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Pollen wall pattern in *Arabidopsis*

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Abstract The pollen wall is a solid and variously sculptured structure. This pattern is determined inside a tetrad. During meiosis, the callose wall is formed outside of the meiocyte/microspore to form a tetrad. Then, primexine is deposited between the callose wall and the microspore plasma membrane which will become undulated. The sporopollenin deposits on top of the undulated membrane and develops into the pollen wall pattern, while the callose wall is gradually degraded. In recent years, much progress has been made in the study of pollen wall pattern formation, at both molecular and genetic levels. In this review, we summarize these achievements mainly in *Arabidopsis*.

Keywords Pollen wall pattern · Sexine · Callose · Primexine · Plasma membrane undulation · Sporopollenin

1 Introduction

The pollen wall is a significant characteristic for pollen grains in flowering plants. It is composed of the outer exine and inner intine [1]. The exine layer can be further subdivided into the outer sexine and inner nexine [2]. The sexine is made of sporopollenin and is variously sculptured [3], while the nexine is simply smooth and relatively conservative in composition. The formation of the exine layer is mainly controlled by sporophytic tissue: the tapetum cell. The nexine can only be observed by transmission electronic microscope (TEM) and its composition is generally considered to be sporopollenin. Recently, the nexine deficient mutant *tek* was reported in *Arabidopsis* [4]. The expression of an arabinogalactan protein 6 (AGP6) in *tek* can rescue nexine formation, suggesting the AGPs are the major composition of nexine [5]. The intine layer is mainly composed of cellulose. Different from that of pollen exine, the formation of the intine layer is mainly controlled by the haploid gametophyte, the pollen grain itself. The major function of the pollen wall is considered to provide physical strength and chemical resistance from external biotic or abiotic attack [6].

The pollen wall pattern refers to the reticular sculpture of the sexine layer. In the past, the understanding of pollen wall patterning largely depended on the cytological observation, although many genetic, biochemical and molecular studies have been done on pollen wall development [1]. The pollen wall pattern is determined inside a tetrad. Under TEM, pollen wall pattern formation includes callose wall synthesis, primexine formation, plasma membrane undulation, sporopollenin deposition and callose wall dissolution [7]. With the development of molecular and genetic technologies in the model plant *Arabidopsis thaliana,* much progress has been made in pollen wall pattern research in recent years. This review presents the recent progresses in pollen wall pattern formation at the molecular and genetic levels in *Arabidopsis* (Fig. 1).

2 Callose wall synthesis

Callose is composed of β-1,3-glucan [8]. According to the ultrastructural observation of pollen development, the

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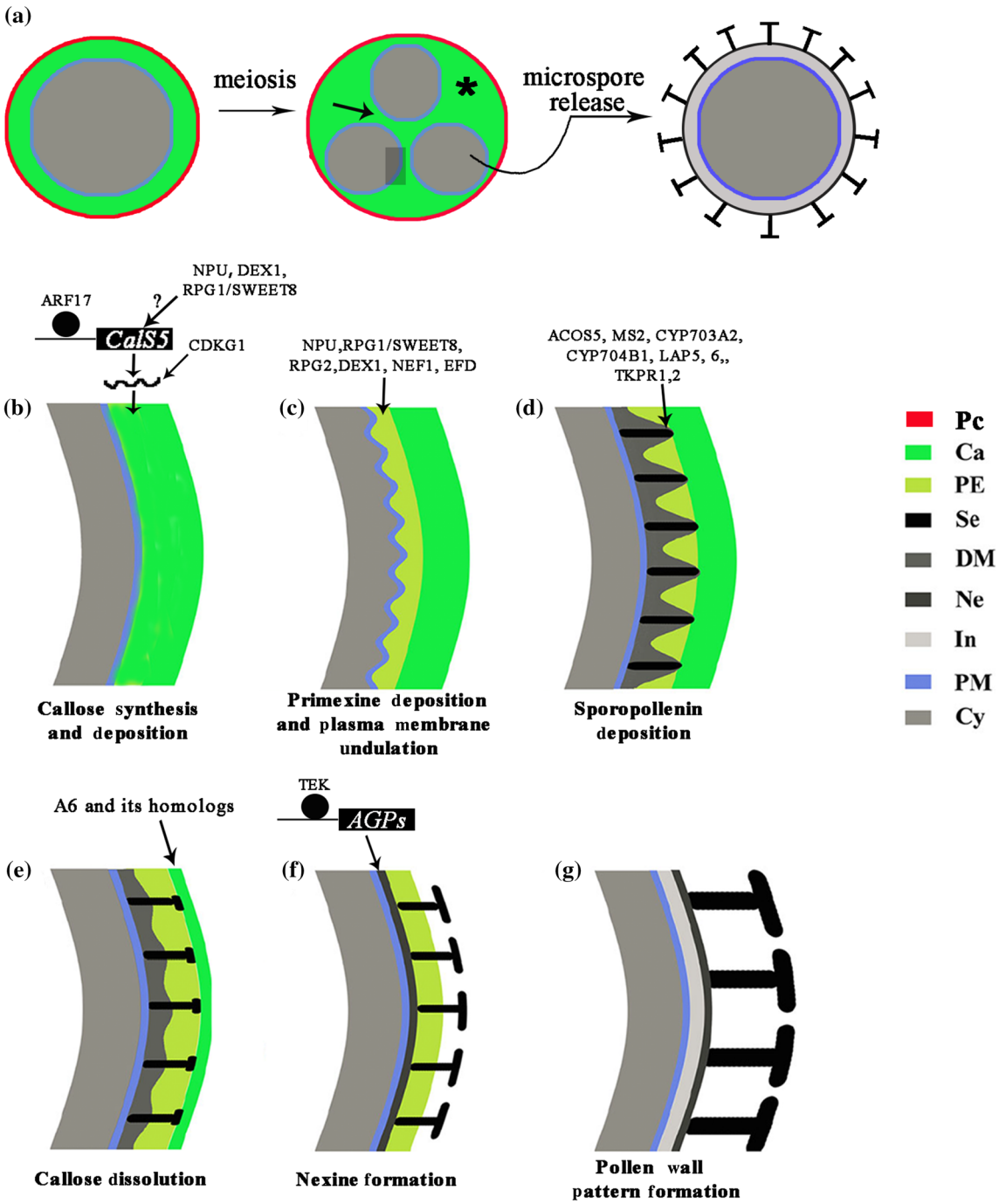

Fig. 1 The developmental processes for pollen wall patterning in *Arabidopsis thaliana.* **a** The progress of microspore development. After meiosis, the four microspores are encased in the callose wall as the tetrahedral structure (only three microspore could be observed on a plane) in *Arabidopsis*. During tetrad stage, the wall pattern is gradually established which are shown in (**b**–**g**). The tetrad callose wall could be separated into the peripheral callose (asterisk) and intestial callose (arrow). **b**–**g** the local amplification of pollen wall development in tetrad as the shadow box in **a**. These figures are based on the developmental model of pollen exine formation in *Arabidopsis thaliana* in [7] with genes involved in the pattern formation. Pc, pectin; Ca, callose; PE, primexine; Se, sexine; DM, deposited material; Ne, nexine; In, intine; PM, plasma membrane; Cy, cytoplasm