South African Journal of Botany 114 (2018) 69–77

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Ultrastructural abnormalities in pollen and anther wall development may lead to low pollen viability in jasmine (*Jasminum sambac* (L.) Aiton, Oleaceae)

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ARTICLE INFO

Article history:
Received 20 January 2017
Received in revised form 28 September 2017
Accepted 14 October 2017
Available online 8 November 2017

Edited by K Balkwill

Keywords:
Jasminum sambac
Anther anatomy
Microspore ultrastructure
Pollen development
Reproductive barrier

ABSTRACT

Jasmine [*Jasminum sambac* (L.) Aiton] rarely sets seed, and its poor pollen fertility significantly influences fecundity. In this study, pollen development of jasmine was investigated at an ultrastructural level, examining the dynamic changes of microspore-tetrads and tapetum and their possible effects on pollen viability. Normally developed microspores are released at the late tetrad phase, whereas the abnormal ones formed large complexes of two to five tetrads with plasmodesmata. Ultrastructural observation also revealed that sterility of some pollen grains might result from defective development of cell walls that failed to absorb their surrounding sporopollenin to form the exine. The secretory type of jasmine tapetum, the usually degenerated middle layer and thickened endothecium were confirmed during the process of pollen development. The epidermis, middle layer and endothecium exhibited no adverse effects on pollen development and dispersal. However, the asynchronous division and delayed degradation of tapetal cells resulted in abnormal development of some microspores and the formation of massulae and empty and flat pollen grains. This is the first ultrastructural characterization of pollen development in *J. sambac* leading to a better understanding of embryology and poor pollen fertility of this important horticultural species.

1. Introduction

Jasmine [*Jasminum sambac* (L.) Aiton] is an important horticultural species originating from the Mediterranean region and extensively used as an ornamental and in bouquets. It has been cultivated in China for over 1500 years (Dong and Zhang, 2001). Although the most widespread jasmine cultivar exhibits high flower productivity and a strong resistance to both biotic and abiotic stresses (Deng et al., 2012a, 2012b; Guo et al., 2004, 2006), breeders are striving to create new cultivars as demands for novel traits continue to increase. However, the most cultivated strain seldom sets any seeds (Lai et al., 1996; Dong and Zhang, 2001; Deng et al., 2016, 2017), severely hampering jasmine breeding via the selection of variants that arise through sexual reproduction.

Characteristics of both female and male reproductive organs and their interactions are closely related to setting of seeds. Therefore, floral bud development in jasmine, including morphology and anatomy of floral ontogeny from emergence to anthesis, sporogenesis and gametogenesis processes, pollen viability, stigma receptivity and pollen-pistil interactions, has been investigated (Deng et al., 2014, 2016, 2017). This study has indicated that failure of pollination and/or fertilization could be caused by a range of malfunctions of the reproductive organs, such as abnormal floral bud growth, low pollen viability, loss of pistil receptivity and ovule sterility (Deng et al., 2014, 2016). Low pollen fertility has been shown to be an important factor for reducing seed production because fertilization probability decreased considerably when sterile pollen grains were deposited on a stigma (Teng et al., 2012; Wilcock and Neiland, 2002; Zhao et al., 2004). Low pollen fertility was responsible for the poor seed yields in *Glycine max* (L.) Merr., *Nelumbo nucifera* Gaertn. and *Bambusa vulgaris* Schrad. ex Wendl. (Koshy and Jee, 2001; Teng et al., 2012; Zhao et al., 2004). In addition, pollen sterility has proven to be a major factor leading to the endangered status of *Opisthopappus taihangensis* (Ling) Shih (Li et al., 2009) and *Pancratium maritimum* L. (Konyar, 2016). These results suggested that further research into microsporogenesis and microgametogenesis would provide a better understanding of the causes of poor seed set in jasmine.

Ultrastructural characteristics change with pollen and anther development, and they are important in embryological development as well. For example, abnormal meiotic development of the pollen mother cells (PMC) of *Picea asperata* Mast. was found to be a cause of low pollen production (Lu et al., 2003). In addition, ultrastructural development of pollen and anthers of *Luehea divaricata* Mart showed the importance of tapetal transfer cells and orbicules of male fertility (Lattar et al., 2012). Moreover, ultrastructural observations of the anthers at various

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https://doi.org/10.1016/j.sajb.2017.10.014

developmental stages revealed which factors affected the quantity of pollen dispersed in *Chrysanthemum morifolium* Ramat. (Wang et al., 2014). Microsporogenesis and microgametogenesis ultrastructure of *Brachypodium distachyon* (L.) Beauv. confirmed that it had a pattern of pollen development that is typical of grasses (Sharma et al., 2015).

A previous study on microsporogenesis and microgametogenesis of *J. sambac* observed general characteristics of pollen development at the microstructural level (Deng et al., 2016), but left questions regarding the reduced pollen viability unanswered. For instance, irregular tapetum and dynamic changes occurring in the tapetal cells during the development were still unknown. In addition, some small and empty pollen grains were observed in mature anthers, but the ultrastructural characteristics of these grains were still unknown. More importantly, jasmine pollen grains frequently clumped into massulae (Deng et al., 2014, 2016). In some plant species, the microspores are naturally held in their original positions in the tetrads and they develop into pollen complexes. For example, in many species of Orchidaceae and Asclepiadaceae, all microspores in a pollen sac are dispersed as a whole pollinium (Hu, 2005). In other species, some tetrads in a sac combine with each other to form massulae containing different numbers of tetrads. For instance, a massula contains 8–16 cells in Mimosaceae (Hu, 2005); it always consists of 16 in *Albizia julibrissin* and hundreds in *Gastrodia elata* of Orchidaceae (Zhou et al., 1987). However, the massulae formed in *J. sambac* severely reduced their germinability (Deng et al., 2014, 2016). Despite the implications of this for the success of breeding programmes, the ultrastructure of the adjacent pollen-tetrads and the cytological mechanism of pollen massulae formation are still poorly understood. Thus, investigation of the ultrastructural features of pollen development is necessary.

The present study focused on the ultrastructural changes during microsporogenesis and microgametogenesis of jasmine. Its objective was to integrate ultrastructural and developmental characteristics using transmission electron microscopy (TEM), focusing on the changes in tetraspores and tapetal cells, in order to provide a better understanding of jasmine pollen sterility. The findings will contribute to novel knowledge of the embryology of this important economic and ornamental species and to a practical solution for overcoming its reproductive barriers.

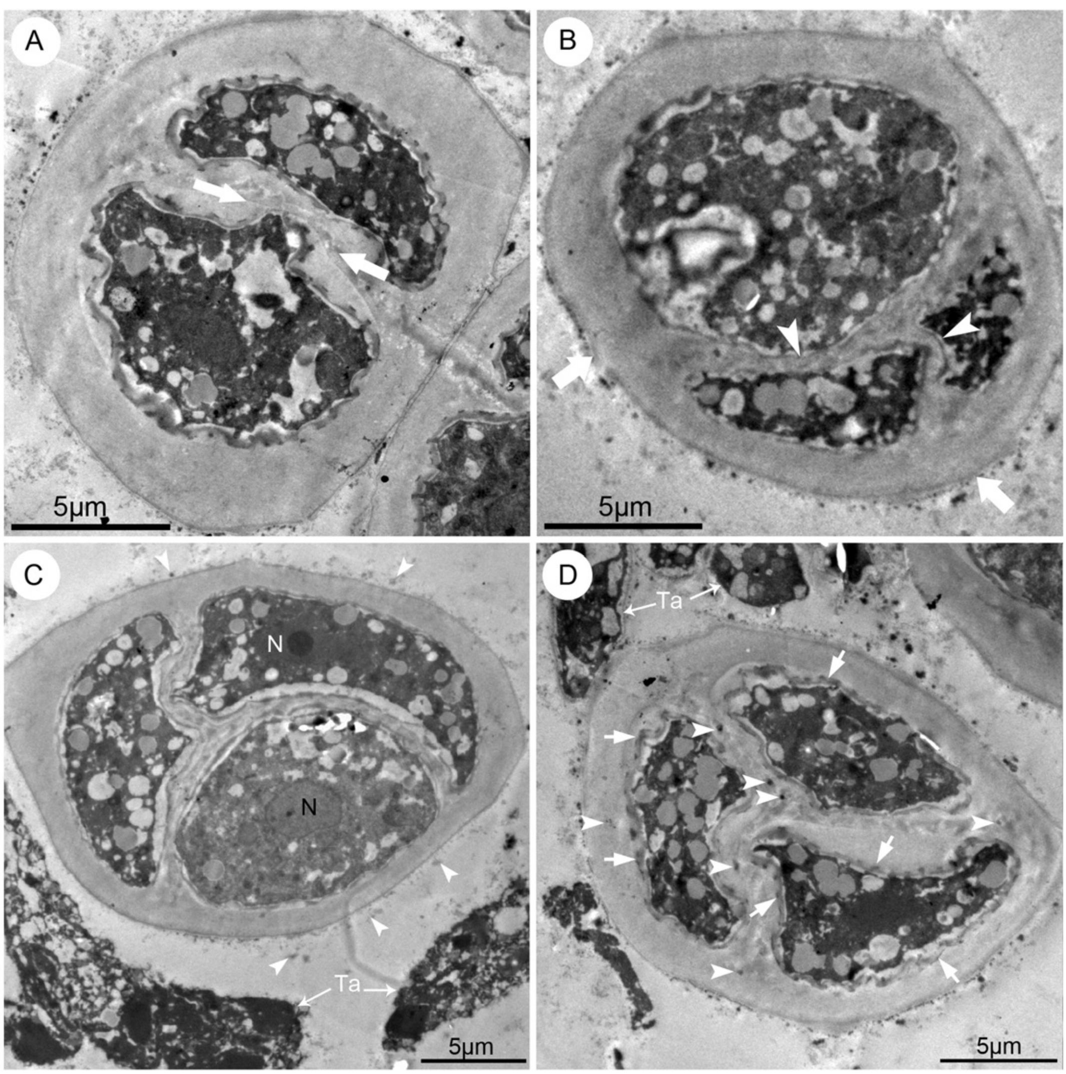

Fig. 1. TEM images of microspore-tetrads of *J. sambac*. (A) A tetrad developed from a PMC, with the tetrad and each microspore surrounded by callose wall and callose accumulated along the wall forming between the recently divided cells (indicated by *arrows*). (B) A tetrad at its early developmental stage. Inner callose walls (*arrowheads*) were narrower than the outer walls (*arrows*). (C) During meiosis, numerous small lipid droplets (*arrowheads*) were inside the anther loculus and around the tetrad. Each tetraspore contained dense cytoplasm, numerous organelles and a central nucleus. (D) A tetrahedral tetrad at late developmental stage. The tetraspore has begun to form its own wall (*arrows*) in the tetrad. *Arrowheads* indicate callose in walls. Ta: tapetum; Te: tetrad.