THE DEVELOPMENT OF ENDOSPERM IN
LANTANA CAMARA L.

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INTRODUCTION

A review of embryological literature on Lantana L. reveals that our knowledge of endosperm development in that genus is inadequate and is involved in ambiguity. Junell (1934) gave a brief comparative account of the formations of endosperm in three species—L. camara L., L. involucrata L., L. chamaedrifolia Cham. In the succeeding year Patermann (1935) followed the development of chalazal endosperm haustorium in L. trifolia. Tatachar (1940) working on L. indica Roxb., refuted some of Patermann's observations and described a non-endospermous origin of the chalazal haustorium. According to him, no endosperm haustorium is differentiated at the chalazal end but instead the antipodal cells together organise themselves into a persistent haustorial apparatus. The observations of Crétè (1942) on L. camara are somewhat casual, brief and indicate no reference to Tatachar's work. According to Crétè, however, the chalazal haustorium is of endospermal origin. In regard to the micropylar haustorium of Lantana again, the descriptions are not uniform. Tatachar described a two-celled micropylar haustorium in L. indica, while according to Crétè (1942) the corresponding structure in L. camara is many-celled.

MATERIAL AND METHODS

Material for the present investigation was collected near Madras, and fixed in Formal Acetic Alcohol. Customary methods of dehydration and infiltration were followed. Sections were cut 8–12μ in thickness and stained with Heidenhain's iron alum hematoxylin. Erythrosin in clove oil was used as counterstain.

OBSERVATIONS

The structure of the mature embryo-sac.—The mature embryo-sac consists of an egg apparatus, two juxtaposed polar nuclei and three multinucleate antipodal cells. Almost immediately after formation, the antipodal cells 420
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rapidly increase in size. The nucleus of each cell undergoes free nuclear mitotic divisions until six to eight nuclei are formed (Fig. 1). The coenocytic antipodal cells enlarge further so as to occupy nearly half or one-third of the vertical length of the embryo sac. It may be noted incidentally that the divisions of the nucleus of the antipodal cell need not strictly follow a simultaneous sequence; not only the divisions of certain nuclei may be accelerated

or retarded, but also some of the nuclei fail to divide. This situation explains the more or less fluctuating number of nuclei in the coenocytic antipodal cells. The antipodal unit begins to show signs of degeneration after four endosperm cells are formed (Fig. 6) and undergoes a somewhat rapid disintegration (Fig. 7). During or prior to degeneration the membranes of the antipodal cells often break down or collapse and the protoplasts of the cells in question merge with one another. At the stage when the endosperm haustoria are
well differentiated, the antipodal unit is completely absorbed and dark remains of its mass can be observed at the chalazal end of the embryo-sac (Fig. 7).

TEXT-FIGS. 5-10. Fig. 5. Three-celled endosperm. Fig. 6. Four-celled endosperm. Fig. 7. Differentiation of haustoria. Fig. 8. First few divisions in the middle tier of endosperm cells. Only two cells of the haustoria are shown. Fig. 9. Diagrammatic representation of the sequence of the planes of division of the primary endosperm nucleus. Fig. 9 a. Cross-sectional view of the micropylar and chalazal tiers of endosperm cells at levels marked aa and bb in Fig. 9. Fig. 10. Diagram of an young seed in longi-section showing haustoria, endosperm and embryo.
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ENDOSPERM

The first division of the primary endosperm nucleus (Fig. 3) is followed by the laying of a transverse wall which divides the embryo-sac into the primary micropylar and chalazal chambers (Fig. 4). Next, the micropylar chamber undergoes division by a vertical wall (Fig. 5). The chalazal chamber divides in the same plane and thus four endosperm cells in two tiers of two cells each are formed (Fig. 6). The two micropylar cells divide by transverse walls. This leads to a three-tiered group of endosperm cells each consisting of two cells—the micropylar tier, the middle tier and the chalazal tier. The micropylar tier differentiates as the micropylar haustorium and the chalazal tier as the chalazal haustorium. The middle tier by successive divisions gives rise to the cellular endosperm. The two cells of the micropylar haustorium soon undergo division by vertical walls so as to form a four-celled tier of more or less elongated cells (Fig. 7). These cells are aligned in a tetragonal configuration, which pattern remains undisturbed during later development (Figs. 7, 9 a, 11). Similar vertical division takes place in the cells of the chalazal tier also, resulting in a similar configuration of the four constituent cells (Fig. 7).

The sequence of the early planes of division of the primary endosperm nucleus are represented in Figs. 9, 9a.

The early few divisions in the middle tier are predominently in transverse plane (Figs. 7, 8), so that the body of the endosperm keeps pace with the elongation of the embryo-sac. Subsequently, however, intercalary divisions set in in diverse planes, thereby increasing in volume (Fig. 10).

The cells of the micropylar haustorium remain uni-nucleate and their free ends assume a more or less tapering appearance (Fig. 11); the cells remain distinct from each other during later stages also, after assuming a more or less falcate contour (Fig. 11). A few layers of endosperm cells lying just below the micropylar haustorium also get deeply stained (Fig. 11). They do not, however, show any change either in size or in shape; or in morphological appearance characteristic of endosperm haustoria. It is doubtful whether these cells function as accessory haustoria.

As has been stated already, the chalazal haustorium is composed of four uni-nucleate cells whose alignment is similar to that of the micropylar haustorial cells. The component cells of the chalazal haustorium are more or less cylindrical with their lower ends tapering (Figs. 7, 8). All the four cells remain uni-nucleate and each of them shows a cylindrical vacuole in the upper part (Figs. 7, 8) while the nucleus occupies the chalazal extremity
of the cell. In late stages the separating walls dissolve, the vacuoles disappear, and complete cytomyxis is accomplished. In longi-sections of young seeds the composite chalazal haustorium appears like a spindle-shaped structure with both ends somewhat tapering (Figs. 10, 12). Even though the lower end of the chalazal haustorium shows some tendency towards the formation of short lobes, no conspicuous branches are produced. The endosperm cells bordering upon the chalazal haustorium get stained deeper and are comparable to similar cells at the micropylar end (Fig. 12).

Discussion

The nature of the antipodal set-up in the genus *Lantana* needs a comment. A critical perusal of available literature indicates that the usual condition in the family Verbenaceae appears to be an early degeneration of the antipodal cells. However, in a few genera like *Lantana* (Junell, 1934; Tatachar, 1940), *Clerodendron* (Misra, 1939) they not only persist but also undergo divisions. Junell’s (1934) account is rather brief and ambiguous in the sense that he interpreted this feature as being due to the persistence of megaspores (or of their derivatives), a conclusion that is not borne out by evidence. Tatachar’s (1940) account clarifies the issue to some extent. According to this author, no megaspores are involved but the nuclei of the antipodal cells themselves undergo two or three free nuclear divisions. That this is so is also confirmed in the present investigation. In contrast to the situation in
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*Lantana, Clerodendron* exhibits actual division of the antipodal cells themselves so that after full development, a group of twenty cells constitute the antipodal apparatus (Misra, 1939).

Tatachar (1940) believed that the three coenocytic antipodal cells in *Lantana* constitute the chalazal haustorium. In his own words, "the three enlarged multinucleate antipodals together seem to form a very aggressive haustorium. Finger-like protrusions directed from them enter the chalazal tissue and their activity is clearly indicated by the degenerating cells of that region."

The sequence of endosperm development described here for *Lantana camara* L. differs in a significant way from the account given by Tatachar for *Lantana indica* Roxb. In the latter the endosperm does not build haustorial structures at the chalazal end. On the other hand, the antipodal unit is said to persist and function as an aggressive haustorium, at the chalazal end of the ovule. In *L. camara* not only an antipodal apparatus similar to the one described by Tatachar has been demonstrated but also the organisation of chalazal endosperm haustorium which is totally independent of the antipodals. Even after the initiation of the chalazal endosperm haustorium, the degenerating antipodal apparatus is clearly seen in every preparation (Figs. 7, 8). Thus, at least in *L. camara*, a normal chalazal endosperm haustorium, as in other members of the family, is organised.

A critical appraisal of Tatachar's (1940) illustrations of *L. indica* indicates the possibility of a different interpretation than the one given by him. It may be mentioned at the outset that Tatachar's Figs. 5–9 correspond in essence to Figs. 1, 2, 12, 5 and 7 respectively (of the present text). A comparison of these two sets of figures indicates the similarity between the two plants. The similarity becomes much clearer if Fig. 4 of the present paper is interpolated as Fig. 7 between Figs. 6 and 8 in sequence of Tatachar's illustrations. It is obvious that Tatachar mistook the more or less persisting antipodal apparatus for the chalazal haustorium. Also, he appears to have missed the complete sequence of the early stages. For example, his Fig. 8 (which corresponds to Fig. 5 of the present text) clearly indicates the initial cell of the chalazal endosperm haustorium being superposed on the antipodal apparatus. Again in Fig. 9 (corresponding to Fig. 7 of the present text) the blocking out of the endosperm haustoria could be seen. Thus in Fig. 9, the cell tiers from the chalazal end are: (a) antipodal apparatus, (b) two-celled chalazal endosperm haustorium, (c) the middle tier of two cells which by subsequent divisions builds the body of the endosperm and (d) the two cells of the apical tier constituting the initials of the micropylar
haustorium. Thus *L. camara* agrees in all essentials with *L. indica* so far as the development of chalazal endosperm haustorium is concerned. The actual number of cells constituting the chalazal haustorium in *L. camara* was not recorded by Crétè (1942). He described a binucleate chalazal haustorium whereas the present work indicates the actual number of cells involved.

Although Crétè (1942) figured a four-celled micropylar haustorium in *L. camara*, in the text he stated that it is composed of many cells. He also agreed with Junell (1934) in regard to the haustorial role of all the constituent cells. The present investigation has revealed that the micropylar haustorium in *L. camara* consists of only four cells at maturity. One point of difference between the present account and that of Crétè lies in the configuration of the four cells of the micropylar haustorium. Crétè’s figure indicates that it consists of two tiers of cells while in my material the cells are observed to lie consistently in a single tier.

It must be remarked that the endosperm cells subjacent to the micropylar haustorium also possess great avidity for stains and in the preparations the cells appear darkly or densely stained as those of the haustoria. This situation is reported in other species of *Lantana* also. As far as I am able to make out, these cells are not the derivatives of the micropylar haustorium. In view of this the statements of Junell (1934) and Crétè (1942) that more than four cells are involved in the micropylar haustorium and that the accessory cells are also functionally haustorial (by virtue of staining reactions) is to be looked upon as being unproven.

The presence of a zone of integumentary cells with ‘reticulate’ thickenings on their walls, around the micropylar haustorium was recorded for *Stachytarpheta indica* by Tatakhar (1940). A similar record for *Lippia nodiflora* was made by Maheshwari (1954). A zone of such integumentary cells has been observed in *L. camara* by Crétè (1942). The present investigation confirms this. The wall structure of the concerned cells here, however, is not due to reticulate thickenings but due to the presence of minute, closely spaced simple pits. Thus the individual cells belong to the category of selereids or stone cells.

**SUMMARY**

The multinucleate antipodal cells in *Lantana camara* L. are described with reference to their duration. The occurrence of mitotic divisions of the antipodal nuclei is confirmed. The antipodal unit begins to degenerate after the second cell generation in endosperm.
The pattern of mature delineation of endosperm is blocked out when the endosperm is composed of three superposed cells. The micropylar cell undergoes two divisions at right angles to each other to constitute a four-celled micropylar haustorium. The chalazal cell differentiates in a similar way into the chalazal haustorium. The middle cell builds up the body of the endosperm. The four cells of the micropylar haustorium remain as such at maturity while cytomixis is accomplished in the chalazal haustorium, at later stages. The reported occurrence of an antipodal haustorium is disproved.

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