Flora 207 (2012) 712–720

Contents lists available at SciVerse ScienceDirect

Flora

journal homepage: www.elsevier.de/flora

Anther structure and pollen development in *Melicoccus lepidopetalus* (Sapindaceae): An evolutionary approach to dioecy in the family

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ARTICLE INFO

Article history:
Received 14 March 2012
Accepted 28 July 2012

Keywords:
Dioecy
Flower morphs
Anatomy
Anther
Pollen grains
Ultrastructure

ABSTRACT

Anther and pollen development in staminate and pistillate flowers of dioecious *Melicoccus lepidopetalus* (Sapindaceae) were examined by light and electron microscopy. Young anthers are similar in both types of flowers; they consist of epidermis, endothecium, two to four middle layers and a secretory tapetum. The microspore tetrads are tetrahedral. The mature anther in staminate flowers presents compressed epidermal cells and endothecium cells with fibrillar thickenings. A single locule is formed in the theca by dissolution of the septum and pollen grains are shed at two-celled stage. The mature anthers of pistillate flowers differ anatomically from those of staminate flowers. The epidermis is not compressed, the endothecium does not develop fibrillar thickenings, middle layers and tapetum are generally persisting, and the stomium is nonfunctional. Microspore degeneration begins after meiosis of microspore mother cells. At anthesis, uninucleate microspores and pollen grains with vegetative and generative nuclei with no cytokinesis are observed. Some pollen walls display an abnormal exine deposition, whereas others show a well formed exine, although both are devoid of intine. These results suggest that in the evolution towards unisexuality, the developmental differences of anther wall tissues and pollen grains between pistillate and staminate flowers might become more pronounced in a derived condition, such as dioecy.
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Introduction

The family Sapindaceae s.str. comprises about 140 genera and 1800 species (Ferrucci, pers. comm.), mainly distributed in tropical and subtropical regions. The species possess climber, tree or shrub habit, and are mostly monoecious, rarely dioecious or polygamous. Radlkofer (1931–1934) reported dioecy in 28 genera from 10 tribes of the family. Both genera of the American tribe *Melicocceae*, *Melicoccus* P. Br. (Radlkofer, 1931–1934) and *Talisia* Aubl. (Ferrucci, 1991), present dioecy. The genus *Melicoccus* consists of 10 tree species, distributed throughout Central and South America, and only *M. lepidopetalus* Radlk. occurs naturally in a larger area comprising parts of Argentina, Bolivia (Santa Cruz), Brazil (Mato Grosso do Sul) and Paraguay (Ferrucci, 1991; Acevedo-Rodríguez, 2003).

Although Sapindaceae is a diverse family with a wide distribution, works on general embryological descriptions have focused on a limited number of species. Most of the available works include Asian species of *Filicium* Thwaites ex Benth. & Hook. f. (Gulati and Mathur, 1977), *Allophylus* L. (Mathur and Gulati, 1980, 1989), *Lepidopetalum* Bl. (Mathur and Gulati, 1981), *Xerospermum* Bl., *Nephelium* L., *Pometia* J.R. Forst. & G. Forst. (Ha et al., 1988), as well as *Cardiospermum halicacabum* L., which is widely distributed (Kadry, 1946; Nair and Joseph, 1960). Moreover, in all these studies, light microscopy was the only technique used to examine anther structure and male gametophyte development.

Sterility mutations that give rise to specialized unisexual flowers are the starting point for the evolution of separate sexes from combined sexes in flowers (Bawa, 1980; Freeman et al., 1997). A common feature in both monoecious and dioecious species of Sapindaceae is the presence of staminate flowers with rudimentary gynoecium and perfect flowers that are functionally pistillate, with nonfunctional stamens, although also perfect flowers exceptionally occur in *Dodonaea* Mill. (Ferrucci, 2005). Thus, these flower morphs are unisexual by abortion of the nonfunctional reproductive organs of the opposite sex, which are recognized in the literature as type I (Ainsworth, 2000; Mitchell and Diggle, 2005), as opposed to unisexual flowers from inception, referred to as type II. Although the stamens of pistillate flowers appear to be always indehiscent, interestingly the mechanisms that could lead to androecial termination development are diverse and may occur at different stages (Ainsworth, 2000), representing several distinct developmental transitions in the evolution from perfect to unisexual flowers (Mitchell and Diggle, 2005). Anatomical examinations in these types of flowers are scarce in the family. However, a recent paper has revealed ultrastructural details on anther development,

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http://dx.doi.org/10.1016/j.flora.2012.07.003

and identified cytological events in the tapetum layer, related to male sterility in functionally pistillate flowers of *Cardiospermum grandiflorum* Sw. and *Urvillea chacoensis* Hunz., both monoecious species with climbing habit (Solís et al., 2010).

Melicoccus lepidopetalus has been studied in terms of taxonomy and pollen morphology, and it has been included in a phylogenetic analysis of Sapindaceae (Muller and Leenhouts, 1976; Acevedo-Rodríguez, 2003; Buerki et al., 2009). However, anther and pollen development in this genus has not been investigated.

The aim of this paper was to provide a comparative description of pollen and anther development in the two flower morphs of *Melicoccus lepidopetalus*, using light and transmission electron microscopy. Features accompanying development in anthers and pollen of pistillate flowers were compared with those of previously studied species to identify possible differences in general mechanisms involved in preventing the production of functional pollen grains.

Material and methods

Light microscopy

Flowers of both types at different developmental stages were fixed in formalin–alcohol–acetic acid 1:1:3 (FAA). Voucher specimens were deposited at the Instituto de Botánica del Nordeste herbarium (CTES), Argentina.

Transverse serial sections of floral buds and flowers at anthesis were made by conventional methods. The material was dehydrated in a series of graded ethanol solutions with a rinsing pre-impregnant of tertiary butyl alcohol (González and Cristóbal, 1997). For infiltration in paraffin, the technique of Johansen (1940) was applied, and the material was later embedded in 'Histoplast®' (Fisher Scientific, Hampton, USA). Sections (12 μm thick) were cut with a rotary microtome, stained with Astra blue-safranin (Luque et al., 1996), and mounted with synthetic Canada balsam (Biopur, Buenos Aires, Argentina). Slides were examined using a Leica DM LB2 (Leica, Wetzlar, Germany) binocular microscope fitted with a digital camera.

Scanning electron microscopy (SEM)

Stamens for scanning electron microscopy were dehydrated by transfer through an acetone series and critical-point dried; the specimens were then sputter coated with gold-palladium. SEM micrographs were obtained with a scanning electron microscope JEOL 5800 LV at 20 kV (JEOL USA, Peabody, MA, USA).

Transmission electron microscopy (TEM)

For transmission electron microscopy examination, fresh anthers at different developmental stages were fixed in 1% glutaraldehyde, 4% formaldehyde in phosphate buffer (pH 7.2) for 2 h and post-fixed in 1.5% OsO_4 at 2 °C in the same buffer for 3 h. The material was dehydrated in an ascending acetone series and embedded in Spurr resin. Ultrathin sections (750–900 nm) were made on a Sorval ultramicrotome and stained with uranyl acetate and lead citrate (OïBrien and McCully, 1981). The sections were examined with a JEOL 100C TEM (JOEL USA, Inc., Peabody, MA).

Material examined

Melicoccus lepidopetalus Radlk.: ARGENTINA. Province of Corrientes: Capital. Corrientes, 8-2008, *Zini & Ferrucci 1*; *Idem*, *Zini & Ferrucci 2*. Province of Corrientes. Departament Capital, 9-1978. *Martínez Crovetto 11313*. Province of Chaco. Departament 1° de Mayo, Colonia Benítez, 10-1951, *Schulz 8119*. Province of Corrientes. Departament Capital, 10-1983. *Ferrucci 196*.

Results

Floral morphology

Flowers of *M. lepidopetalus* are actinomorphic, 5 mm in length; staminate flowers have eight stamens, exserted, 4 mm in length, with dehiscent anthers (Fig. 1A), and a gynoecium reduced to a pistillode, whereas pistillate flowers have smaller stamens, 2 mm in length, with indehiscent anthers (Fig. 1B), and a fully developed pistil.

Anther development

Anthers of both staminate and pistillate flowers are bithecal and tetrasporangiate. At anthesis, SEM observations show that the epidermal cells of staminate flower anthers are dehydrated and show a cuticle slightly striated, whereas in pistillate flowers, those cells are turgescent and smooth (Fig. 1C and D). Unlike in staminate flowers, pollen grains of pistillate flowers are dehydrated (Fig. 1E and F). Both types of flowers share the anatomy of the filament; in transverse sections, two or three layers of subepidermal tanniferous cells are observed, and a single periphloematic vascular bundle supplies each stamen.

Archesporial isodiametric cells differentiate in young anthers, dividing periclinally to form outer primary parietal cells and inner sporogenous cells. The latter undergo periclinal divisions to form secondary sporogenous cells, which finally differentiate into microspore mother cells. Primary parietal cells undergo periclinal divisions, resulting in two layers of secondary parietal cells. The outer one divides periclinally, forming two cell layers, namely the endothecium and the upper middle layer, whereas the inner one forms the lower middle layer and the tapetum. The two middle layers may further divide periclinally.

At microspore mother cells stage the anther wall consists of an epidermis, an endothecium with thin-walled cells and conspicuous nuclei, two-four middle layers and a secretory tapetum.

For a clear interpretation, the results are organized by ontogenetic stages. Four stages were identified: microspore mother cell, tetrad, free microspore and mature pollen grain stages.

Microspore mother cell stage

Staminate flowers

Sporogenous tissue differentiates into microspore mother cells (MMC), which are surrounded by callose deposited between the plasmalemma and the MMC wall (Fig. 2A). The cytoplasm of the MMC presents numerous mitochondria, rough endoplasmic reticulum (ERr) with expanded cisternae, free ribosomes and dictyosomes (Fig. 3A and B).

The tapetum is well differentiated and can be clearly distinguished from the other anther wall layers by the denser cytoplasm of its cells (Fig. 2A) and the abundant mitochondria, ERr and dictyosomes with numerous vesicles (Fig. 3C). At this development stage, most tapetal cells suffer nuclear divisions, giving rise to two-nucleate cells. Cytoplasmic connections between these cells were not observed.

Pistillate flowers

Microspore mother cells contain a conspicuous nucleus (Fig. 4A); the cytoplasm of these cells has some mitochondria and abundant free ribosomes (Fig. 4B). The tapetum cells present a similar ultrastructure but with less ERr than staminate flowers (Fig. 4B).

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