STRUCTURE AND ONTOGENY OF FOLIAR NECTARIES AND STOMATA IN BIGNONIA CHAMBERLAYNII SIMS

BY J. A. INAMDAR

(Department of Botany, Sardar Patel University, Vallabh Vidyanagar, Gujarat, India)

Received November 27, 1968

(Communicated by Prof. V. Puri, F.A.Sc.)

ABSTRACT

The present paper describes the distribution, structure, ontogeny, function of foliar nectaries and structure and ontogeny of stomata in Bignonia chamberlaynii Sims. The mature nectaries are patelliform and originate from a single papillate epidermal cell. They consist of 1-layered base (foot), 2-layered stalk and 1-2-layered palisade-like epithelial cells which secrete sugary fluid.

The mature stomata are anisocytic, anomocytic, paracytic, perigenous (tetracytic and amphicyclic), with a single subsidiary cell. The ontogeny of anisocytic, paracytic and stomata with a single subsidiary cell conforms to the mesogenous type, while that of the anomocytic, tetracytic and amphicyclic ones is perigenous. Abnormalities noticed here are contiguous (juxtaposed and superposed) stomata, stomata with a single guard cell and aborted guard cells.

INTRODUCTION

Several angiosperm families are known to have foliar nectaries. In the family Bignoniaceae, they are reported to be present on various foliar and floral organs of the plant (see Rao, 1926; Parija and Samal, 1936). Solereder (1908) recorded patelliform glands in Pyrostegia venusta and Adenocalymma impressum. Water-excreting glands were observed on the inner margin of the calyx in Spathodia campanulata (Haberlandt, 1914), S. stipulata (Rao, 1926), Bignonia grandiflora and Tecoma stans (Morini in Solereder, 1908). However, our knowledge regarding the structure, ontogeny and function of the extra-floral nectaries is scanty. The structure, ontogeny and function of these organs have been described for Tecoma capensis by Parija and Samal (1936). In Bignonia chamberlaynii, the foliar nectaries occur in shallow depressions on the lower surface of the leaf (Fig. 2, A, B, E), bract (Fig. 2, A, D) and outer surface of the calyx (Fig. 2, C). The mature nectaries
Foliar Nectaries and Stomata in Bignonia chamberlaynii Sims

appear as dark green small glistening dots on the leaf bract and pearl-like
glistening dots on the calyx to the naked eye.

According to Metcalfe and Chalk (1950), the stomata in the family
Bignoniaceae are mostly anomocytic, occasionally paracytic and rarely dia-
cytic. As far as the author is aware no report exists on the ontogeny of
stomata in the Bignoniaceae.

The distribution, structure, development, function of foliar nectaries
and structure, ontogeny of stomata in Bignonia chamberlaynii form the
subject of the present investigation. Terminology of Metcalfe and Chalk
(1950) and Pant (1965) is used here.

MATERIALS AND METHODS

The material of Bignonia chamberlaynii was collected from the depart-
mental garden, where it is cultivated as an evergreen beautiful ornamental
climber. Young and mature leaves, bracts and calyx were fixed in FAA,
then stored in 70% alcohol. Camera lucida drawings were prepared from
the temporary whole mounts of epidermal peels of leaves stained with
Delafield’s hamatoxylin. The development of foliar nectaries were studied
in the surface as well as sectional view of the leaf, bract* and calyx.
Microtome sections were also taken. For the presence of sugars in the
secretory fluid, the leaves, bracts and calyx were tested with Fehling’s
solution A and B.

OBSERVATIONS

I. Foliar Nectaries

Development

Usually the nectaries initiate from the cells of the lower epidermis of
the foliar or floral organs of the plant. The nectary initial is distinguish-
able by its papillate nature, prominent nucleus and dense staining properties
(Fig. 2, F). It divides periclinally to form a basal and outer cell (Fig. 2, C).
The latter divides again periclinally to give rise to a stalk cell and a terminal
cell (Fig. 2, H). The first four divisions in the terminal cell are anticlinal
as a result of which 16 cells are formed (Fig. 3, A–E). Further divisions
in the terminal cell are either anticlinal, periclinal or irregular (Fig. 3, F, G).
This histogenic activity results in a broad, multicellular, saucer-shaped head

* This is the term used for pair of small leaves situated at the base of the inflorescence and
in the axils of the leaves.
or shield (Fig. 2, I-K; 3, F, G). The primary stalk cell divides periclinally and then anticlinally so as to form a short but broad stalk (Fig. 2, J-K). The basal cell also divides anticlinally simultaneously in order to keep pace with the increased breadth of the stalk region (Fig. 2, J-K). The cells of the basal region remain in continuation with the epidermis and differ in having larger nuclei and denser cytoplasm.

**Structure and Function**

The mature nectaries are patelliform and situated in shallow depressions. The main body of the nectary consists of 1–2–layered palisade-like epithelial
Foliar Nectaries and Stomata in Bignonia chamberlaynii Sims

II. Stomata

Mature Epidermis

The leaves of Bignonia chamberlaynii are hypostomatic. The epidermal cells are polygonal or elongated and irregularly arranged. The epidermal cells have mostly straight or arched thick anticlinal walls. The surface of the cuticle shows parallel and straight striations radiating from the guard cells or hair bases (Fig. 4, C). Simple uniseriate conical trichome with compound foot have been observed on leaves and bracts (Fig. 3, H).

Mature Stomata

The mature stomata are anisocytic (Fig. 1, G), anomocytic (Fig. 1, H), paracytic (Fig. 1, K), perigenous and with a single subsidiary cell (Fig. 1, L). Perigenous stomata may be tetracytic (Fig. 1, F) or amphicyclic (Fig. 1, M). Contiguous stomata are either juxtaposed (Figs. 1, J; 4, F) or superposed (Fig. 1 E). Abnormal stomata with a single guard cell (Fig. 4, A, B) and one or both the guard cells aborted (Fig. 4, C, D) are common in yellowing leaves which were about to drop down, while they are rare in the green leaves. In some instances (Figs. 1, I; 4, A, B), rarely, a cell, in a position regularly occupied by another guard cell, is either a guard cell or a subsidiary cell which may be stretched (Fig. 4, A) or may or may not show division (see also Dehnel, 1961). Occasionally, between adjacently placed stomata a cytoplasmic connection bridge (Fig. 4, E) was observed.

Ontogeny

Protoderm cells in a young leaf are either polygonal, elongated or tetragonal. A stomatal initial (meristemoid) is cut off from any cell of the
protoderm. The meristemoid is more or less squarish and is easily recognisable from the adjacent protoderm cells by its smaller size, prominent nucleus and dense cytoplasm (Fig. 1, A, B). Meristemoids occur in a random fashion rarely between mature stomata. The development of different types of stomata is as under:

1. Anisocytic stomata.—The meristemoid divides unequally by a curved wall to form a small triangular cell in a corner and a large flat, more less rectangular cell on the other side (Fig. 1, A, B). The larger cell differentiates as the first subsidiary cell. The small triangular one then enlarges and divides by a curved wall to give rise to the second subsidiary cell (Fig. 1, A, B). Later, the triangular meristemoid divides again on the

![Fig. 2. Foliar nectaries (A-K). A. Twig showing distribution of nectaries on the leaf and bract in the form of dots, × 1/2.; B. Portion of leaf enlarged showing nectaries, × 19; C. Flower showing position of nectaries on calyx ×1/2; D. T.S. bract, diagrammatic showing position of nectaries in depressions, × 70; E. T.S. leaf, diagrammatic, showing position of nectary, × 290; F. Nectary initial; G. Formation of a basal and an outer cell; H-I. Formation of stalk cell and terminal cell; note anticlinal division in head cell; J. Periclinal division in the alk cell and anticlinal divisions in terminal cell; K. Patelliform nectary (F-K, × 440).]
third side to form a third subsidiary cell (Fig. 1, A, B). At this stage, the small triangular meristemoid is surrounded by three subsidiary cells. The central cell now functions as the guard mother cell which becomes rounded and divides by a straight wall parallel to the last into two guard cells which develop an intervening pore (Fig. 1, A). Here, the meristemoid behaves like an apical cell with three cutting faces to produce three subsidiary cells in a spiral fashion, as has been reported by earlier authors. It is the smaller cell which remains meristematic and keeps on dividing repeatedly (see also Shanks, 1965; Pant and Banerji, 1965; Pant and Kidwai, 1967; Paliwal, 1967; Inamdar, 1969). The mature stomata are anisocytic (cruciferous) surrounded by three unequal subsidiary cells (Fig. 1, G).

2. Anomocytic stomata.—Here, the meristemoid, which directly becomes a guard mother cell without cutting off any subsidiary cells, divides vertically into two equal guard cells and develops an intervening pore (Fig. 1, E). Sometimes, in anomocytic stomata, the adjacent epidermal cells divide and look like subsidiary cells. The stoma, thus, becomes perigenous. The perigenous stomata may be tetracytic (Fig. 1, F) or amphicyclic (Fig. 1, M).
3. **Paracytic stomata.**—The meristemoid divides into two unequal rectangular cells (Fig. 1, A, C). The larger rectangular cell differentiates into the first subsidiary cell, while the smaller divides again forming two unequal cells (Fig. 1, A). Of these, the central is smallest and becomes the guard mother cell and the flanking cells differentiate into the subsidiary cells. The guard mother cell divides vertically parallel to the previous divisions into two equal guard cells which develop an intervening pore (Fig. 1, C). The flanking subsidiary cells which are mesogenes divide and sometimes due to spatial readjustment the adjacent epidermal cells, which are perigenes, assume the form of subsidiary cells. The mature stomata are, thus, paracytic with 2–6 parallel flanking subsidiary cells (Fig. 1, K).

4. **Stomata with a single subsidiary cell.**—Sometimes of the two unequal rectangular cells, the larger differentiates as a subsidiary cell while the smaller becomes a guard mother cell. It divides vertically forming two equal guard cells. The mature stoma thus has a single flanking subsidiary cell (Fig. 1, L).

The development of anisocytic, paracytic and stomata with a single subsidiary cell resembles the mesogenous type of Pant (1965), since the subsidiary cells and the guard cells originate from the same initial. The ontogeny of anomocytic, tetracytic and amphicyclic stomata conforms to the perigenous type (Pant, 1965).

**DISCUSSION**

Foliar nectaries originate from a single epidermal cell. At maturity, they are patelliform consisting of 1-layered base, 2-layered stalk and 1–2-layered palisade-like epithelial cells. According to Haberlandt (1914), Rao (1926) and Parija and Samal (1936) the extra-floral nectaries originate from the glandular hairs. The present observations are in accordance with this view.

Haberlandt (1914) suggested that the function of the extra-floral nectaries is a further addition to the secretory function of the normal floral nectaries which in these plants are not in a high state of differentiation. Parija and Samal (1936) pointed out that patelliform glands keep away the unwelcome ants from visiting the flowers and thereby probably favour self-pollination, hindering cross-pollination which would have been otherwise possible. According to Chakravarty (1937, 1948) and Maheshwarji (1954), the extra-floral nectaries are said to allure protective ants against pests and excrete superfluous fluid from the plant body. The view of Haberlandt (1914) seems to be more probable. It has been consistently
observed that the ants enter deep into the flower even when the nectaries are present on the outer surface of the calyx and corolla. Anyway, the function of the extra-floral nectaries is to secrete sugary fluids.

Strasburger (1866–1867), Tognini (1897), Yarbrough (1934), Pant and Verma (1963), Gupta et al. (1965) and Inamdar (1969) described the ontogeny of anisocytic stomata. The meristemoid behaves like an apical cell and cuts off subsidiary cells in a spiral sequence along its three sides. Occurrence of diverse types of stomatal development on the same surface of the leaf has been observed. Different types of stomatal development on the same surface of the leaf depends upon the orientation of the spindle and plane of division in a meristemoid (see also Pant, 1965). A combination of different types of mature stomata on the same surface of the leaf has been reported by several workers (Sen, 1958; Pant and Kidwai, 1964; Pant and Mehra, 1964; Pant and Banerji, 1965; Paliwal, 1965; Inamdar, 1967, 1968, 1969). Juxtaposed contiguous stomata are common, while superposed ones are rare. Abnormal stomata with a single guard cell and aborted guard cells are also common.

ACKNOWLEDGEMENTS

I am deeply indebted to Professor V. Puri for critically reviewing the paper, encouragement and interest in my work. Thanks are due to Dr. J. K. Maheshwari for confirming the identification of this plant and Mr. M. A. Francis for help. I am grateful to Principal J. G. Chohan for his keen interest in my work.

REFERENCES


Inamdar, J. A.  

Maheshwari, J. K.  

Metcalfe, C. R. and Chalk, L.  

Paliwal, G. S.  


Pant, D. D.  

.. and Banerji, R.  

.. and Kidwai, P.  


Pant, D. D. and Mehra, B.  

.. and Verma, B. K.  

Parija, P. and Samal, K.  

Rao, L. N.  

Sen, S.  

Shanks, R.  

Solereder, H.  

*Strasburger, E.*  

*Tognini, F.*  

Yarbrough, J. A.  

*Zimmermann, J. G.*  

*Not seen in original.
Fig. 4. Abnormal Stomata (A–F, × 590). A. Stoma with a guard cell (Cell 'a' represents either a guard cell or a subsidiary cell). B. Anisocytic stoma with a single guard cell (cell 'a' is in the position of a guard cell or a subsidiary cell). C. Stoma with one of the guard cells aborted (arrow); note cuticular striations. D. Stoma with both the guard cells aborted (arrow). E. Adjacently placed stomata showing cytoplasmic connection bridge between them. F. Juxtaposed parallel contiguous stomata.