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Review

The biosynthesis, composition and assembly of the outer pollen wall: A tough case to crack

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ABSTRACT

The formation of the durable outer pollen wall, largely composed of sporopollenin, is essential for the protection of the male gametophyte and plant reproduction. Despite its apparent strict conservation amongst land plants, the composition of sporopollenin and the biosynthetic pathway(s) yielding this recalcitrant biopolymer remain elusive. Recent molecular genetic studies in *Arabidopsis thaliana* (Arabidopsis) and rice have, however, identified key genes involved in sporopollenin formation, allowing a better understanding of the biochemistry and cell biology underlying sporopollenin biosynthesis and pollen wall development. Herein, current knowledge of the biochemical composition of the outer pollen wall is reviewed, with an emphasis on enzymes with characterized biochemical activities in sporopollenin and pollen coat biosynthesis. The tapetum, which forms the innermost sporophytic cell layer of the anther and envelops developing pollen, plays an essential role in sporopollenin and pollen coat formation. Recent studies show that several tapetum-expressed genes encode enzymes that metabolize fatty acid derived compounds to form putative sporopollenin precursors, including tetraketides derived from fatty acyl-CoA starter molecules, but analysis of mutants defective in pollen wall development indicate that other components are also incorporated into sporopollenin. Also highlighted are the many uncertainties remaining in the development of a sporopollenin-fortified pollen wall, particularly in relation to the mechanisms of sporopollenin precursor transport and assembly into the patterned form of the pollen wall. A working model for sporopollenin biosynthesis is proposed based on the data obtained largely from studies of Arabidopsis, and future challenges to complete our understanding of pollen wall biology are outlined.

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1. Introduction

For the evolution of plant life on land, a number of adaptations were required to support terrestrial life and its inherent stresses (Cronk, 2009; Kenrick and Crane, 1997). Among these adaptations, external barriers encasing the dominant plant body and its reproductive offshoots were forefront in preventing desiccation and ensuring the transmission of genetic information (Wallace et al., 2011). The cycling between the sporophytic and gametophytic generations characteristic of land plants is made possible by the reproductive cells they produce, namely the haploid spores produced by the sporophyte through meiosis and the haploid gametes produced by the gametophytes through mitosis. However, these reproductive cells often require prolonged survival as independent entities, necessitating the fortification of their cell walls with polymers capable of withstanding terrestrial stresses. Sporopollenin, a structurally robust biopolymer, served this critical function in the evolution of land plants by enveloping and protecting the spores of early non-seed-bearing plant lineages and the pollen grains (microgametophytes) formed by the male reproductive organ, the anther, of seed-producing plants (Wallace et al., 2011). Sporopollenin appears to be conserved in its properties and to have been critical in the evolution of land plants.

Sporopollenin fortifies the outer wall (exine) of pollen grains, forming a durable casing around the male gametophyte. The surfaces of pollen grains often appear intricately decorated due to species-specific sculpturing of sporopollenin present in their outer walls, commonly assuming a regular hexagonal pattern, as in *Arabidopsis thaliana* (Arabidopsis) (Fig. 1A and B). Apertures or colpi intercept the outer wall of pollen in species-specific locations and frequencies, and serve as the typical sites of pollen tube emergence (Fig. 1A). Pollen surface features have facilitated plant identification in the fossil record, aiding our understanding of the evolution and distribution of land plants over geological time. However, our understanding of the function of these features in plant reproductive success are limited. In some species, such outer wall features are presumably adaptations that aid pollen dispersal or hold additional wall materials such as tapetum-derived pollen coat constituents that are important for the physiology of the pollen in its interaction with the stigma.

Despite the great diversity of pollen surface structure, spore/pollen walls exhibit common structural features observed in cross-sections of developing and mature spores and pollen grains using transmission electron microscopy (TEM). These features typically include an inner intine composed of pectin, cellulose, and hemicellulose, and an outer exine composed of sporopollenin (Heslop-Harrison, 1968a). The intine appears as a light band by TEM, directly external to the pollen plasma membrane (Fig. 1C and D). The cellulosic intine maintains the structural integrity of pollen grains, as Arabidopsis plants with mutations in primary cell wall cellulose synthases produce collapsed or malformed pollen grains with aberrant pollen walls that lack or have uneven intine cellulose (Persson et al., 2007). Sporopollenin provides the rigid and sculptured framework of the exine, which serves to encapsulate and protect the contents of spores/pollen, and to assist in stigmatic capture (Fig. 1). For many species, including Arabidopsis, this structured backbone is additionally covered by a heterogeneous pollen coat (also called tryphine), which primarily serves in pollen stigmatic adhesion, recognition, and hydration and can be extracted from the underlying sporopollenin with organic solvents (Edlund, 2004; Murphy, 2006; Piffanelli et al., 1998). After pollen tube emergence from the exine shell, the intine serves as the only cell wall encasing the growing pollen tube, and is rapidly remodeled to assist growth while preventing premature rupture (Chebli et al., 2012).

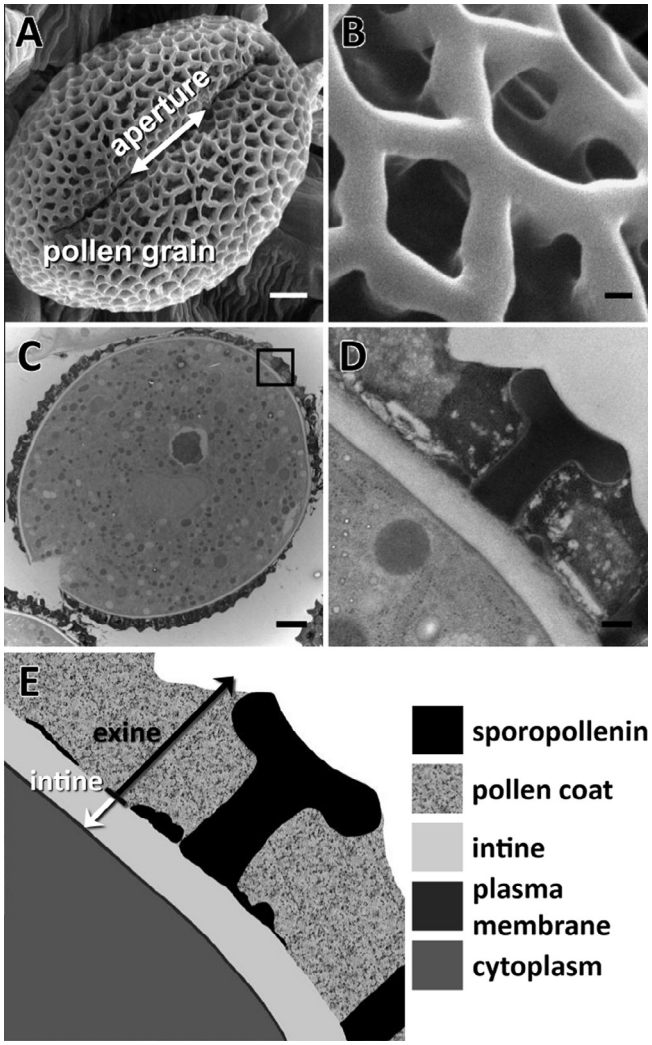

Fig. 1. Surface structure and cross-section morphology of the mature Arabidopsis pollen wall. Scanning electron micrographs (A, B) and transmission electron micrographs (C, D) of wild-type pollen at maturity. (A) Critical point dried pollen grain with reticulate exine and one visible aperture (of three). (B) Pollen wall surface structure. (C) High-pressure frozen and freeze substituted pollen grain in cross-section with dense cytoplasmic contents encased by a pollen wall. Region boxed in panel C is magnified in panel D. (D) Stratified pollen wall with electron-lucent intine, electron-dense sporopollenin and heterogeneous pollen coat. The plasma membrane separates wall components from pollen cytoplasm. (E) Diagrammatic representation of the pollen wall from panel D. Arrows indicate the broad categorization of wall layers into intine (light grey) and exine. Within the exine, the structured sporopollenin (black) of the wall appears homogeneous, in contrast to the heterogeneous pollen coat (mottled grey). Bars = 2 μm (A, C) and 0.2 μm (B, D).

Current understanding of pollen wall biogenesis is that components of the intine are generated by the microspore vegetative cell (Hess, 1993), while components of the exine are synthesized by the surrounding sporophytic tapetal cells and deposited on the surface of developing microspores within the locule (Ariizumi and Toriyama, 2011). Tapetal cells form the innermost cell layer of the sporophytic anther wall, and their direct proximity to developing microspores and loss of their cell walls at maturity facilitates their nutritive role in pollen development (Goldberg et al., 1993; Owen and Makaroff, 1995). Tapeta in spermatophytes are broadly grouped into the secretory (or parietal or glandular) type or the amoeboid (or periplasmodial or invasive) type, differing primarily in the extent of their intrusion into the locule during microspore development (Pacini, 2010). Amoeboid tapeta intrude into the locule, encasing microspores and providing direct nutrition to

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