

Lipids in pollen – They are different[☆]

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ABSTRACT

During evolution, the male gametophyte of Angiosperms has been severely reduced to the pollen grain, consisting of a vegetative cell containing two sperm cells.

This vegetative cell has to deliver the sperm cells from the stigma through the style to the ovule. It does so by producing a pollen tube and elongating it to many centimeters in length in some species, requiring vast amounts of fatty acid and membrane lipid synthesis.

In order to optimize this polar tip growth, a unique lipid composition in the pollen has evolved. Pollen tubes produce extraplasmidial galactolipids and store triacylglycerols in lipid droplets, probably needed as precursors of glycerolipids or for acyl editing. They also possess special sterol and sphingolipid moieties that might together form microdomains in the membranes.

The individual lipid classes, the proteins involved in their synthesis as well as the corresponding Arabidopsis knockout mutant phenotypes are discussed in this review. This article is part of a Special Issue entitled: Plant Lipid Biology edited by Kent D. Chapman and Ivo Feussner.

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1. Lipids in pollen

Pollen grains represent the male gametophyte of higher land plants. These cells derive from diploid precursor cells, the microsporocytes, also called pollen mother cells. Maturation takes place in the pollen sac of the anther, encapsulated and protected by the sporophytic tissue and nourished by the tapetum cells (Fig. 1), the most inner layer of the anther surrounding the pollen sac [1]. The development of pollen (Fig. 2) starts with several rounds of mitotic divisions of the microsporocytes before they enter meiosis, leading first to a tetrad stage and then to four individual haploid microspores. These microspores undergo an asymmetric cell division (mitosis I) resulting in a small generative cell and a large vegetative cell. The generative cell later divides again (mitosis II) to form the two sperm cells, while the vegetative cell produces the pollen tube. Before this, however, the microsporocyte grows into a mature pollen grain and further strengthens its cell wall [2] consisting of a thin intine and a thick exine made up mostly by sporopollenin.

This very resistant biopolymer is composed of phenolics and lipids such as fatty acids and carotenoids. It is deposited from the outside of the pollen, as it is synthesized and secreted by the tapetum (Fig. 1). Towards the end of pollen development, the tapetal cells rupture after programmed cell death [3], setting free lipids and proteins that were previously accumulated in tapetosomes and elaioplasts (Fig. 1; [4,5]). Tapetosomes consist of ER derived membranes and lipid droplets [6–8], and elaioplasts are specialized plastids filled with lipid-rich plastoglobuli [9–11]. These tapetum derived substances overlay the exine and form the so called tryphine with the lipids therein also referred to as pollen coat or pollenkitt (for the German word for pollen glue).

During the last period of development, the pollen also accumulates internal substances including most of the proteins needed for tube growth [12], polar lipids in the form of densely packed membranes, and neutral lipids such as triacylglycerols (TAGs) in lipid droplets (also referred to as oil bodies; [13,14]).

Therefore, the mature pollen contains two types of lipids, the ones in the pollen coat deriving predominantly from the diploid tapetal cells and the ones formed by the haploid vegetative cells of the pollen grains. The coat lipids are not only important to protect the pollen during its desiccation stage and transport, but are also involved in the attachment of the pollen to the stigma and the following interaction and signaling processes [15].

On the stigma, the pollen grain germinates, the vegetative cell forms a tube that grows out through one of the apertures of the pollen coat and enters the female tissue. This way, the lipids coating the pollen grain are left behind. At least there is no evidence that they are internalized and used for pollen tube growth. Therefore, the pollen cell depends

Abbreviations: TAGs, triacylglycerols; GPAT, glycerol-3-phosphate acyltransferase; LPAAT, lysophosphatidic acid acyltransferase; PA, phosphatidic acid; DAG, diacylglycerol; FAX1, Fatty acid export 1; PI, phosphatidylinositol; PECT1, CTP:phosphorylethanolamine cytidyltransferase; PE, phosphatidylethanolamine; PC, phosphatidylcholine; MGDG, monogalactosyldiacylglycerol; DGDG, digalactosyldiacylglycerol; PS, photosystem; DGAT, Acyl-CoA:diacylglycerol acyltransferase; PDATs, phospholipid:diacylglycerol acyltransferases; LDAP, lipid droplet associated protein; SDP1-like, SUGAR DEPENDENT 1-like; LCB, long-chain base; GlcCers, glucosylceramides; IPCs, inositolphosphoceramides; GIPCs, glycosylinositolphosphoceramides.

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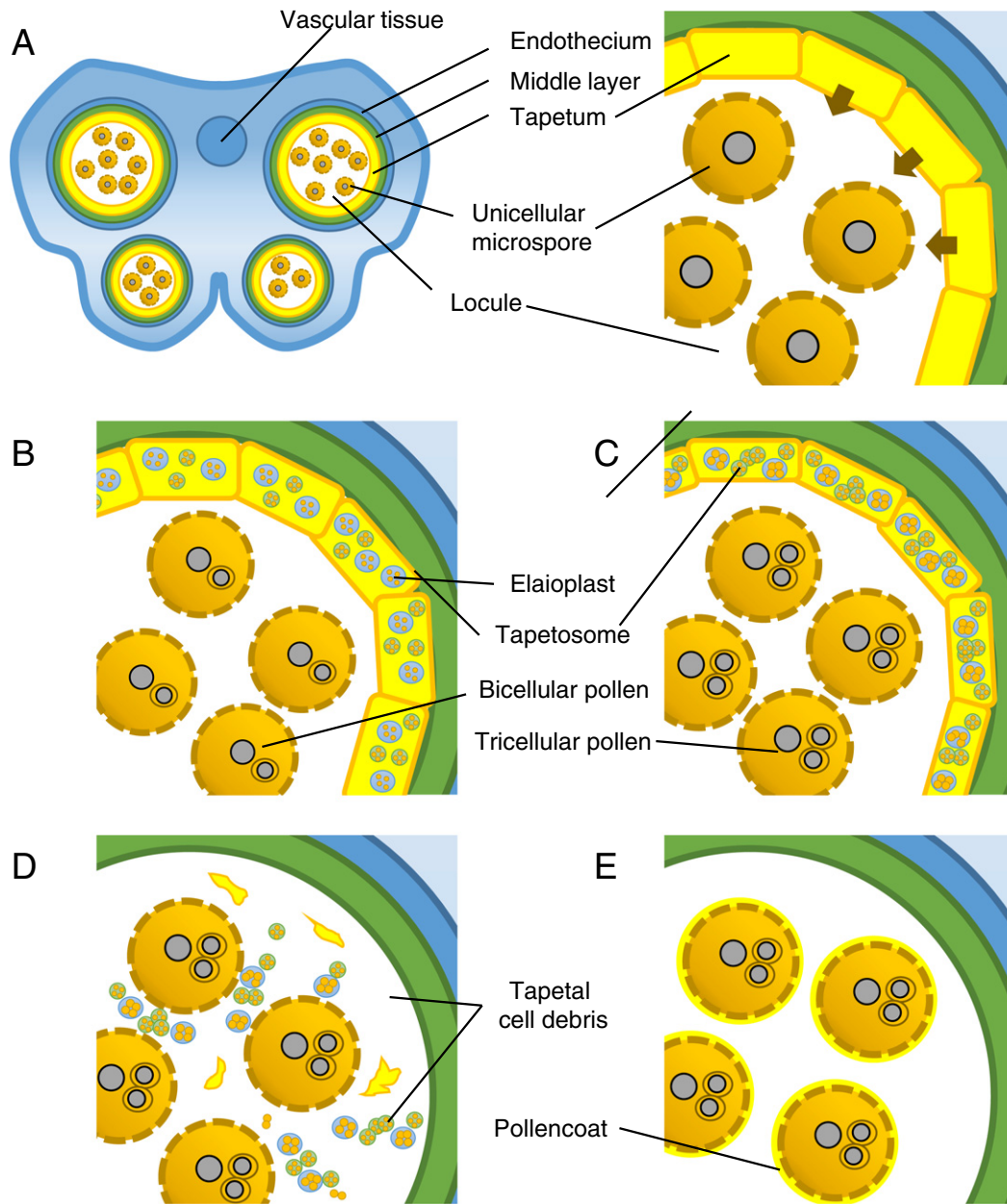


Fig. 1. The pollen coat derives from the tapetum. Overview of the later stages of *Arabidopsis* pollen development displayed in a cross-section of an anther bud. A, During the microspore stage, the tapetum secretes precursors for the sporopollenin that forms the exine of the pollen grains. B, During the bicellular pollen stage, the plastids of the tapetum differentiate into elaioplasts and start to accumulate neutral lipids. Tapetosomes appear. C, During the tricellular pollen stage, the tapetal cells are made up mostly of elaioplasts and tapetosomes. D, The tapetal cells lyse setting free elaioplasts, tapetosomes and cell debris into the locule. E, The remnants of the tapetal cells overlay the exine of the pollen grains to form the Pollen coat. For a full overview of pollen development see Fig. 2. This figure is based on work by Quilichini et al. [2].

solely on its own lipids that have to be either synthesized before desiccation inside the grain or on the way through the pistil to the female gametophyte. The proportion of newly synthesized lipids might vary from species to species, especially considering the differences in length the pollen tube has to reach, ranging from less than a mm in watermeal (genus *Wolffia*, estimated from the size of the flower [16]) to 50 cm in maize [17]. It is clear that at least longer pollen tubes require the synthesis of large amounts of membrane lipids during their elongation. Even though the shank of the pollen tube is strongly vacuolated, a 10 μm diameter pollen tube would need 2.4 pmol of membrane lipids per cm of length for the tonoplast and the plasma membrane alone (calculating with 2.86×10^6 molecules per μm^2 in a pure lipid bilayer [18] and 80% of area covered by lipids). This amount corresponds to roughly 1.8 ng. The dry weight of

individual pollen grains ranges from 1 ng in nettle (*Urtica dioica*) to 50 ng in beech (*Fagus sylvatica*; [19]). The weight of *Arabidopsis* pollen grains has to my knowledge not been determined, but is likely less than the 5 ng of pollen from kale [20], which has bigger pollen grains. As a lot of this weight originates from the pollen wall, it is probably impossible for pollen of most species to store enough lipids to carry them through the fertilization process. Therefore, sugars are likely taken up from the female apoplast and metabolized into lipids at a fast pace (this has so far only been shown for pollen tubes grown in medium [21]), as for example maize pollen tubes elongate by more than 1 cm per hour [17].

The enzymatic machinery of the pollen needed for the synthesis of lipids resembles the one found in sporophytic tissues, but differs in the quantitative composition, resulting in a distinct pollen lipidome (Fig. 3).

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