Chapter 3

POLLEN GERMINATION AND POLLEN TUBE GROWTH

Tip Growth Mechanism in Sexual Plant Reproduction

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1. Introduction

Pollen, the male gametophyte of higher plants, is a biological system playing a central role in sexual plant reproduction (Cresti \textit{et al.}, 1992). The understanding of the mechanisms controlling the various aspects of pollen tube development has a direct relevance to biotechnological applications since it represents a starting point to modify crop production and it enhances the knowledge on molecular and cellular events controlling the tip growth mechanism. When pollen arrives on the surface of a compatible stigma it undergoes a complex series of regulated cytoplasmic rearrangements leading to the emergence of a cylindrical structure known as pollen tube, with the main purpose to carry and deliver sperm cells to the embryo sac for the double fertilization. \textit{In vivo}, pollen tubes grow through the transmitting tissue in the style and, since they never penetrate stigmatic cells, the mechanisms involving cell-cell recognition and signalling must exist to guide pollen tubes to the ovary. For this purpose, specific molecules of the transmitting tissue acting as adhesive substrate, attractants and stimulators of pollen tube elongation (Lord and Sanders, 1992) have been identified and characterized in several angiosperms but pollen tube targets of these external

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stimuli and the nature of these interactions have not been fully understood at the molecular level (Frankling-Tong, 1999).

At present, most of the data on pollen germination and pollen tube growth have been obtained from in vitro studies, using artificial media that mimic the in vivo growth. Even on optimum media, pollen tubes in in vitro systems sometimes show structural anomalies and grow to about 40% of the length attained in vivo; in some other species, such as Arabidopsis thaliana pollen do not germinate in artificial media (reviewed by Taylor and Hepler, 1997). Nevertheless, studies on in vitro growth showed many cellular and molecular aspects of pollen and pollen tubes, and since many stylar factors have been characterized at the molecular level, their effects on pollen germination and tube elongation can be studied in in vitro systems (Cheung, 1996; Cheung et al., 1995).

Pollen germination and tube elongation depends on regulated exocytosis of Golgi derived secretory vesicles to a restricted area of the apical zone. This tip growing mechanism requires the integrity of the endomembrane system and of the cytoskeletal apparatus (Li et al., 1997). As a matter of fact, interactions among cytoskeletal elements and membranous organelles play a central role in carrying and maintaining enough secretory vesicles (SVs) at the tip region where they fuse with the apical plasma membrane under the control of the tip focused Ca\(^{2+}\) gradient (Malhó, 1999). Although the correct mechanism of tube growth represents a basic condition for the transfer of sperm cells to the embryo sac for fertilization, the generative cell (GC)/sperm cells (SCs) organization and movements will not be treated in this chapter. Some of these aspects are dealt with in Chapter 2.

In this chapter the crucial aspects controlling the polarity of pollen cytoplasm and tip growth as the organization and function of cytoskeleton and cytoskeletal motor proteins will be analysed and related to the membrane trafficking following a Ca\(^{2+}\) controlled pathway.

2. Modifications Accompanying Pollen Germination

Pollen is released from the anther in a dehydrated and metabolically quiescent state, which allows it to be transported to long distances until it reaches the female apparatus (Lin and Dickinson, 1984). At anthesis, pollen appears to be bound by an inner pecto-cellulosic layer and an outer exine made of sporopollenin (Wiermann and Gubatz, 1992), enclosing the vegetative cytoplasm. An additional outer layer, comprising waxes, lipids, proteins and other small molecules (tryphine or pollenkitt layer), is deposited on the exine surface of pollen grains following the degeneration or disintegration of tapetum. It is believed that pollenkitt components are responsible for generating signals required for pollen adhesion and further germination after it lands on the stigmatic surface. Mutants with impaired