Nectaries are well covered by the stamens and are present on the torus. The flowers produce abundant nectar and pollen grains which serves as a staple food for visiting insects. Different types of bees and flies were observed to forage the flowers for nectar as well as pollen collection. All these characters clearly indicate that the flowers of *L. acutangula* are entomophious.

DISCUSSION

The extrafloral and floral nectaries must be considered as independent entities as in the members of Turneraceae and Bignoniaceae (Elias *et al.*, 1975, Elias and Prance, 1978, Subramainan and Inamdar, 1986). The present work confirms the observations of these authors. The extrafloral nectaries show specialization of tissue into nectary base, secretory region and subsecretory region, together with their vascular supply. These characters are typical of the extrafloral nectaries that remain active over a long period of time.

The rapid decline of starch during secretory stage in floral nectaries is well known. Such instances have been reported in the floral nectaries of *Passiflora* (Durkee *et al.*, 1981), *Kiqelia pinnate* and *Biononia illicium* (Subramanian and Inamdar, 1985, 1986).

The secretory products of extrafloral nectaries attract variety of ants. The ants may help to ward off other herbivorous insects and plant-predators and save more flowers for pollination. The persistent nature of the calyx in the female flowers probably aid in protecting the young unferilized ovaries. Such instances have been reported by Koptur(1979) and Beckman Stucky (1981). The nectaries are scattered almost all over the plant parts, which is advantageous for the plants as reported by Chakravarthy (1948). Ants were found foraging on extrafloral and floral nectaries probably helping in pollination and plant protection (Chakravarthy, 1948).

The floral nectary is strategically situated at the end of the corolla lobes to aid in pollination.

The plant is monecious and hence cross pollination is highly necessary (Percival, 1965). The pollinators land on the corolla to collect nectar and the head portion of the visiting insects come in direct contact with the stamens in male flowers. These pollen grains are probably transported to the female flowers when the same insects visit them in search of nectar, since both male and female flowers exihibit the same features.

Thus, the floral biological characters exhibited by *L. acutangula* indicate that these flowers are cross-pollinated. Sprengel (1973) and later Percival (1956) confirmed the manifestation of such characters in insect pollinated flowers. The hymenopteran members probably collect pollen grains and nectar for food and while foraging pollinate the flowers.

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Explanation of Figures

Fig. 1. A. Tessovar photograph showing the abaxial surface of lamina bearing mature extrafloral nectaries (120 X). Note arrow pointed toward a nectary. B–F. Longitudinal sections of calyx showing various developing stages of calycine nectary. (B, 1536 X; C, 1536 X; D, 1024 X; E, 768 X; F. 640 X). G. Cross-section of mature laminar nectary showing different regions (190 X). H. Cross-section of a laminar nectary a section showing secretory and subsecretory tissue along with a prominent stalk cell alyer (450 X). I. Cross-section of a mature laminar nectary during secretion (510 X). Note. Arrow pointed towards lifted cuticle due to secretion. J. Cleared leaf showing distribution of veins below the nectary (320 X). Note. Arrow pointed towards a vein.
NI, Nectary initial; ST, Secretory tissue; SST, Subsecretory tissue; SCL, Stalk cell layer; N, Nnectary.

Fig. 2. A. Tessovar photograph showing nectaries on leaf-probract-axilar region in the form of four cups. (8 X). B. Cross-section of a mature calycine nectary prior to secretion showing different regions (192 X). Note. Arrow pointing towards a vascular bundle present underneath the nectary. C. Cross-section of a mature nectary present on leaf-probract-axilar region during secretion (384 X). Note. Arrow pointing towards a lifted cuticle due to secretion. D. Cross-section of a mature pedicellar nectary (300 X). Note. Arrow pointing towards a lifted cuticle due to secretion. E. Longitudinal section of a young bud showing developing young floral nectary (200 X). F. Longitudinal section of an open flower (120 X). G. Longitudinal section of a mature flower stained with PAS reaction(Periodic acid-Schiff's reagent) (200 X). Note. The presence of dense starch grains. H. Longitudinal section of a flower with floral nectary during post-secretory stage stained with PAS (300 X). Note. The decline in the quantity of starch grains.
N, Nectary; ST, Secretory tissue; SST, Sub-secretory tissue; SCL, Stalk cell layer; S, Starch grains; P, Phloem strands.

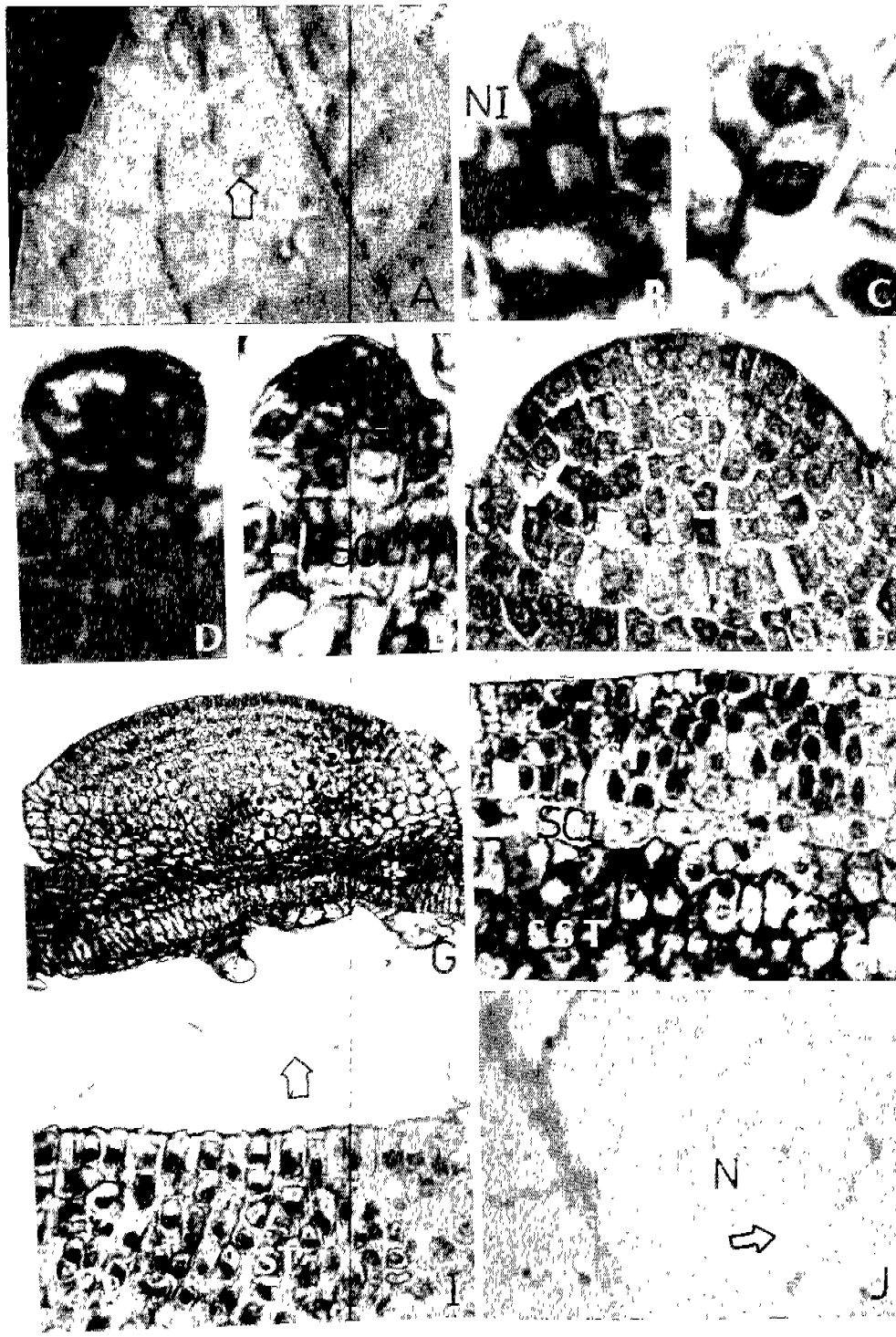

Fig. 1

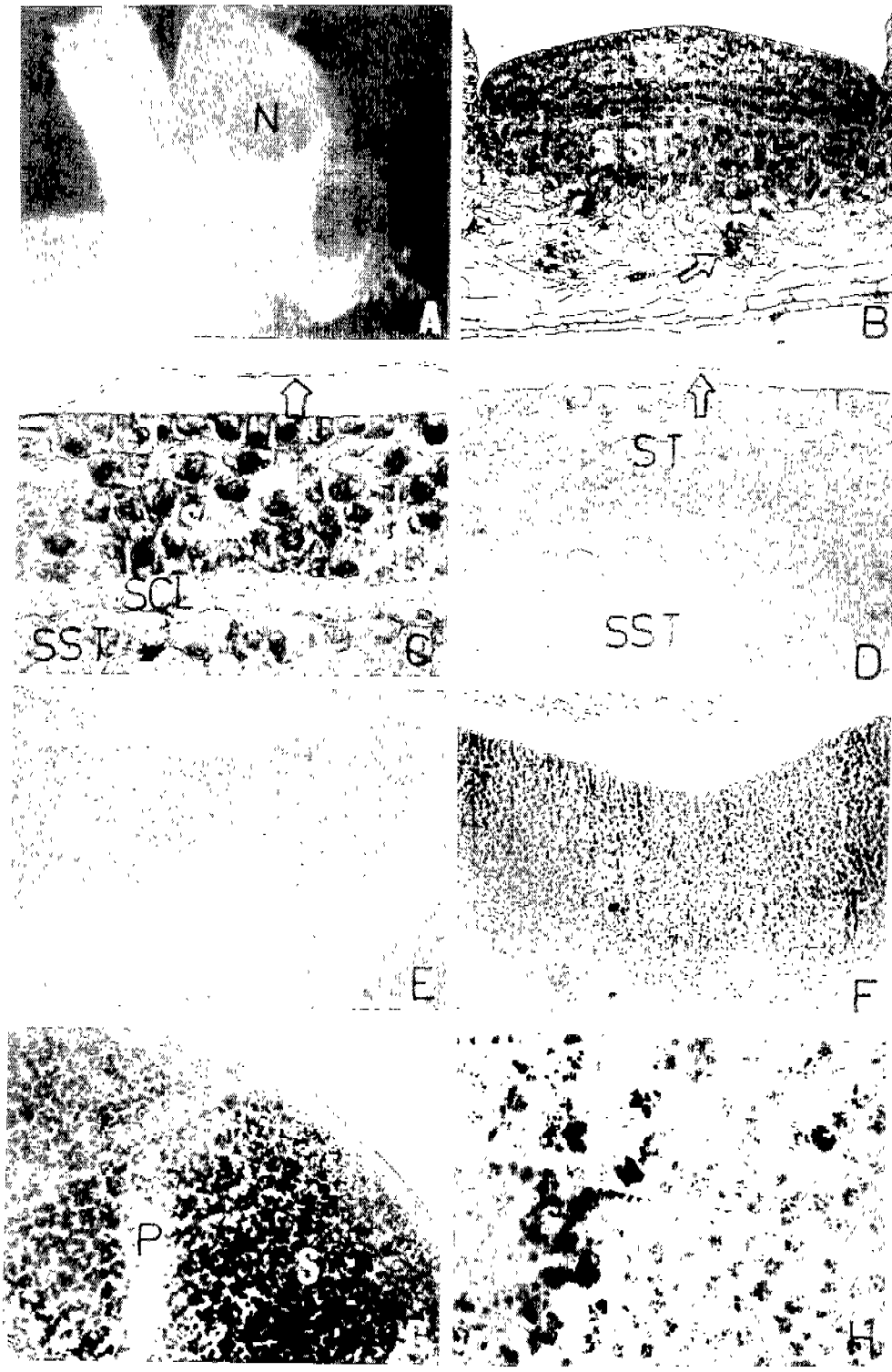

Fig. 2