



Research article

Embryology of *Mammillaria dioica* (Cactaceae) reveals a new male sterility phenotypeDaniel Sánchez^a, Sonia Vázquez-Santana^{b,*}^a CONACYT – Laboratorio Nacional de Identificación y Caracterización Vegetal, Departamento de Botánica y Zoología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan, C.P. 44171, Jalisco, Mexico^b Laboratorio de Desarrollo en Plantas, Departamento de Biología Comparada, Facultad de Ciencias, Universidad Nacional Autónoma de México, Coyoacán, C.P. 04510, Ciudad de México, Mexico

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ABSTRACT

Although most of angiosperms have bisexual flowers, unisexuality has evolved in different angiosperms lineages. Bisexual flowers have been reported for the majority of species in Cactaceae; however, three of four subfamilies have members with unisexual flowers. *Mammillaria dioica* (Cactoideae) has been reported having unisexual flowers in gynodioecious, dioecious or trioecious breeding systems. However, a developmental study is missing to clarify the breeding system and the anther or ovule abortion process. This study describes breeding system and embryology of *M. dioica* from a population at Baja California Sur, México, through the careful examination of floral morphology and by using light and scanning electron microscopy at different stages of floral development. Hermaphrodite and female individuals were identified in the population with a ratio of 67.5% and 32.5% respectively. In pistillate and bisexual flowers, the ovary presents many campylotropous, bitegmic and crassinucellate ovules with well-formed style and stigma, likewise both morphs produce fruits and seeds. Moreover, in bisexual flowers, stamens are well-developed and contain pollen grains, anther wall development is of the monocotyledonous type, the microspore tetrads are tetrahedral, and mature pollen grain is three-celled with reticulate exine and tricolpate. In pistillate flowers, the anthers develop just before the meiosis of the microspore mother cells, and are collapsed at anthesis; the tapetum is bi-layered and exhibits abnormal growth, each cell is uninucleate in both layers. The inner layer of tapetum develops fibrous reticulate cell wall thickenings, while endothecium develops U-shapes cell wall thickenings. No tapetal secretory layer was observed, which means a fail to support the development of microspore mother cells. This male sterility phenotype has not been reported for other species of Cactaceae with unisexual flowers neither flowering plants.

1. Introduction

In angiosperms, flowers show a great diversity of size, shapes, colour, and matting systems (Barrett, 2002); however, 90% of them develop bisexual flowers while the remaining 10% have evolved some form of unisexuality (Ainsworth, 2000; Bawa and Beach, 1981). Dioecy and other breeding systems have independently originated in many flowering families, and are found in several floras around the world (Geber et al., 1999). Sexual diversity in plants has been explained as a mechanism that promotes allogamy to reduce inbreeding depression (Barrett, 2002). A flower becomes unisexual from the lack of initials of androecial or gynoecial organs, or as a result from the abortion or sterilization of the sexual whorls at different developmental stages (Mitchell and Diggle, 2005). The latter, commonly results in unisexual flowers that show vestiges of the aborted or non-functional sexual

whorl (Ainsworth, 2000; Lebel-Hardenack and Grant, 1997). In Cactaceae, ca. 23 species have been reported displaying unisexual flowers with a breeding system different to hermaphroditic one (Table 1). *Mammillaria dioica* belongs to the subfamily Cactoideae, it has unisexual flowers and has been referred as having a trioecious (Brandege, 1897) or gynodioecious breeding system (Ganders and Kennedy, 1978). Bemis et al. (1972) suggest that the pistillate flowers of *M. dioica* and related species have “indehiscent anthers with malformed pollen”, while Ganders and Kennedy (1978) mention that pistillate flowers bore “indehiscent anthers with no pollen”; however, precise information regarding the nature of unisexuality in *M. dioica* is still lacking.

Few publications in Cactaceae include embryological studies describing the development and the stage in which floral unisexuality is established. Some species of *Consolea* present a subdioecious or dioecious breeding system, where pistillate flowers have a well-developed

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Table 1

Cacti species with unisexual flowers and sexual systems updated from Orozco-Arroyo et al. (2012). Taxonomic status following Hunt et al. (2006). Unisexuality is present in three subfamilies, seven genera and 24 species.

| Species | Breeding system | Distribution | Reference |
|-------------------------------------------------------------------------------------------------------|---------------------------------------------------------|---------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------|
| Subfamily Pereskioideae (4 species) | | | |
| <i>Pereskia marcanoi</i> | Dioecious | Eastern Dominican Republic | (Areces-Mallea, 1992) |
| <i>Pereskia portulacifolia</i> | Dioecious | Dominican Republic and Haiti | (Leuenberger, 1986) |
| <i>Pereskia quisqueyana</i> | Dioecious | Western Dominican Republic | (Leuenberger, 1986) |
| <i>Pereskia zinniiiflora</i> | Dioecious | Cuba | (Leuenberger, 1986) |
| Subfamily Opuntioideae (11 species) | | | |
| <i>Consolea macracantha</i> (incl. <i>C. millspaughii</i> , <i>C. nashii</i> and <i>C. picardae</i>) | Dioecious | Bahamas, Cuba, Dominican Republic, Haiti, Cayman Islands, Puerto Rico, United States, British Virgin Islands. | (Strittmatter et al., 2006, 2008) |
| <i>Consolea moniliformis</i> (incl. <i>C. rubescens</i>) | Dioecious | Cuba, Dominican Republic, Haiti, Puerto Rico | (Strittmatter et al., 2006, 2008) |
| <i>Consolea spinosissima</i> (incl. <i>C. corallicola</i>) | Subdioecious or dioecious | Jamaica, Cayman Islands, United States | (Strittmatter et al., 2002, 2006) |
| <i>Cylindropuntia molesta</i> (incl. <i>C. calmalliana</i>) | Gynodioecious | Western Mexico | (Rebman, 1998; Rebman and Pinkava, 2001) |
| <i>Cylindropuntia sanfelipensis</i> | Gynodioecious | Western Mexico | (Rebman, 1998; Rebman and Pinkava, 2001) |
| <i>C. chuckwallensis</i> | Gynodioecious | California, USA, | (Baker and Cloud-Hughes, 2014) |
| <i>Cylindropuntia wolfii</i> | Gynodioecious | Northwestern Mexico and southwestern United States | (Rebman, 1998) |
| <i>Opuntia quimilo</i> | Gynodioecious | Northern Argentina and southern Bolivia | (Díaz and Cocucci, 2003) |
| <i>Opuntia quitensis</i> | Dioecious | Ecuador and Peru | (Anderson, 2001) |
| <i>Opuntia robusta</i> | Hermaphrodite, dioecious, gynodioecious, and trioecious | Central Mexico | (Del Castillo and González-Espinosa, 1988; Janczur et al., 2014) |
| <i>Opuntia stenopetala</i> | Dioecious | Central and northern Mexico | (Bravo-Hollis, 1978) |
| Subfamily Cactoideae (9 species) | | | |
| <i>Echinocereus coccineus</i> | Dioecious | Northern Mexico | (Hoffman, 1992; Hernández-Cruz et al., 2018) |
| <i>Echinocereus mombergerianus</i> | Dioecious | Northwestern Mexico | (Baker, 2006; Hernández-Cruz et al., 2018) |
| <i>Echinocereus pacificus</i> | Dioecious | Northwestern Mexico | (Baker, 2006; Hernández-Cruz et al., 2018) |
| <i>Echinocereus polyacanthus</i> | Dioecious | Northern and northwestern Mexico | (Sánchez et al., 2013; Hernández-Cruz et al., 2018) |
| <i>Echinocereus yavapaiensis</i> | Dioecious | Southern United States | (Baker, 2006) |
| <i>Mammillaria dioica</i> (incl. <i>M. estebanensis</i>) | Gynodioecious or trioecious | Northwestern Mexico and southwestern United States | (Lindsay and Dawson, 1952) |
| <i>Mammillaria neopalmeri</i> | Gynodioecious or trioecious | Northwestern Mexico | (Lindsay and Dawson, 1952) |
| <i>Pachycereus pringlei</i> | Trioecious or gynodioecious | Northwestern Mexico | (Fleming et al., 1994) |
| × <i>Aporberocereus innesii</i> (<i>Selenicereus innesii</i>) | Gynodioecious | St. Vincent, Lesser Antilles | (Kinnach, 1982) |

gynoecium, and bare stamens with short filaments, collapsed and indehiscent anthers with no pollen due abnormalities in the tapetum (Strittmatter et al., 2002, 2006). Staminate flowers have a normal androecium and a well-developed gynoecium, although the stigma remains closed and ovules collapse by anthesis (Strittmatter et al., 2002, 2006). In *Opuntia stenopetala* a dioecious sexual system has been documented, where pistillate flowers possess a normal gynoecium and produce indehiscent collapsed anthers that exhibit anomalies in tapetum development, and thus do not form pollen grains (Flores-Rentería et al., 2013). Staminate flowers have pollen-bearing stamens, an anomalous gynoecium formed by a stylodium with no stigma, and ovary, which when present produces a few aborted ovules (Orozco-Arroyo et al., 2012). In dioecious species of *Echinocereus*, pistillate flowers display a well-developed gynoecium and collapsed stamens with no pollen anthers (Hoffman, 1992; Hernández-Cruz et al., 2018). Staminate flowers show a fully developed gynoecium with ovules, but seeds are aborted at early stages of development (Hernández-Cruz et al., 2018)

Programed cell death (PCD) has been documented as the process that causes the loss of function of the androecium and gynoecium in unisexual species of *Consolea* (Strittmatter et al., 2006, 2008), dioecious *Echinocereus* (Hernández-Cruz et al., 2018), as well as in the androecium of *O. stenopetala* (Flores-Rentería et al., 2013). PCD is an active cell death process involved in the selective elimination of unwanted, unnecessary cells or, tissues and organs (Ellis et al., 1991) or tissues with temporary functions as tapetum (Papini et al., 1999). A type of PCD is the autophagy (Shi et al., 2014), which is divided in

microautophagy and macroautophagy. Microautophagy is the uptake of cellular constituents by the vacuolar membrane and macroautophagy occurs farther away from the vacuole, and it is performed by autolysosomes, these organelles contain hydrolases (van Doorn, 2011; van Doorn et al., 2011; van Doorn and Papini, 2013). The macroautophagy was mentioned in normal development of tapetum in *Lobivia rauschii* (Cactaceae) (Papini et al., 2014; Papini and van Doorn, 2015). However, autophagy of tapetum at an abnormal stage is considered to be the main cause of male sterility in *Consolea* and *Opuntia* species (Strittmatter et al., 2002, 2006; Flores-Rentería et al., 2013) and it shows chromatin condensation and DNA fragmentation.

Other species of Cactaceae with non-hermaphroditic breeding systems (Table 1) share some external morphological characteristics observed in *Consolea* and *Opuntia*, however little information is available regarding the developmental changes that originate unisexuality in those taxa. Therefore, we consider necessary undertaking embryological studies in unisexual flowers to generate a structural framework for future physiological and molecular research on the evolution of dioecy in cactus family. The present study aims to characterize the unisexual and bisexual flowers found in *M. dioica* in order to recognize its breeding system, and describe both anther and ovule embryology, to understand the structural changes that cause sexual whorl sterility and the developmental stage in which unisexuality is determined.

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