Some Observations on the Reproduction of
Tridax procumbens L.
II. Development of the embryo sac and embryo

S. Rogers

Department of Biology, Queen Elizabeth College (University of London),
Campden Hill, W. 8, London, England

Received April 2, 1968

Abstract

Observations of megaspore mother cell meiosis, fertilization and embryo development show Tridax procumbens to have a straightforward amphimictic type of reproduction. The embryo sac is monosporic and eight nucleate with prominent synergidae and the antipodal nuclei are contained within a short tubular haustorial outgrowth of one or three cells.

Fertilization follows within twelve to eighteen hours of pollination and embryo development conforms to the asterad pattern. No meiotic irregularities have been seen during division of the megaspore mother cell but this does not eliminate the possibility that a proportion of the observed 15% of sterile cypselas may result from meiotic failure rather than from failure of pollination or fertilization.

Introduction

Since apomictic mechanisms are widespread in the Compositae and particularly among taxa where polyploidy is known to have played a significant role in speciation, the possibility of some form of apomictic development of the embryo sac in Tridax procumbens cannot be eliminated without observation of the course of meiosis leading to the development of the embryo sac, fertilization, and the subsequent development of the embryo.

Materials and methods

Development of the embryo sac was followed in serial sections of whole capitula prepared in the same way as for pollen mother cell meiosis.

Fertilization and embryo development were studied using the ligulate florets only. Since these are the first to flower, the hermaphrodite disc florets can be removed prior to anthesis and the chance of unintentional contamination of the ligulate stigmas by self pollen is thereby eliminated. A proportion of the ligulate florets was invariable damaged or inadvertently removed during emasculation but leaving the ligulate florets on the capitulum gave more consistent and satisfactory results than pollinations carried out on detached florets maintained on damp filter paper in small petri dishes. The florets were fixed at 24, 36, 48, 72 and 96 hour intervals following self or cross pollination, and subsequently embedded singly and cut at 10μ. Acid
fuchsin, Meyers haemalum and Feulgen all gave satisfactory staining.

**Observations**

1. *Development of the embryo sac*

   Development appears to follow a normal amphimictic pattern. The ovule is anatropous and tenuinucellate. Only a single archesporial cell, which develops directly into the megaspore mother cell, can be distinguished. This lies in a hypodermal position surrounded by nucellar cells, three or four of which form a cap over it at the micropylar end. It can be readily recognised by its longitudinal elongation and prominent nucleus (Fig. 1a).

   Meiosis takes place subsequently to that in the pollen mother cells, divisions of the megaspore mother cell being found in florets whose anthers contain disintegrating tetrads and thickening endo-extines around the pollen grains. 18 bivalents are visible at diakinesis I (Fig. 2a) and the first megaspore division proceeds normally. There is a definite interphase between the two divisions and the spindles for the second lie in the same plane as those of the first, resulting in a chain of four megaspores (Figs. 4a–d Fig. 1b). The embryo sac develops from the chalazal megaspore, the other three spores soon disintegrating (Fig. 4e). The embryo sac is thus monosporic. Degeneration of the nucellus parallels the enlargement of the
embryo sac which thus comes to lie adjacent to the inmost integumental layer. This has already differentiated into a well defined endothelium whose cells contain dense cytoplasm and large nuclei. It persists until development of the embryo and endosperm causes tangential stretching of the cells resulting in their breakdown.

2. The embryo sac

Development of the megaspore results in a normal type of 8 nucelate sac (Fig. 3a) which shows the following characteristic features:

a) The synergidæ. These are well developed and break through the wall of the embryo sac at the micropylar end forming conspicuous projections into the micropyle (Fig. 4). Their tips are densely staining and either are very densely cytoplasmic or contain fine cellulose fibrils analogous to the filiform apparatus seen in Viola (West 1930). The tips appear to twist round one another and persist for 2–3 days after fertilization but are no longer visible in sacs containing multicellular capi-

---

Fig. 2. Megaspore mother cell at diakinesis showing eighteen bivalents. ×1110. b, three uninucleate antipodal cells. ×560.

Fig. 3. a, embryo sac prior to fertilization. b, embryo sac 24 hours after pollination showing two divisions of the fertilized oosphere and endosperm nucleus. In each the three antipodal nuclei are closely grouped within a single cell. Both ×350.
tate embryos 96 hours after pollination.

b) The oosphere. This is a large cell lying between the synergidae. At
its micropylar end it projects forward between the synergidae but does not extend beyond the limits of the embryo sac.

c) The primary endosperm nucleus. The two polar nuclei have fused prior to pollination and the resultant nucleus lies closely adpressed to the oosphere.

d) The antipodal nuclei. These are contained within a short tubular haustorial outgrowth. In some cases this consists of 3 distinct uninucleate cells (Fig. 2b), in others there is a single large cell in which the 3 antipodal nuclei are grouped closely together (Figs. 3a and b). The haustorium is non-persistent and plays no part in the nutrition of the developing embryo.

3. Post-fertilization development

Development follows rapidly on fertilization. Divisions of the endosperm nucleus give rise to a short free nuclear phase which is followed walling of the endosperm proceeding from the periphery of the sac inwards. Preparations made 24 hours after pollination show that where fertilization has been successful, at least two divisions of the endosperm nucleus have already taken place. Fertilization must, therefore, occur within 12-18 hours of pollination.

Division of the oosphere commences simultaneously and in 24 hours preparations the nucleus has generally divided once demarcating a smaller caplike head cell from a larger basal cell. A second division has occasionally taken place within this time giving a 4-celled embryo consisting of a head cell, two suspensor cells and the basal cell (Fig. 3b and Fig. 4g).

Further development of the embryo follows the asterad pattern and by the fourth day after pollination endosperm walling is complete and the embryo consists of a large actively dividing head, a multicellular suspensor and a small basal cell (Fig. 4h).

Discussion

These observations show that *Tridax procumbens* is a normal amphimictically reproducing species and that its success as a camp follower of man cannot be attributed as in many other species of Compositae, to the evolution of an apomictic system of reproduction superimposed upon the mechanism of amphimixis. Some of the 15% of unfilled fruits characteristic of open pollinated capitula may result from meiotic irregularities similar to those described in normal pollen mother cells i.e. quadrivalent or univalent formation, lagging bivalents and anaphase bridges. Such irregularities have not been observed in megaspore mother cell meiosis but the number of these cells that are seen in division is small compared with pollen mother cells and a low frequency of irregular divisions would easily pass unobserved.

Fertilization is successful following both self- and cross pollinations, and comparable stages of development are reached after the same time intervals. The low set of seed obtained when capitula are bagged and allowed to self pollinate unaided thus points to defective pollination or to failure of pollen
development on the stigmas rather than to a positive inhibition of the pollen tubes or failure of fertilization. This aspect of the reproductive biology of *Tridax procumbens* will be considered in the final paper of this series.

**Literature cited**