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Full Length Article

Microsporogenesis, Megasporogensis and Male and Female Gametophyte Development in *Feijoa sellowiana* (Myrtaceae)

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Abstract

Feijoa sellowiana Berg is cultivated as a non-timber forest tree in New Zealand, Colombia and France, and is well known for its high dietary value fruit. *F. sellowiana* was introduced into China during the 1980s. However, it is particularly prone to erratic fruit set and very little work has been conducted on its reproductive biology. *F. sellowiana* 'Mammoth' cultivar was subjected to a light microscopy analysis to clarify male and female gametogenesis. The results showed that the formation of anther wall conforms to the basic type. The tapetum is of the glandular type. Cytokinesis in microsporocyte meiosis is of simultaneous type, and the micropore tetrads are tetrahedral. Mature pollen grains are two-celled with three germ pores. The ovules are anatropous, bitegminous, and tenuinucellate. The megaspore tetrads are arranged linearly, and the megaspore at the chalazal end is functional. The functional megaspore undergoes three successive mitoses resulting in the formation of an 8-nucleate embryo sac of the *Polygonum* type. Our results elucidate the mechanism that regulates sexual reproduction in *F. sellowiana*, thus expanding the prospects for *F. sellowiana* breeding programs and further molecular and genetic analyses of this species.

Keywords: *Feijoa sellowiana*; Microsporogenesis; Megasporogensis; Male gametophyte; Female gametophyte

Introduction

Feijoa sellowiana (Berg) of Myrtaceae family is commercially cultivated as a fruit tree. It is native to the highlands of Northern Uruguay and Southern Brazil, and also found in western Argentina and Paraguay (Sharpe *et al*., 1993). It grows at altitudes > 800 m in Southern Brazil (Finatto *et al*., 2011), and is resistant to frost down to -9.4~–11.4ºC (Cui, 2010). This species is cultivated in several countries, including New Zealand, Colombia, France, Italy, USA, Japan, and China. Researchers at Shanghai Botanical Garden first brought *F. sellowiana* to China from Europe in the 1980s (Han *et al*., 2009). Thereafter, it was introduced to Jiangsu, Sichuang, and Hunan provinces. In 2007, we planted 3-year-old *F. sellowiana* on the campus of the Central South University of Forestry and Technology (Hunan, China). In China, flowering occurs from May to June, and fruiting from late October to November (Cui, 2010). The flowers have a pleasant scent and can be consumed when used to decorate dishes, salads, and desserts. The *Feijoa* fruit is rich in vitamins, minerals, and iodine and also contain many phenolic compounds, such as catechins, leucoanthocuanins, proanthocuanidins, and flavonols (Necati Barış Tuncel and Neşe Yılmaz, 2015). Its unique flavor makes it a potentially attractive fruit for farmers to grow, while providing an opportunity for a non-wood forest product to contribute to forest conservation (Santos *et al*., 2009).

The male and female gametophytes are critical for plant reproduction (Yadegar and Drews, 2004; Zou *et al*., 2013a). Fallen *Feijoa* fruit when sporogenesis of the gametophyte, pollination, or fertilization is abnormal. Therefore, it is important to study the reproductive biology of *Feijoa*. However, only a few published accounts of *Feijoa* sexual reproduction are available (Pescador *et al*., 2009; Finatto *et al*., 2011). This lack of basic knowledge is more evident for *Feijoa* trees. These are difficult, when not impossible, to grow in controlled conditions and seasonal flowering is not easy to overcome. This creates strong experimental constraints and the need to conduct most of the experimental work within a few months. It is generally accepted that better knowledge of the pollination and fertilization mechanisms may increase productivity (Zou *et al*., 2013a). Thus, knowledge of the embryology and the development of reproductive organs in *F. sellowiana* is essential to solve these problems.

Embryological studies are often useful, as they encompass virtually all events relevant to sexual

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reproduction. *F. sellowiana* male and female gametogenesis has not been investigated previously. The objective of this study was to investigate male and female gametogenesis in the 'Mammoth' *F. sellowiana* cultivar and provide basic information for our research projects.

Materials and Methods

Plant Material

The experimental site was a non-wood forest garden on the Changsha campus of Central South University of Forestry and Technology (longitude: east 112°59′32″; latitude: north 28°8′14″; altitude: 100 m). The site, which slopes gently and has been re-soiled, is located in the warm temperate zone of a humid region, with mean annual precipitation of 1360 mm and a mean annual temperature of 18.5°C. The experiment was conducted during 2009 and 2010 using 6-year-old *F. sellowiana* 'Mammoth' planted at a distance of 3 × 3 m. The other cultivars planted were *F. sellowiana* 'Unique', 'Coolidge', and 'Triumph' (Cui, 2010).

Bud Fixation and Sample Preparation

Complete male and female gametophyte development was observed in *F. sellowiana* 'Mammoth'. Representative flower buds were collected about every 3 days during 2009 and 2010. The material was fixed in FAA (70% alcohol: formalin: acetic acid = 89: 5: 6, v/v) and stored at 4°C prior to sectioning (Chehregani *et al*., 2011; Zou *et al*., 2013b).

Light Microscopy

The material was dehydrated in a graded ethanol series from water through 10–100% ethanol, embedded in paraffin with a 58–60°C melting point, and sectioned at 10-μm thickness using a microtome (Zou *et al*., 2013a). The sections were stained with Heidenhain's iron alum hematoxylin (Zou *et al*., 2014). Observations and photographs of the sections were obtained using a BX-51 microscope (Olympus, Tokyo, Japan).

Results

Formation of the Anther Wall

Floral emergence and development occurred over 2 months (mid–April to June; Table 1). We first observed the archesporial stage of microsporogenesis in buds in the middle April (Fig. 1A). These archesporial cells could be recognizable by their large volume, dense cytoplasm and conspicuous nuclei, and appeared at the corners of young anthers (Fig. 1A). The anthers were tetrasporangiate in late May (Fig. 1C). The archesporial cells differentiated below the anther epidermis during early development. These cells divide periclinally to form a primary parietal cell to the outside and a primary sporogenous cell to the inside (Fig. 1B). The primary parietal cells divided repeatedly through periclinal and anticlinal divisions to form the subepidermal endothecium and two middle layers (Fig. 1B). The outer cell layer began to form the massive nucleus by periclinal and anticlinal division. The inner cells formed sporogenous cells (Fig. 1B). The endothecial cells elongated gradually and acquired a thick fibrous shell at anthesis (Fig. 2H). The middle layers had a common histogenetic origin with the endothecium. It was detected by the microspore tetrad stage (Fig. 2A) and disappeared by the time the two-nucleate microspores (Figs. 2G–H). The middle layers appeared to undergo further divisions to form two layers. The rich starch in the mid-layer cells was digested and disappeared gradually, providing nutrition for pollen during development. The walls of the endothecium thickened after the microspores formed (Fig. 2C). The endothecium was a single layer when the pollen matured (Fig. 2H). The anther wall was usually comprised of five cell layers before maturation; i.e., single epidermis, endothecium, two middle layers, and the glandular tapetum. Thus, wall formation conformed to the basic type (Davis, 1966).

Microsporogenesis and Microgametogenesis

The anther primordium began to form as a teat comprising meristematic tissue enveloped by an epidermal layer (Fig. 1A). Simultaneously with the changes occurring in the walls of the microsporangia, four groups of hypodermal cells differentiated near each of the four corners of young anthers (Fig. 2B). A row of sporogenous cells derived from archesporial cells produced a large number of microspore mother cells after several mitotic divisions (Fig. 2C). The primary sporogenous cells underwent mitosis, forming secondary sporogenous cells, from which the microsporocytes were derived. The microsporocytes were discernable by their large volume, dense cytoplasm, and conspicuous nuclei (Figs. 2D–E). The microsporocytes underwent two cell divisions of meiosis. Meiosis I included prophase, metaphase (Fig. 1F), anaphase and telophase (Fig. 1G). As a result, the microspores formed a dyad. Microspore tetrads were formed via prophase II, metaphase II, anaphase II, and telophase II (Fig. 1H). Meiosis II resulted in a microspore tetrad from each dyad. The majority of the tetrads were tetrahedral (Fig. 2A), and a thick callose wall surrounded the microspore tetrad (Fig. 2A). The callose was deposited in the pollen mother cells at the onset of meiosis, reached a peak at metaphase II or anaphase II by enveloping the pollen mother cells or microtetrads (Fig. 2A), and disappeared at the end of meiosis. Callose cycling (or cellulose synthesis) during microsporogenesis may play an important role in protecting pollen mother cells from various environmental stressors and release of the microspores from the microtetrads. The second divisions in all sections occurred only after a wall formed between the microspores.

Table 1: Phenology of microspore and megaspore development in *F. sellowiana* 'Mammoth' in Hunan, China 2009–2010

Date	Developmental event in stamens	Developmental event in pistils
April 23 ~April 26	Young anther	Ovule primordial arise
April 27 ~April 30	Microspore mother cell stage	The nucellus started protrusions
May 1 ~ May 3	Meiosis of microspore mother cell stage	Nucelli continue projection
May 4 ~ May 7	Microspore tetrad stage	Inner and outer integument initiation to elongation
May 7 ~ May 10	Central nucleus microspore stage	The megaspore mother cell formation
May 11 ~ May 13	The late uninucleate stage	The megaspore mother cell meiosis to form tetrad
May 14 ~ May 16	Binucleate stage	The uninucleate embryo sac
May 17 ~ May 18	Two-celled pollen	Binuclear or four nuclear embryo sac
May 18 ~ May 20	Mature pollens	Eight nuclear embryo sac
May 21 ~ June 20	Pollen grains released	Mature embryo sac

The microspores soon separated from each other and were released from the tetrads as free microspores (Figs. 2B–C). Each microspore had a dense cytoplasm, conspicuous wall, and a prominent and centrally placed nucleus (Fig. 2B). The uninucleate microspores gradually increased in volume and the number of vacuoles (Figs. 2D–E). The nucleus took a peripheral position as the central vacuole developed (Fig. 2F). Microspore development was divided into three periods: early or mid-uninucleate (Figs. 2D–E), late-uninucleate (Fig. 2F) and binucleate. At this stage, the uninucleate microspore underwent an asymmetric mitotic division (microspore mitosis) to give rise to two cells, but the vegetative cell and the generative cell was not observed. The mature pollen grains contained two cells in mid-May and formed an approximate equilateral triangle with three germ pores (Figs. 2G, H). The anthers were dehiscent and the pollen grains were shed on May 21 (Table 1).

Ovule Development

The parenchyma cells beneath the epidermis of the ovule in the micropyle end developed into an archesporial cell in late April (Fig. 3A). The nucellar epidermal layer and the subdermal layer cells developed by anticlinal division (Fig. 3A) and the nucellar cells below the subdermal layer constantly increased and developed into primary archesporial cells (Fig. 3A). The archesporial cells easily were recognized by its large size as compared with that of the adjacent cells. The nucellar epidermal cells underwent rapid mitosis, which leaded to formation of the inner integument primordium (Fig. 3B). However, the primordium of the outer integument was initiated a little later than the inner one (Fig. 3B). Finally, both the inner and outer integuments were two or three cell layers in thickness (Fig. 3B).

The inner and outer integuments elongated rapidly and almost enclosed the nucellus (Fig. 3B). The archesporial cell in the nucellus formed a primary parietal cell by periclinal cell divisions (Fig. 3B). The outer integument overgrew the inner integument and completely enclosed the nucellus. At a later stage, the ovules occupied part of the ovarian cavity (Fig. 3B).

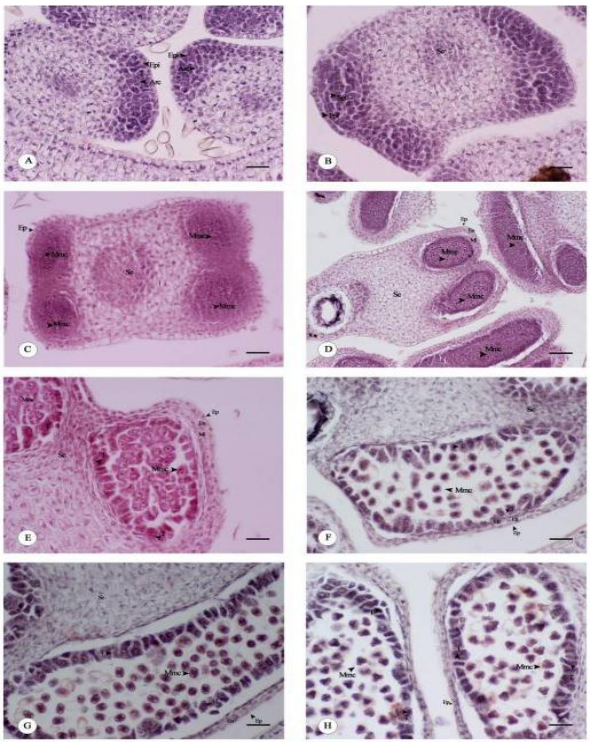

Fig. 1: Formation of microspores and development of the male gametophyte in *F. sellowiana* 'Mammoth'. A, The archesporial cells and protoderm appeared at the corners of young anthers. B, Details of the anther showing the sporogenous cell and primary parietal layer. C, Details of the anther showing the microspore mother cells. D-E, Details of the anther showing the microspore mother cell, the epidermal layer, endothecium, the two middle layers, and the tapetum. F, Details of a late microspore mother cell wall at metaphase in meiosis I. G, Details of a late microspore mother cell wall at telophase in meiosis I. H, Details of a late microspore mother cell wall at telophase in meiosis II. Arc, archesporial cell; En, endothecium; Ep, epidermis; Epi, protoderm; Mi, middle layers; Mmc, microspore mother cell; Ppl, primary parietal layer; Se, septum; Sgc, sporogenous cell; T, tapetum. Scale bars: D = 100 μm; A–C and E–H = 50 μm

The ovaries were superior, bicarpellate, and unilocular or multilocular with parietal placentae. The integuments started with periclinal and oblique divisions at the base of the nucellus. The integument reached the top of the nucellus and formed a micropyle through continuous cell division. The ovules in *F. sellowiana* 'Mammoth' were anatropous (Fig. 3B), and their structure resembled that described for other *Feijoa* species (Pescador *et al*., 2009).

Megasporogenesis and Megagametogenesis

A single archesporial cell differentiated under a single layer of epidermal cells in the young nucellus (Fig. 3B). This archesporial cell functioned as a megasporocyte and was easily distinguished from other cells because of its large size, prominent nucellus and dense cytoplasm (Fig. 3B). The archesporial cell did not develop into a parietal layer. However, the nucellar epidermis produced a subdermal layer by periclinal division between the epidermis of the ovule and the megaspore mother cell (Fig. 3B). Thus, the ovule was crassinucellate, as reported by Davis (1966).

The megasporocyte produced a dyad of megaspores by meiosis. A megaspore tetrad was formed after nuclear divisions. Finally, a linear tetrad of megaspores was formed (Fig. 3C). Three megaspores in the tetrad degenerated and the chalazal megaspore became functional (Fig. 3D). This functional megaspore developed into a two-nucleate embryo sac after the first successive meiotic division (Fig. 3E). Second mitosis resulted in the formation of the four-nucleate embryo sac. Later, by anther mitotic division, an eight-nucleate embryo sac was produced (Figs. 3F–H). The embryo sac began to mature when the flowers were blooming in late May (Table 1). Three cells (or nuclei) were grouped together at the micropylar end and constituted the egg apparatus (Fig. 3F). The cells were initially similar, then one of them developed into an egg cell, whereas the other two became synergid cells with a large vacuole at the micropylar end (Figs. 3F–G). Two polar nuclei (positioned close to each other) fused at the center and moved close to the egg apparatus. The synergid cell at the micropylar end degenerated (Fig. 3H), whereas the three antipodal cells at the chalazal end were ephemeral and degenerated soon after fertilization. The development of the female gametophyte thus conformed to the *Polygonum* type.

Discussion

The anther of *F. sellowiana* 'Mammoth' is microdiodanges. The mature anther wall consists of an epidermis, a one-layered endothecium, two middle layers, and a single-layered tapetum. Cytokinesis in microsporocyte meiosis is of the simultaneous type, and the micropore tetrads are tetrahedral. Formation of the anther wall conforms to the basic type. The pollen grains are monocolpate and two-celled with three germ pores at shedding. The ovules are anatropous, bitegminous and tenuinucellate.

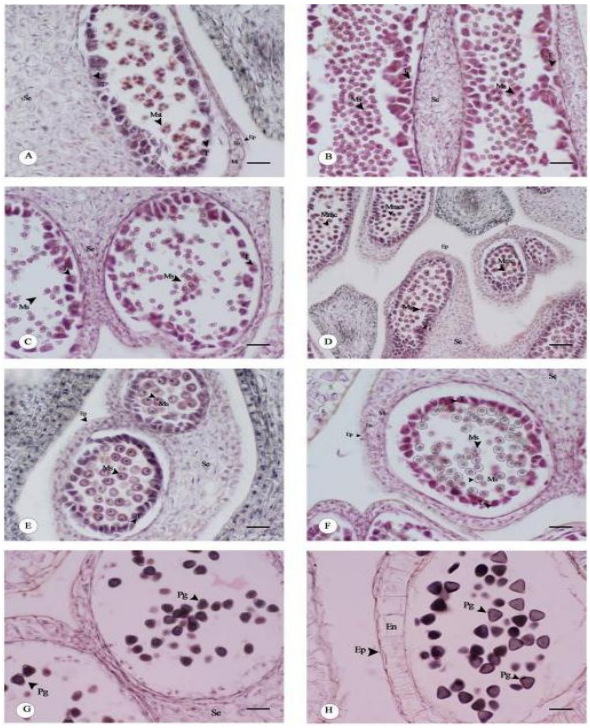

Fig. 2: Formation of microspores and development of the male gametophyte in *F. sellowiana* 'Mammoth' A, Details of a microspore showing tetrahedral microspore tetrads enclosed in the callose. B, C, Details of the anther showing microspore cells at the free stage. D, Details of the anther showing the central nucleus microspore stage. E, High magnification of D showing the central nucleus microspore stage. F, Details of the anther showing the late-nucleus microspore stage. G-H, Details of anthesis showing the anther wall composed of the epidermis, endothecium, and mature pollen grains. En, endothecium; Ep, epidermis; Mmc, microspore mother cell; Mi, middle layers; Ms, microspore; Mst, microspore tetrad; Se, septum; T, tapetum; Pg, pollen grains. Scale bars: D = 100 μm; A–C and E–H = 50 μm

The archespore, which is directly under the nucellar epidermis, develops into the megaspore mother cell. The megaspore tetrad is arranged linearly, and the megaspore at the chazlazal end is the functional megaspore. The eight-nucleate sac is formed by three divisions of the functional megaspore and therefore of the *Polygonum* type of development.

Some striking features are found in *Feijoa*. (1) The anther wall is usually comprised of five cell layers; i.e., a single epidermis, an endothecium, two middle layers, and the tapetum. Davis (1966) classified development of the anther wall into four types of basic, dicotyledonous, monocotyledonous and reduced. Formation of the anther wall in *Feijoa* conforms to the basic type. Because data on the embryological characters of Myrtaceae are insufficient,

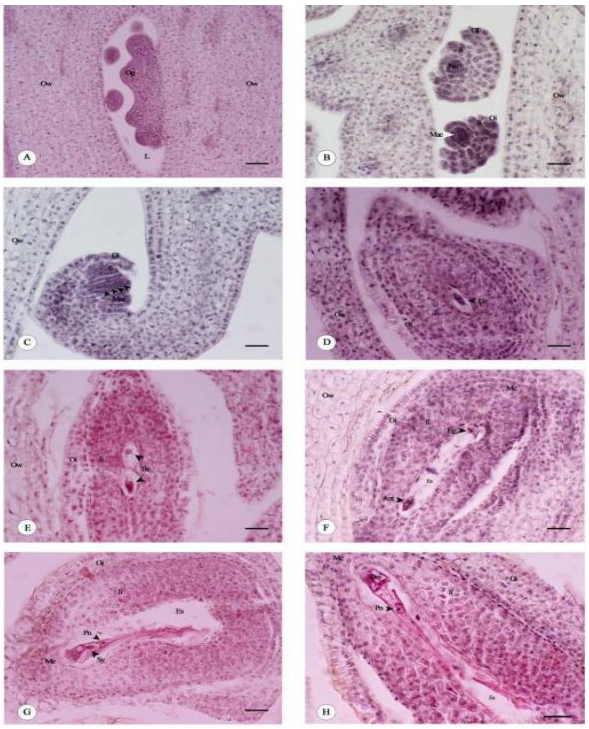

Fig. 3: Formation of megaspores and development of the female gametophyte in *F. sellowiana* 'Mammoth' A, Longitudinal section showing ovule primordium, locus, and ovarian wall. B, Longitudinal section showing initiation and development of the inner and outer integuments, nucellus, megaspore mother cell, and ovarian wall. C, Longitudinal section showing a megaspore mother cell at the tetrad stage. D, Longitudinal section showing a uninuclear embryo sac, inner and outer integuments, and ovarian wall. E, Longitudinal section showing a binuclear embryo sac, inner and outer integuments, and the ovarian wall. F–H, Developmental stages of a mature embryo sac. F, Longitudinal section showing an egg cell at the micropylar end, three antipodal cells at the chalazal end, and the inner and outer integuments. G, Longitudinal section showing a synergid cell at the micropylar end, polar nuclei, and the inner and outer integuments. H, Longitudinal section showing a degenerated synergid cell, two central polar nuclei, and the inner and outer integuments. Ant, antipodal cells; Be, binuclear embryo sac; Dsy, degenerated synergid cell; Eg, egg cell; ES, embryo sac; II, inner integument; L, locus; Me, micropylar end; Mac, megaspore mother cell; Nu, nucellus; Oi, outer integument; Op, ovule primordial; Ow, ovary wall; Pn, polar nuclei; Sy, synergid cell; Ue, uninuclear embryo sac. Scale bars: A = 100 μm; B–H = 50 μm

the formation patterns of the anther walls in taxa other than *Feijoa* are unknown. Pescador *et al*. (2009) reported that the main cellular events occur synchronously in the zygotic embryogenesis structures in *F. sellowiana*, but details for the male gametophyte developmental process are lacking. (2) Five microspore tetrad arrangement patterns are generally recognized in angiosperms: tetrahedral, isobilateral, linear, T-shaped, and decussate (Xue *et al*., 2005). We observed that the *F. sellowiana* tetrads were tetrahedral in shape. (3) The tapetum during anther wall development is of the glandular type. This tapetum type has been reported in other species of Myrtaceae (Baskorowati *et al*., 2010a, b). At about the time the pollen tetrad appears, the walls of the tapetal cells become indistinct, and the tapetal cells degenerate at their original site. The tapetal cells degenerate completely when the anthers dehisce. The main functions of the tapetum include producing the pollen wall components, providing nutrients for pollen development, and providing the enzymes necessary for release of the microspores from the tetrads. In addition, all nutrients reaching the sporogenic cells must pass through the tapetal cells (Qu *et al*., 2010). (4) Microsporogenesis of *F. sellowiana* is successive. Mature pollen grains contained two cells in late May, and formed an approximate equilateral triangle with three germ pores. The morphology of *Feijoa* pollen agreed with the main features of Myrtaceae pollen (Yang *et al*., 2012). Male sterility may be an important factor influencing fruit production (Zou *et al*., 2013a). Male sterility is the result of a failure to form functional stamens, microspores, or gametes. According to Qu *et al.* (2010), some failed plants develop normal pollen, probably caused by abnormal development in the sporogenous tissue, the tapetum layer, and the microspore. Male sterility is usually accompanied by abnormal callose deposition or anomalies in the tapetum (Kaul, 1988). However, we did not find any abnormal callose deposition or anomalies in the tapetum during microsporogenesis in *F. sellowiana* 'Mammoth', indicating that the male gametes were fertile and could pollinate. (5) Davis (1966) classified the embryo sac development into 11 types: *Polygonum*, *Oenothera*, *Allium*, *Endymion*, *Plumbago*, *Peperomia*, *Fritillaria*, *Drusa*, *Adoxa*, *Penaea* and *Plumbagella*. We found that the *Feijoa* embryo sac conformed to the *Polygonum* type. The pattern of formation megagametogenesis of taxa other than of *F. sellowiana* is unknown because sufficient data on embryological characters of Myrtaceae are lacking. (6) Three megaspore tetrad arrangement patterns are generally recognized in angiosperms, including two column, linear and T-shaped (Davis, 1966). We found linear tetrads in *F. sellowiana* 'Mammoth'.

The embryological attributes of all Myrtaceae family members need to be clarified.

Conclusion

We clarified the reproductive stages and considered similarities among *F. sellowiana* cultivars. Microgametogenesis resulted in binucleate pollen in *F. sellowiana* 'Mammoth', as observed in other *Feijoa* plants. Macrogametogenesis was of the *Polygonum* type.

We studied the cytological and embryological characteristics of *F. sellowiana* 'Mammoth' for the first time. The reproductive biology of *F. sellowiana* cultivars remains poorly understood and various aspects remain to be studied in depth. Only when more is known about the reproductive biology of Myrtaceae will we be able to understand and control fruit yield and quality in *F. sellowiana*.

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