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EMBRYOLOGY OF CASSAVA*

by P. N. RAO† *and* D. SARVESWARA RAO

Department of Botany, Andhra University, Waltair, A. P.

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Embryology of a perennially, vegetatively propagated cultivar H 97-of Cassava-*Manihot esculenta* Crantz. has been studied. Degeneration of the secretory anther tapetum, pollen mother cells, and pollen tetrads has been observed at various stages of development. Embryo sac development is of the Polygonum type. Though, healthy embryo sacs are formed, due to absence of pollination, seed set does not occur. Continuous asexual propagation appears to have upset the balance of sexual phase of the reproduction and resulted in a genetically blind stock. A critical appraisal of the existing data related to embryology of the crop has also been made.

INTRODUCTION

Manihot esculenta Crantz., commonly called as the cassava or tapioca, a native of Brazil, is a member of the Euphorbiaceae. This is a source of edible tuber and is cultivated as a field crop in several parts of India in a wide range of soil and climate conditions. The root tubers are a rich source of starch and sago. The cultivation of the crop is to be encouraged as it is grown easily, has large yields, is relatively free from pests and diseases and above all due to the low cost involved. Investigations on genetics, anatomy, cultural procedures, variety trials, productivity and cyanogenetic glucoside content (see Rogers 1963; Magoon *et al.* 1974) have been made on a large scale. But little is known about the embryology of the species of the genus *Manihot* Mill. which has about 200 spp. Previous work was confined to the report of a Polygonum type of embryo-sac development in *M. dichotoma* (see Schnarf 1931) and *M. palmata* (Ventura 1940); enumeration of pollen nuclear number in a few species of the genus (Hans 1973; Webster & Rupert 1973); reports on pollen grain structure (Punt 1962; Singh *et al.* 1968), and embryogeny in *M. carthaginensis* (Liem 1962). So far, there is practically no data on the embryology of *M. esculenta.* Some aspects of the pre-pollination embryology of a cultivar H 97 of cassava, together with a critical appraisal of the existing related data which may form a sound basis for further work, constitute the contents of the present paper.

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†*Present address :* Department of Botany, Nagarjuna University, Nagarjuna Nagar 522 510, Guntur Dist. (A.P.).

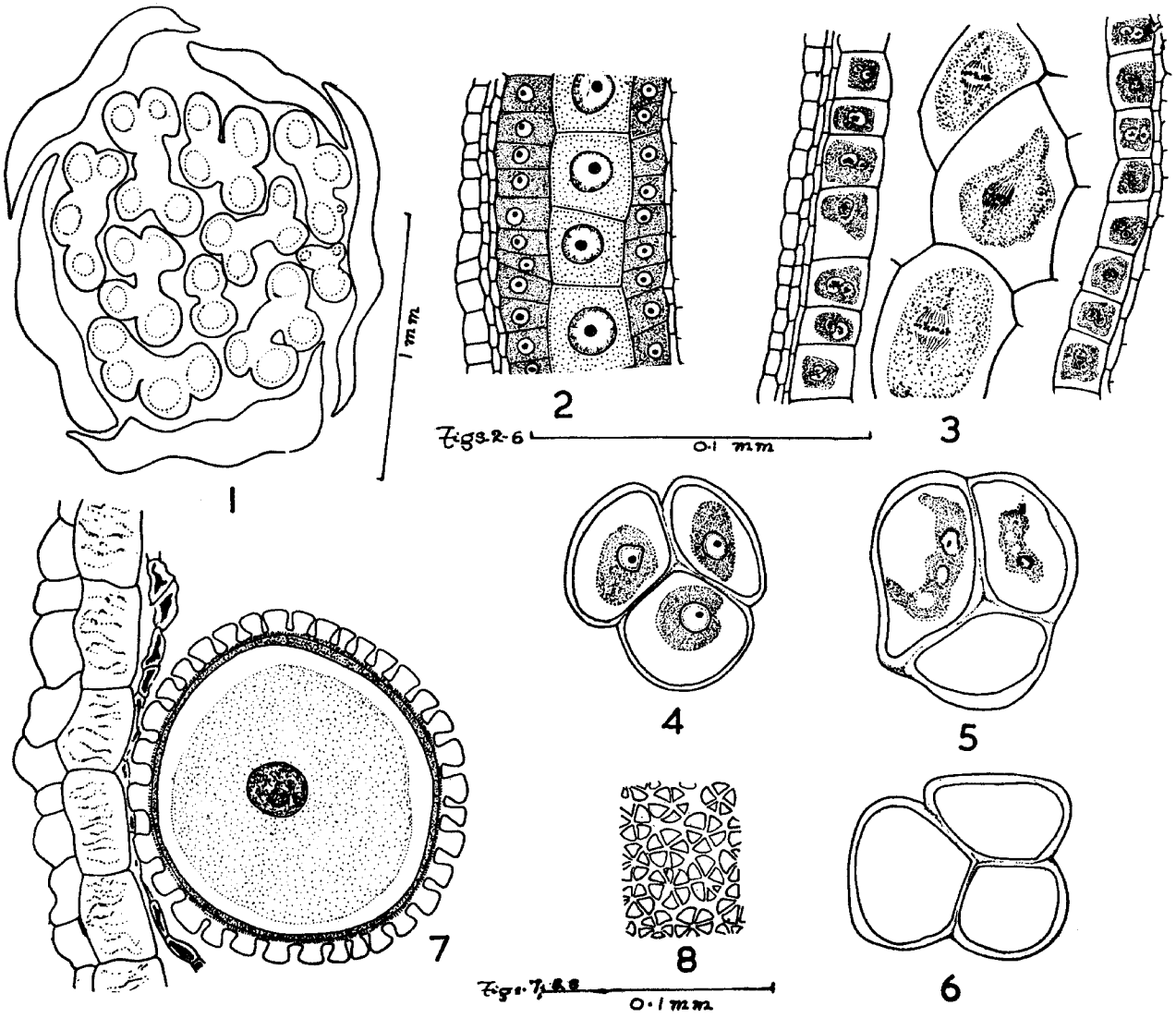
Materials and Methods

Flower buds of the crop were fixed in FAA, from the plants cultivated in fields in Waltair during November–December, 1975. Customary methods of study have been followed in dehydration and embedding. The sections were stained in safranin and fast green or Delafield's Haematoxylin.

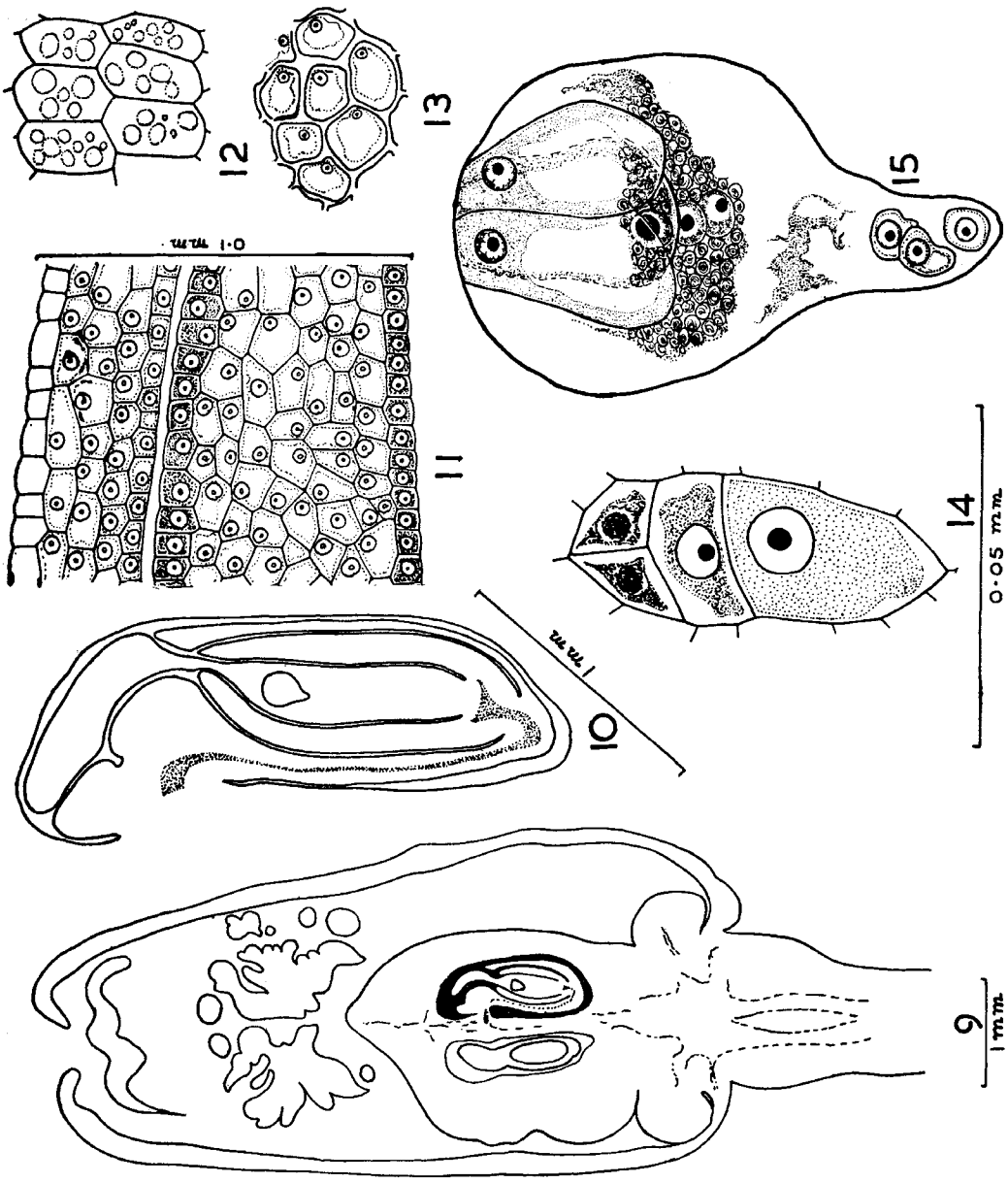
Results and Discussion

Development of anther and pollen—The plants are monoecious with flowers in dichasial cymes. The male flowers have a uniseriate perianth and ten dithecous, quadrisporangiate stamens (Fig. 1). The anther wall is tetraseriate with the epidermis, two middle layers and secretory tapetum of binucleate cells (Figs. 2, 3). Cytokinesis is simultaneous and pollen tetrads are of the tetrahedral type (Figs. 4, 5). Degeneration of the tapetum, pollen mother cells, and pollen tetrads occurs at various stages of development (Figs. 3-6). Occassionally, growth progresses up to the formation of 1-celled pollen (Fig. 7). At this stage the cells of the hypodermal wall layer show distinct fibrous thickenings. The development of the pollen could not be traced very far due to sterility and the anthers fail to dehisce. The pollen grains are of the 'Croton' pattern (Punt 1962) and are designated further to conform to 'Manihot' type. They are spheroidal with the outer exine showing uniform teeth-like columellae (Figs. 7, 8). No apertures could be observed at 1-celled stage as also cited by Singh *et al.* (1968). Mature pollen was described as periporate or pantoporate, spheroidal and tectate (Punt 1962; Singh *et al.* 1968). The pollen grains are among the largest in flowering plants ranging from 105.8 μ to 168.5 μ. Singh *et al.* (1968) studied pollen in 30 cultivars of cassava and came across 3 size groups: small (< 90 μ), medium (90-150 μ) and large (>150 μ). Often they may occur intermixed in a cultigen. Maurizio (1956) reported that an increase in the number of apertures occurs in connection with an increase in the chromosome number. There are diploid, triploid and tetraploid forms in the crop which has a basic number of 9 (Koshy 1947; Magoon & Krishnan 1974). The pore count may be used to distinguish polyploid material from diploids as is done with stomata as well as select 'palynoforms' from a population. Germination of the fertile pollen *'in vivo'* occurs within 8 hr and completed within 20 hr, while *'in vitro'* experiments were not yet successful (Singh *et al.* 1968). The same workers showed that the pollen fertility studies (as decided by morphological sterility determined by stainability with 1% acetocarmine) revealed fertile, sterile, partly sterile as well as male sterile lines in the different varieties of cassava.

Megasporogenesis and female gametophyte—The female flowers have a cup-shaped, slightly-petaloid, perianth with a glandular disc surmounted by the tricarpellary syncarpous and trilocular ovary. The pendulous anatropous ovules are attached to the axis in the upper half region (Figs. 1-2). They are oblong, narrow, bitegmic and crassinucellate. The nucellar beak is very long, serpentine and arches beyond the integuments (Fig. 10) towards the loosely arranged, vacuolated parenchymatous cells of the placental obturator (Figs. 10, 13). Koshy (1947) described that the placental obturator in *M. esculenta* grows towards the ovule, curves round the caruncle and enters the nucellus through the micropyle. This is erroneous because no true micropylar passage occurs in *M. esculenta* due to the long nucellar beak. It is the nucellar beak



FIGS. 1–8. 1, T. S. male flower; 2 & 3, Longisections of portions of the anther showing wall and pollen mother cells; 4–6, Formation of pollen tetrads and their degeneration; 7, L. S. portion of anther showing epidermis, hypodermal fibrous endothecium, remnants of the secretory tapetum and 1-celled pollen; 8, Portion of the exine surface.



FIGS. 9–15. 9, L.S. female flower; 10, L.S. mature ovule; 11, L.S. portion of the integument at the mature embryo sac stage; 12, Cells of the nucellar beak showing starch grains; 13, Enlarged view of the cells of the obturator; 14, 'T' shaped tetrad of megaspores; 15, Mature embryo sac.

that comes out of the micropyle to meet the obturator. The obturator never enters the ovule. Further, he mentioned that at the tip of the outer integument a soft tissue, caruncle is formed which caps the ovule. However, as evidenced by the present study in cassava and previous studies in Euphorbiaceae there is no development of the caruncle before fertilization. It is a post-fertilization phenomenon. The funicular vascular supply terminates at the chalaza (Fig. 10). There is no integumentary vascular supply. The embryo-sac development conforms to the Polygonum type (Figs. 14, 15) and is confined to the upper part of the narrow nucellus. The cells of the nucellar beak are packed with starch grains (Fig. 12). Considerable starch accumulates in the egg cell and around the secondary nucleus (Fig. 15). In the absence of pollination, the embryo-sac gradually degenerates. Among the thousands of plants observed, no seed was found. Continuous vegetative propagation is the reason for the sterility.

Post-pollination embryology— Due to reasons cited above, post-pollination embryological data could not be furnished. But Koshy (1947) remarked that in cassava the pollen tube in its passage to the embryo-sac directs its course through the obturator and that this interesting mechanism serves as a short cut to the micropyle besides being a nutritive tissue for the pollen tube. Apart from this, it is natural that the obturator and the nucellus degenerate after fertilization. The endosperm becomes cellular at maturity. It is massive and encloses the embryo (Koshy 1947). The embryogenesis is traced so far in only one species of the genus *Manihot carthaginensis* (Liem 1962) which is considered to be closely related to *M. esculenta* (Rogers 1963). Here it conforms to the *Myosurus minimus* type, as in the majority of the Euphorbiaceae investigated so far. Among the various cultigens of cassava, Magoon & Krishnan (1974) recognised three categories: those which flower and produce normal seeds, those which flower but produce sterile gametes and those which never flower at all. The material of the present study of the variety H 97 falls into the second category. It is in the individuals of the first category that intervarietal and interspecific hybridization can be attempted to realise the main cassava-breeding objectives, such as high protein and starch contents, low HCN content and breeding cassava mosaic virus resistant types. Mosaic resistent types have been obtained by hybridization with Caera rubber plants, *Manihot glaziovii* (Koshy 1947); Magoon & Krishnan 1974). High starch and protein varieties have been obtained by hybridization with *M. melanobasin* and *M. saxicola* as well as by mutation breeding by irradiating with doses of 4000 r and 7000 r (Magoon & Krishnan 1974).

Koshy (1947) described the seeds of cassava to be elliptical, black, grey or mottled, shining, resembling a castor seed. The seed coat is thick, hard and polished. In the seed the two thin cotyledons are pressed against each other by the endosperm.

The failure of pollen formation, and post-pollination development in the present study is ascribed to the continuous asexual propagation resulting in accumulation of high genetic load of deleterious recessive mutations leading to a genetically blind alley.

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