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Chapter 14

Callose in Plant Sexual Reproduction

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Additional information is available at the end of the chapter

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1. Introduction

The typical plant cell wall is composed of cellulose, hemicellulose, pectin and protein. Cellulose is a polymer of 1,4- β- glucan and found as microfibrils in the cell wall. Callose, a specialized polysaccharide, is also one of the cell wall components in plants, and it appears in some cells or in some cases. It is a 1,3- β- glucan polymer with some 1,6 branches, and it differs from cellulose. Callose and cellulose are synthesized by callose synthase and cellulose synthase located on the plasma membrane, respectively. Callose synthase locates vectorially in the plasma membrane with substrate being supplied from the cytoplasmic side, and the products are deposited on the cell surface [1].

Callose was initially identified by Mangin [2] more than 100 years ago. Afterwards, it is defined by Frey-Wyssling and Muhlethaler [3] as a component of cell walls in higher plants. Although it is not as common as cellulose, its role is very significant. It generally exists in small quantities in structurally different plant tissues, and it has individual properties: (1) High impermeability, (2) Rapid synthesis and easy degradation [4-6]. Callose can be identified with aniline blue by fluorescence microscope or resorsine blue (lacmoid) by light microscope. Aniline blue technique based on the emittance of secondary fluorescence was standardized by Eschrich and Currier [7] and it has been extensively used to identify callose deposition.Callose is deposited between plasma membrane and cellulosic cell wall, and it appears electron-lucent in transmission electron micrographs [8].

Callose plays important roles in many processes during plant development (Table 1). It plays a significant role in the reproductive biology of angiosperms, particularly. Callose wall surrounds the sporocytes while meiosis occurs. Because of its structure, it may provide an isolation barrier sealing off one meiotic cell (pollen mother cell or megaspore mother cell) from another [9]. Waterkeyn [10] suggested that callose plays an important biological role: It acts as a temporary wall to prevent the products of meiosis from cohesion and fusion, and its

dissolution results in the release of free spores. It has been proposed that the callose wall functions as a molecular filter isolating the developing microspores from the influence of the surrounding diploid tissue or sister spores [11]. The molecular filter also transmits only signals that are indispensable for meiosis into the meiocytes [12-13]. The temporary isolation of the sporocyte (male as well as female) may be connected with the process of differentiation of the sporocyte. Callose accumulates in the walls of incompatible pollen grains and tubes, and in certain cases, in papillae of stigma following rejection [14].

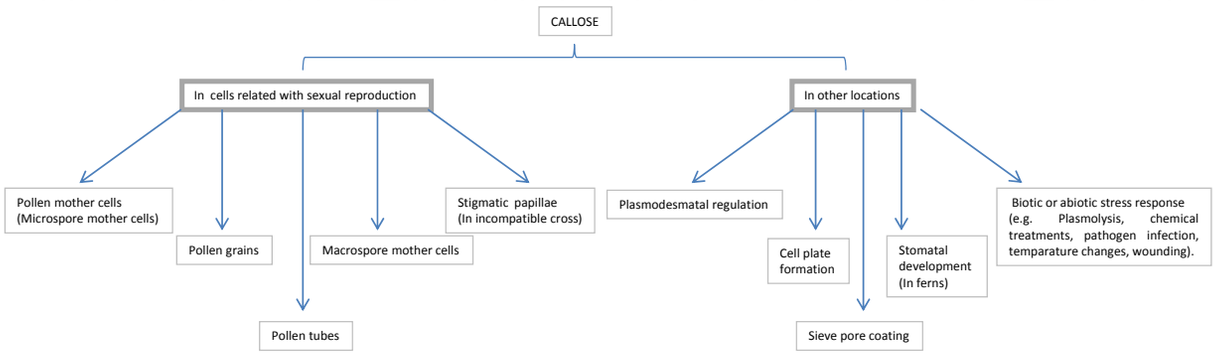

Table 1. Schematic summary of callose deposition in the plant cells.

The synthesis of callose can also be induced by wounding, pathogen infection and physiological stresses [15-16]. Callose is not only a component of the normal sporophytic cell wall when produced in response to wounding [17], but also participates in the formation of a physical barrier against pathogen invasion. It is formed at the penetration sites of fungal hyphae [8] and around lesions in virus-infected plants where it may help to prevent spreading of the virus [18]. Callose localizes at other locations as well, including the cell plate, plasmodesmata, and in sieve plates of phloem [19].

All the events mentioned above point that callose existence is a well organized process. It seems that it provides an isolation period to the cells in normal development and under stress conditions. Although the synthesis and deposition of callose have been studied for many years, the understanding of synthesis mechanism is still incomplete. Over the last several years, however, significant progress has been made, in particular using the model plant *Arabidopsis thaliana* [20]. In the model plant *Arabidopsis thaliana* two independent research groups identified twelve genes encoding putative callose synthase [21-24]. The group of Desh Verma [21] uses the CalS (callose synthase) system to name the twelve genes: *AtCalS1-AtCalS12*. Each of these genes may be tissue-specific and/or regulated under different physiological conditions responding to biotic and abiotic stresses.The callose synthase complex exists in at least two distinct forms in different tissues and interacts with phragmoplastin, UDP-glucose transferase, Rop1 and, possibly, annexin. The Somerville group [24] also refers to the twelve *Arabidopsis* genes as GSL (glucan synthase-like) genes, and has designated them as *AtGSL1* to *AtGSL12* [16]. Phylogenetic analysis of the *AtGSL* family suggests that the *GSL* family can be classified into four main subfamilies according to the phlogenetic analysis based on aligning deduced

GSL amino acid sequences. The first subfamily contains *AtGSL1*, *AtGSL5*, *AtGSL8* and *AtGSL10*, the second subfamily contains *AtGSL2*, *AtGSL3*, *AtGSL6* and *AtGSL12*, the third subfamily contains *AtGSL7* and *AtGSL11*, and the last subfamily includes *AtGSL4*. A single *GSL* gene can also have diverse functions; for instance, *GSL5* is responsible for the synthesis of wound- and pathogen-inducible callose in leaf tissue, and it also plays an important role in exine formation and pollen wall patterning [16, 25-27].

Although this review will cover the role of callose in the course of sexual reproduction, our purpose is also to draw attention to the formation and importance of callose during normal development and response to biotic and abiotic stresses.

2. Callose in the cells related with sexual reproduction

2.1. Callose in microsporogenesis

Pollen grains in flowering plants are produced as an outcome of meiotic division in pollen mother cells (PMCs). In preleptoten stage, PMCs look alike somatic meristematic cells those are surrounded by a typical cellulose wall. They are connected by plasmodesmata in 200–280 A° diameters. Plasmodesmatal connections also exist between PMCs and tapetal cells, innermost layer of anther wall, at that stage. With the initiation of meiosis, callose deposition starts between plasma membrane and cell wall of microsporocytes, and cytoplasmic connections between tapetum and PMCs are broken. At the prophase I, the PMCs are interconnected by wider cytoplasmic channels which provide cytoplasmic continuity in all microsporocytes of an anther locule. Thus, all PMCs of a pollen sac form a single cytoplasmic entity, the meiocytic syncytium. Although the importance of syncytium is not clear, the cytoplasmic continuities impose a mutual influence of one cell over the other. This probably helps maintaining a close synchrony in meiotic prophase I [28], and with the blockage of cytoplasmic channels, usually at end of prophase I, synchrony is gradually lost. Callose deposition continues through meiosis so that each of the products of meiosis, the tetrad of microspores, is also surrounded by a dense callose (Figure 1a-d). After the completion of meiosis, the callose wall is broken down by callase enzyme activity that is secreted by tapetum releasing free microspores into the pollen sac [29-31].

The development of callose and its degradation a little after the completion of meiosis suggests that callose layer performs some special functions. The callose wall isolates not only the sporogenous tissue from the somatic tissue but also the individual microspores. It gives mechanical isolation to the developing microspores, thereby preventing cell coherence, and by their rapid and total dissolution, sets the microspores free. This layer also functions as a kind of chemical isolation, establishing a selective barrier between genetically different haploid cells that must pass through their developmental stages unexposed to the influence of their sister spore, or of adjoining spores and somatic tissue [28, 32, 33]. Heslop-Harrison and Mackenzie [11] used labelled thymidine in the anthers of *Lilium henryi* and suggest that callose not only acts as a barrier or "molecular filter" to the exchange of at least some macromolecules, but also provides genetic autonomy to each developing sporocyte.

It has also been suggested that callose wall protects the developing sporocytes from harmful hormonal and nutritional influence of the adjoining somatic cells [34, 35]. According to Shivanna [36], isolation is necessary for the PMCs for transition, from the sporophytic phase to the gametophytic phase, and gametophytic genome expression without interference either from other spores or parent sporophytic tissue.

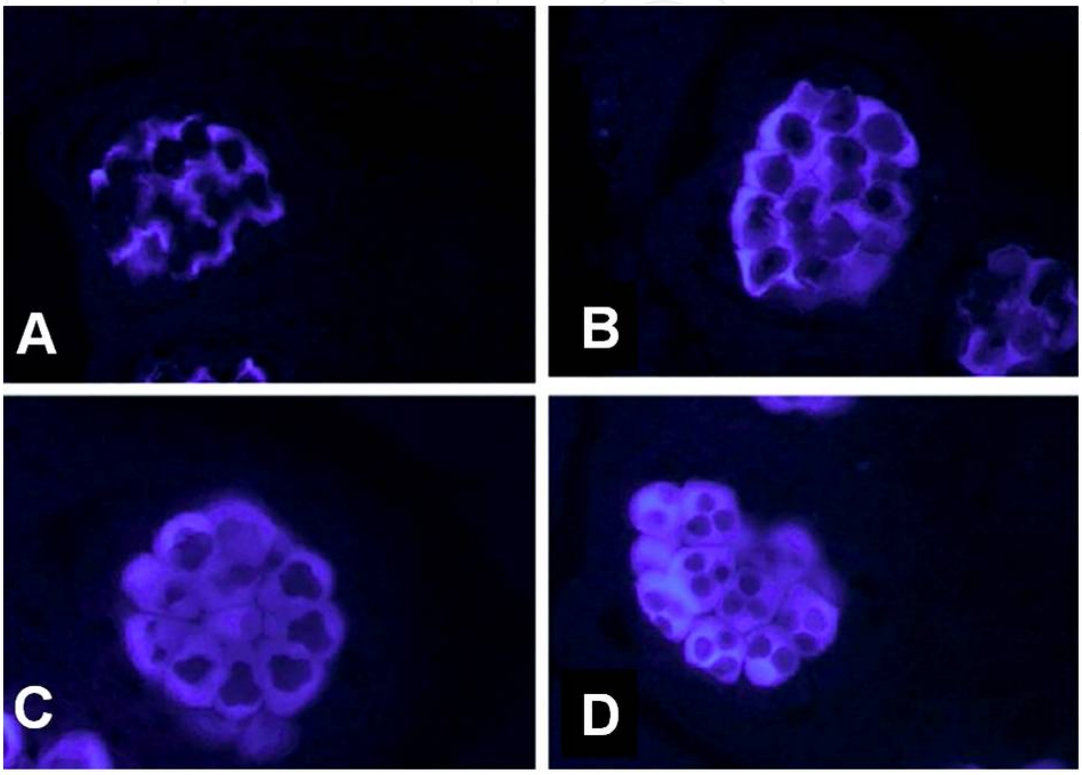

Figure 1. Callose accumulation in the anthers of *Lathyrus undulatus* during microsporogenesis stained with aniline blue. A, B. Prophase I. C. Telophase II. D.Tetrad [129].

Barskaya and Balina [37] studied in Sax beans in order to enlighten the role of callose in the anthers, and examined the effect of atmospheric drought on microsporogenesis. They pointed that moderate drought inflicts considerable damage on sporogenous cells from dehydration, and cells surrounded by callose are not harmed by drought for a certain period of time. The effect of callose is achieved by its ability of water absorption. Undoubtedly, the callose protection is not unlimited. It depends on both the intensity and duration of the drought and the plant's resistance to the drought. When the drought is long and intensive, callose's water source is consumed rapidly, and the anther dies. Similarly Li *et al.* [38] stated that the callose wall isolates meiocytes from other sporophytic tissues and, concurrently, prevents them from dehydration in water stress conditions.

According to Barskaya and Balina [37], callose is a source of carbohydrates for the developing microspores. Following its breakdown, the soluble carbohydrate can be used in their metabolism during their development. Despite the fact that this idea is quite interesting, we think that it seems to have more work.

Irregularities in the deposition of callose around the PMCs and its prematurely breakdown seem to be responsible for male sterility. It has been shown that the PMCs of male sterile lines of *Petunia hybrida* are not enclosed by callose wall after prophase I [39]. It is thought that this abnormality is due to the mistiming of callase in both male sterile *Petunia* [39] and male sterile sorghum lines [40]. In fertile plants, callase enzyme appears only at microspore tetrad stages while in sterile plants strong callase activity is detected during prophase I. It could be concluded that earlier activation of callase enzyme is responsible for cytoplasmic male sterility in *Petunia*. However, it is not known whether this is the only factor that contributes to male sterility. The male sterile plants, therefore, provide only circumstantial evidence that the callose wall has a vital function in microsporogenesis. There is a positive relationship betweeen pH, callase activity and dissolution of callose. Activation of callase in both sterile and fertile anthers is associated with a drop in pH in the anther locule from over pH 7 to around pH 6 that is optimal for callase activity. It is suggested that the time of activation of callase is controlled by regulation of pH in the anther locule [39].

Winiarczyk *et al.* [41] examined callase activity in anthers of sterile *Allium sativum* (garlic) and fertile *Allium atropurpureum*. In *A. sativum*, the extracted callase from the thick walls of microspore tetrads exhibited maximum activity at pH 4.8. Once microspores were released, *in vitro* callase activity reflected the presence of three callase isoforms peaked at three distinct pH values. One isoform, which was previously identified in the tetrad stage displayed maximum activity at pH 4.8. The remaining two novel isoforms were most active at pH 6.0 and 7.3. In contrast to *A. atropurpureum*, three callase isoforms, active at pH 4.8–5.2, 6.1, and 7.3, were identified in the microsporangia that had released their microspores. The callose wall persists around meiotic cells of *A. sativum*, whereas only one callase isoform, with an optimum activity of pH 4.8, is active in the acidic environment of the microsporangium. However, this isoform is degraded when the pH rises to 6.0 and two other callase isoforms, maximally active at pH 6.0 and 7.3, appear. Thus, the researchers concluded that factors that alter the pH of the microsporangium may indirectly affect the male gametophyte development by modulating the activity of callase, and thereby regulating the degradation of the callose wall. They also indicated that a reduction or inhibition of enzyme activity may be caused by the presence of some inhibitors. A number of such inhibitors have been isolated and characterized from legume seeds, cereals, and tubers [42, 43].

Several studies performed on *Arabidopsis* demonstrated that multiple *GSL* genes are involved in pollen development. Enns *et al.* [27] reported that *GSL1* and *GSL5* are necessary in pollen development, and they are responsible for the formation of the callose wall that separates the microspores of the tetrads. They also indicated that these genes also play a gametophytic role later in pollen grain germination.

Callose wall also plays an effective role in the orderly formation of exine. It provides the compounds of cellulosic primexine [44]. Waterkeyn and Beinfait [45] suggested that the callose wall acts like a template or mold for the formation of the species-specific exine sculpturing patterns seen on mature pollen grains. This hypothesis is also supported by the studies in Epacridaceae [46].

It has been reported that there is no callose wall formation during microsporogenesis in *Pergularia daemia* and the exine wall is thin, fragmentary, and it lacks ornamentation [47]. Some hydrophylic plants such as *Amphibolis antartica* [48] and *Halophila stipulaceae* [49] exhibit no detectable callose around microspore tetrads, and pollen grains show no ornamented exine either. Similarly, *Arabidopsis* mutants that produce no callose wall show no ornamented exine either [50]. These results suggest the essential role of callose in the formation of outer wall of pollen grains.

Albert *et al.* [51] investigated the relationship between intersporal wall formation, tetrad shape and pollen aperture pattern ontogeny in *Epilobium roseum* (Onograceae) and *Parranomus reflexus* (Proteaceae). Comparison of apertures within tetrads indicates that the position of apertures is correlated to the last point of callose deposition.

2.2. Callose stage of generative cell in a pollen grain

The mitotic division of a pollen grain results into two unequal cells; a larger vegetative cell and a smaller generative cell. Initially, they are separated by two plasma membranes. The wall of the generative cell is soon formed in between the two plasma membranes [52]. Callose first appears in the region of the wall between the two cells in the pollen grain, and then progresses around the generative cell, completely enveloping it. Gorska-Brylass [53] was the first researcher who pointed that callose exists in the area where the generative cell is separated from the vegetative cell. Later studies have shown that the callose alone, or along with cellulose, is a component of the early formed wall around the generative cell of pollen grains of certain other plants [53-57]. The general rule in researched species is that the callose disappears just before the generative cell moves to the centre of vegetative cell. Generally, the time period where the callose wall appears is short. The isolation period with the callose, comes before the DNA synthesis. Because of that reason, the callose stage of the generative cell is a period where structural and physiological differentiation takes place, and considering the fact that there is no isolation stage in male gamete formation in higher plants, it becomes more significant. Callose provides an adequate isolation barrier for the differentiation of cells related with sexual reproduction. As a result of the isolation, the generative cell confronts a different differentiation period than the vegetative cell has. The callose that becomes visible for a period of time in the border between the two cells in the closed system of the pollen grain has a significant role in both vegetative and generative cell differentiation. It is a well-known fact that isolation is necessary for the expression of gametophytic genome without interference from neighbors [36].

2.3. Callose in pollen tubes

After pollen hydration, a pollen tube emerges at the germination pore. If many germination pores are present, their outgrowth is generally blocked by deposition of callose [58]. When a pollen tube grows out of a pollen grain, the entire cytoplasm that contains the germ units flows continuously towards the tube apex [59]. The pollen tube is surrounded by an outer pectocellulosic wall and an inner homogeneous callose wall [60-61]. Besides as a wall substance, callose occurs as a plug in pollen tubes (Figure 2). A few authors [6, 62, 63] assumpted that inner tube

wall layer and the plug consist exclusively of callose, and concluded that the inner tube wall layer and the plugs contain, in addition to callose, pectin and cellulose. Kroh and Knuimann [64] reported that, in the inner pollen tube wall, and plugs contained microfibrils of cellulose in addition to callose, and "non-cellulosic" microfibrils that had "pectin-like" properties.

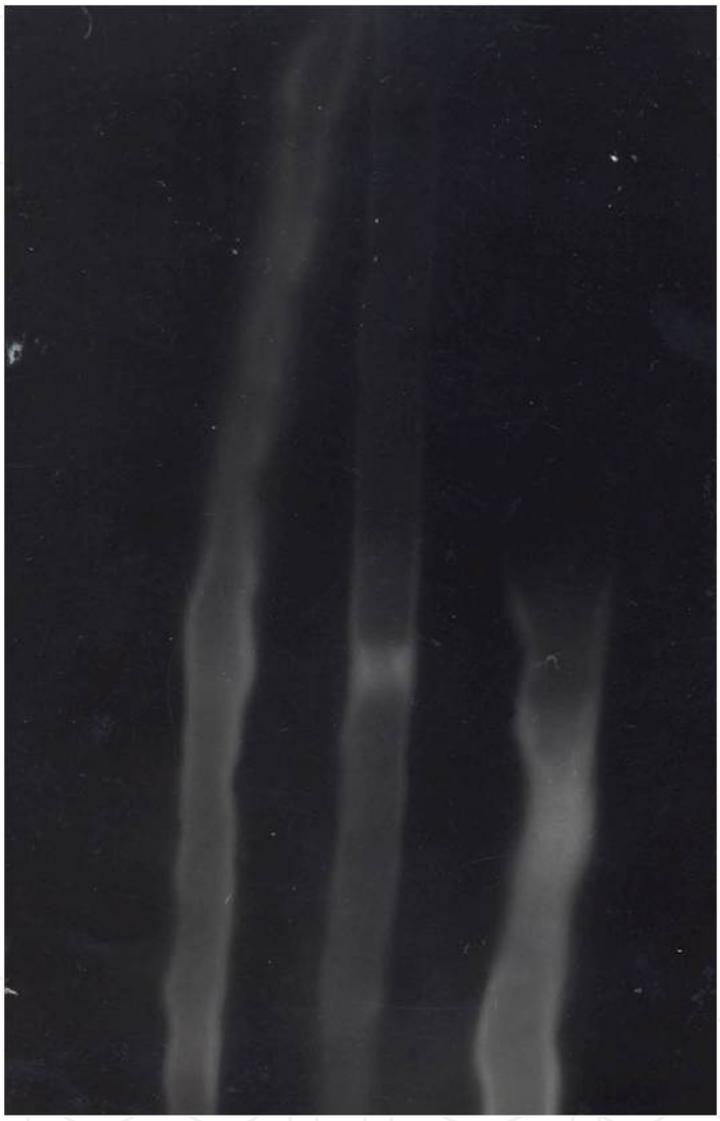

Figure 2. Fluorescence of callose in the compatible pollen tubes of *Petunia hybrida* [78].

As the pollen tubes grow down of the style, depending on the length of pollen tube and the rhythmic growth, a series of callose plugs (Figure 3a,b) sealing off the pollen tube are formed transversely at a regular distance behind the tip [65]. As a result, a fully grown pollen tube is divided into many compartments by callose plugs. The tip of the pollen tube contains only pectin, hemicellulose and cellulose [64, 66]. Closely behind the tip zone an additional cell wall layer is deposited, containing callose. Callose is not deposited on the tip of growing pollen tube.

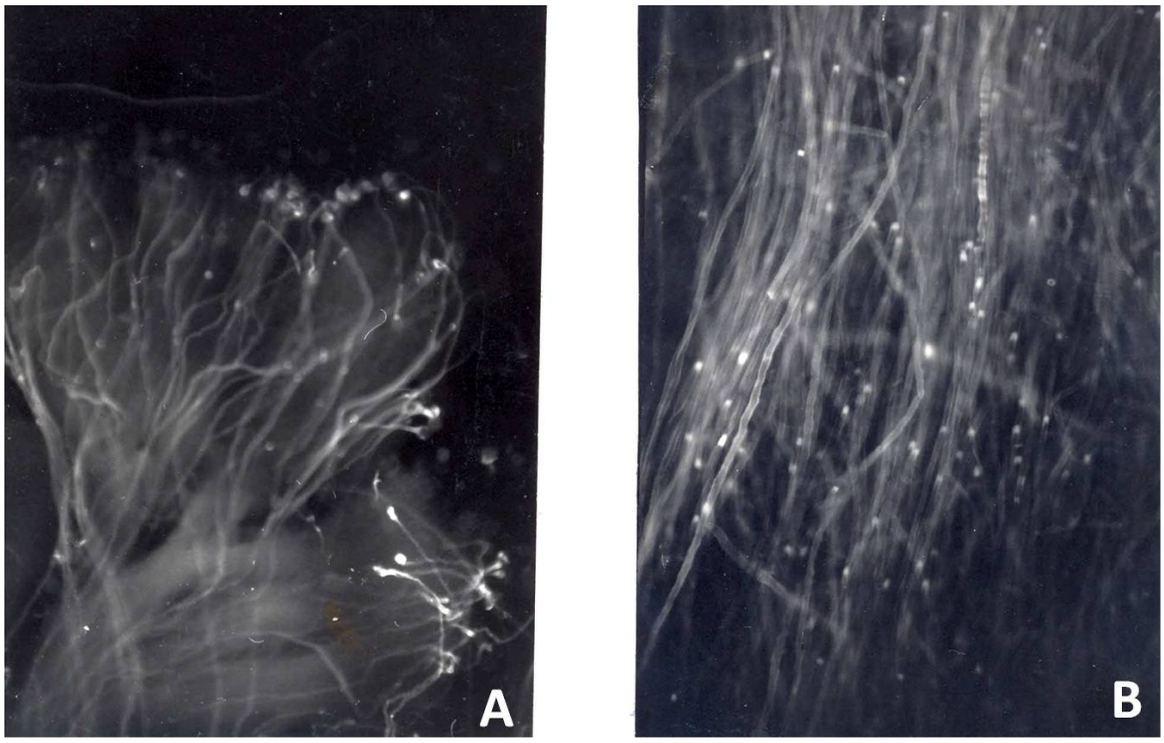

Figure 3. Fluorescent micrographs of compatible pollen tubes of *Petunia hybrida*. A. In stigma B. In style [78].

Generally, callose plugs are believed as mechanical barriers those prevent the plasma at the apex to flow backwards. According to Jensen and Fischer [67], plugs prevent the tubes to shrink. According to Müller-Stoll and Lerch [62], callose is a significant product of the pollen tube metabolism. It arises as a result of a mechanical stimulation of the cytoplasm movement, and this stimulation activates the callose synthesizing enzyme. According to Tsinger and Petrovskaya–Baranova [63], plugs are formed to support the pollen tube wall from the factors such as pressure, dehiscence and mechanical tensions. The callose in the pollen tube wall takes also a role in maintanence of osmotic balance in pollen tubes [65]. As a wall material, however, there must be another reason for the callose deposition. According to the Rubinstein et al. [68] the callose sheath of pollen tube in maize is the target of accumulation of a maize pollen-specific gene, PEX-1, with an extensin-like domain. It might be expected that proteins like extensin would ultimately be involved in supporting the growth of the pollen tube or in facilitating cell to cell signalling between the pollen tube and the style [68]. Much more work is needed before we can truly assess generality and significance of extensin and callose sheat of pollen tube. Giampiero *et al.* [69] examined the distribution of callose synthase and cellulose synthase in tobacco pollen tubes in relation to the dynamics of cytoskeleton and the endomembrane

system. Both enzymes are associated with the plasma membrane, but cellulose synthase is present along the entire length of pollen tubes (with a higher concentration at the apex) while callose synthase is located in distal regions. Actin filaments and endomembrane dynamics are critical for the distribution of callose synthase and cellulose synthase.

There is a close relation between incompatibility and callose deposition on pollen tubes. Sexual incompatibility in plants may be interspecific or intraspecific. The latter is also called self-incompatibility and it is of two types: gametophytic self-incompatibility (GSI) and sporophytic self-incompatibility (SSI). An important manifestation of gametophytic incompatibility systems includes abnormal behavior of pollen tube and heavy deposition of callose in it. Linskens and Esser [70] are the first investigators to point the relationship between the incompatibility and the callose amount in pollen tubes. In GSI systems, the rejection reaction take place in the style and the growth of the pollen tube after growing to various extents, about one-third of the transmitting tissue of style ceases. In GSI systems inhibition of pollen tube is generally associated with extensive deposition of callose in the pollen tube [71-76]. Callose deposition increase in the walls and in the plugs of incompatible pollen tubes. In others, callose is deposited even inside the pollen grain, beginning at what appears to be the site of pollen tube emergence [77].

In incompatible pollen tubes of *Petunia hybrida*, the amount of callose is greater than in compatible ones [78]. According to the results of the study on *P. hybrida*, incompatible tubes are characterized by an abnormally increased deposition of callose in the wall. Often, a callose plug is located at the tip to prevent the sperm cells to reach the tip (Figure 4). Furthermore, the callose plugs in these tubes are much longer and greater in number compared to those in compatible tubes (Figure 5a,b). The incompatibility of pollen tubes is also marked by swelling of tips until they burst to death within the style. While some of the incompatible pollen tubes carrying sperm cells in transmitting tissue may burst. Eventually, incompatible tubes stop growing and die. These events have not been found in compatible tubes. The first callose plug formation in incompatible tubes of *P. hybrida* was observed 4 hours after self-pollination, but 8-10 hours after cross pollination in compatible ones. This fact indicates that the formation of callose plugs in incompatible tubes is earlier than the one in compatible ones [78]. According to Tupy's [71] experiments in apple and tobacco, the callose amount in incompatible tubes is twice that of in compatible tubes. The reason of more callose in incompatible tubes of apple and tobacco is longer plugs and intensive callose, respectively.

Although the most common self-incompatibility system is of the gametopytic type, amazingly, little is known about the location of pollen recognition factors in this group plants. After incompatible pollination, when the pollen grains also come in contact with the stigmatic papillae, a callose plug develops at the tip between the cell wall and the plasma membrane [79-80]. There is no plug formation after compatible pollination. The formation of the callose plug in the papillae is very rapid and often visible within 10 minutes after pollination (Figure 6a,b) [81]. The stigmatic papillae react with the production of callose in the papillate cells near the pollen or pollen tube in order to prevent the penetration of pollen tube into stigma and the style. The deposition of callose in *Raphanus* is possibly related to the perforation of the cuticle by the pollen tube, and it can be compared with a wounding effect [82].

Figure 4. Terminal callose plug in the incompatible pollen tube of *Petunia hybrida* [78].

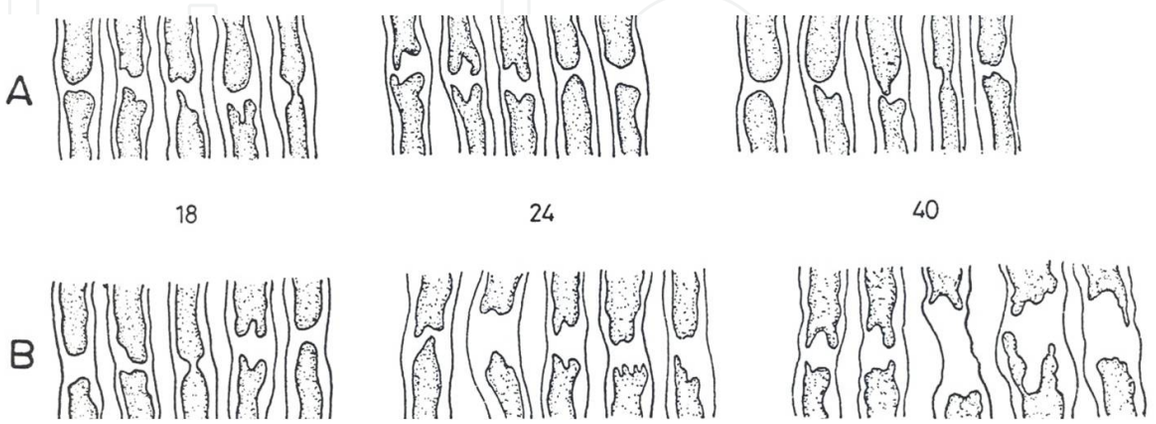

Figure 5. Callose plugs after 18, 24 ,40 hours compatibly pollinated (A) and incompatibly pollinated pistil (B) of *Petunia hybrida* [78].

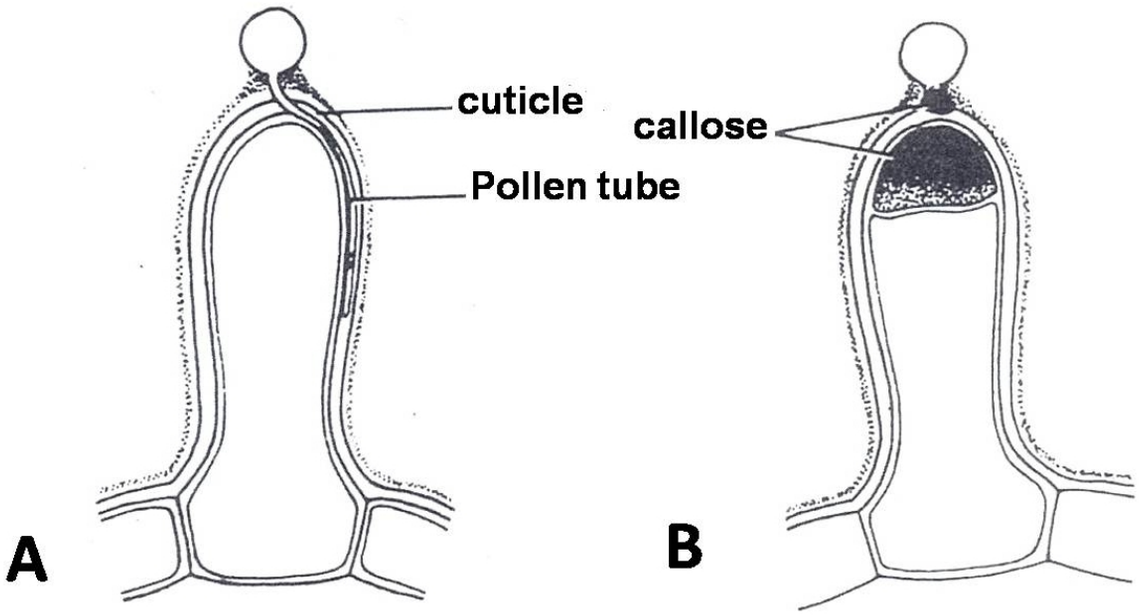

Figure 6. Stigmatic papilla in cross-pollination (A) and self-pollination (B). Note deposition of callose at the tip of pollen tube and in the papilla in self-pollinated stigma [36].

Callose deposition appears to be a Ca^{+2} –dependent process in self-pollinated *Brassica oleracea* since it is abolished by deprivation of Ca^{+2} [83]. Callose formation in the stigma is not a requirement for the demise of self-pollen or incompatibility functions [84].

2.4. Callose in megasporogenesis

Despite there is a similarity on the deposition of callose during megasporogenesis and microsporogenesis, there are evident differences. These differences basically depend on the strong polarization of megaspore mother cell (MMC) and megaspore tetrad. In the course of meiosis of PMCs and microspore tetrads, such polarization does not exist. The polarization in the megasporocyte and megaspore tetrad is very obvious, resulting in the formation of an active megaspore. The unusual accumulation of callose in megasporogenesis is clearly connected with the strong polarization of the cells. The starting of callose deposition in the wall of megasporocyte and its disapperance corresponds with the localization of the active spore in the tetrad [85].

Callose always appears in the early meiotic prophase I. In the *Polygonum* type of embryo sac development callose first deposited at the chalazal pole of the meiocyte in the early prophase I, and the entire meiocyte is usually surrounded by a callose wall at metaphase I. Subsequently, it surrounds the entire cell. Callose deposition continues through meiosis so that each of the products of meiosis, the tetrad of megaspores, is also surrounded by callose. The callose deposites on the cross walls separating individual megaspores, as well. After completion of megasporogenesis, the callose disappears from the wall of the functional megaspore, whereas it frequently remains present in the walls of megaspores which will degenerate. The temporary

isolation of the megasporocyte may be connected with the process of differentiation of the sporocyte for basically a new type of development [85].

In such cases, the cell organelles and starch grains are more intensively located in the side of megasporocyte of the active spore in the tetrad. Additionally, cell division occurs in unequally resulting in a larger functional megaspore and smaller non-functional megaspores which will degenerate. Invariably, the active functional megaspore has a callose free wall to allow the passage for the movement substances into it [85]. On the other hand, the non-functional megaspores are surrounded by callose wall for a long time and eventually undergo programmed cell death and degenerate [86].

In the meiotic division of MMC, callose formation was first demonstrated in orchids by Rodkiewicz and Gorska–Brylass [87]. Subsequently, Rodkiewicz [88] identified the callose existence in 43 species from 14 families in angiosperms (Figure 7a-e). We have, now, an impressive list of plants in which callose formation during megasporogenesis has been demonstrated [89-96]. In the course of megasporogenesis, callose exists transiently in the cell walls of plants with mono- or bisporic type of embryo sac development, but it is not detected in the species with a tetrasporic type [88]. It is assumed that the callose wall plays a significant role in the type of embryo sac development, forming a molecular filter that decreases the permeability of the cell wall. In this way, MMC becomes temporarily isolated from the surrounding sporophytic tissue. This isolation enables the cells to undergo an independent course of differentiation, accompanied by the shift from sporophytic to gametophytic gene expression.

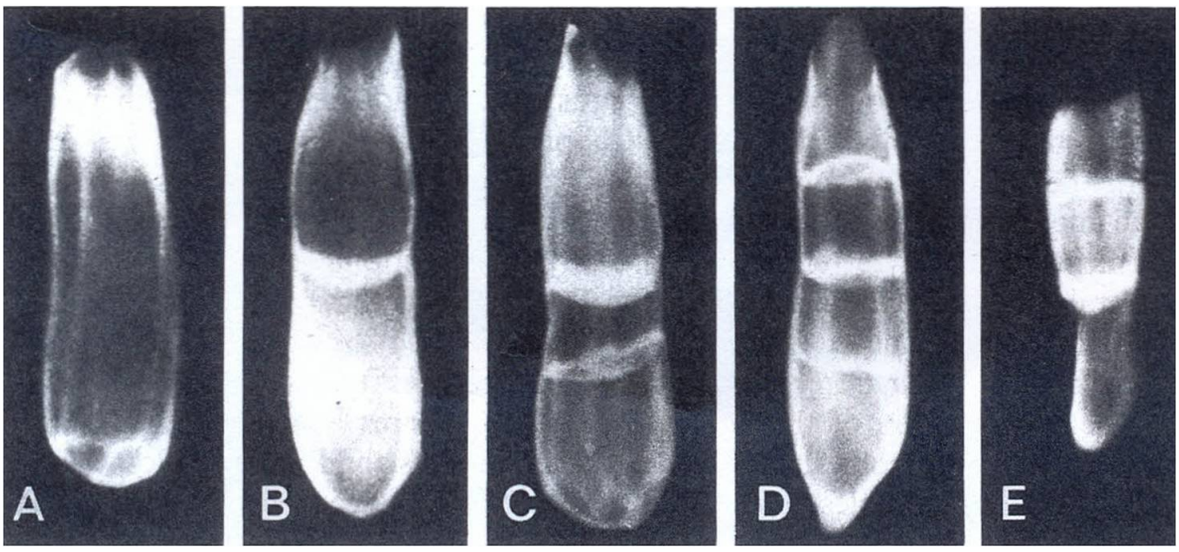

Figure 7. (A-E) Fluorescence of callose in the walls of megasporocytes in *Fuchsia hybrida* [88].

Moreover, callose has alternative roles in sexual reproduction. In *Catananche betacea*, *Nicotiana tabacum* and *Petunia hybrida*, the two sperm are connected together by a transverse wall as is in *Plumbago zylenica* [97]. However, in *N. tabacum*, the wall appears to be further specialized by the presence of fibrils, small tubules, and callose [98].

It has been known that the pollen tube enters to embryo sac through the filiform apparatus, and after growing, it arrives in the synergid cytoplasm. The content of the pollen tube is discharged in the synergid. In cotton, the content is discharged through a subterminal pore which is invariably on the side facing the chalaza [99]. The end of the discharge is signaled by the formation of a callose plug over the pore, effectively preventing any cytoplasmic flow between the pollen tube and the synergid [100].

Soon after syngamy, the zygote undergoes some changes. Before fertilization, the cell wall that is restricted to the micopylar part of the egg cell, is now complete around the zygote. In several species of *Rhododendron* and in *Ledum groenlandicum* (Ericaceae), a callose wall is laid off around the zygote during the first two days after fertilization [101]. The fact that the wall essentially insulates the newly formed zygote from the influence of cells of a different genotype in the immediate neighborhood probably has some significance in the subsequent induction of the sporophytic divisions [97]. Zygote becomes an isolated cell in the sence that the plasmodesmatal connections with the surrounding cells are blocked.

In apomictic species, the nucellar cells which start an embryonic pathway also show isolation from surrounding nucellar cells with a callose wall [102]. This event is an excellent example of the mystery of callose existence in the cells related with reproduction. It suggests that if a cell takes a role in reproduction, it needs to be isolated for a period by a callose wall.

3. Several other locations of callose and its deposition in response to stress

As we mentioned above, callose plays important roles during sexual reproduction in plants. Besides, callose also appears in several other locations such as plasmodesmata regulation, cell plate formation and responses to multiple biotic and abiotic stresses (including plasmolysis, high and low temperature, many harmful chemical compounds including heavy metals, ultrasounds, pathogen infection and wounding). After stimulation callose synthesis occurs rapidly, and it is deposited as plugs and drops [103, 104].

Callose has been localised particularly to plasmodesmata [105-106]. It has been known that plasmodesmata are the intercellular connections between plant cells that allow cell-to-cell transport of sugars, amino acids, inorganic ions, proteins, and nucleic acids [107]. The accurate function of plasmodesmata depends on what plants require to respond to developmental and/or environmental signals [108]. Thus, callose is deposited at plasmodesmata to regulate the cell to cell movement of molecules by controlling the size of them. Callose can also be deposited at plasmodesmata in response to abiotic and/or biotic stresses [16].

In higher plants during cell division, the first visible evidence of the new cell wall is deposition of the cell plate in an equatorial plane between daughter nuclei. Samuels *et al*. [109] indicated that the callose is the main luminal component of forming cell plate and it forms a coat-like structure on the membrane surface. Callose deposition is followed by the deposition and organization of cellulose and other cell wall components; at the same time, cell plate callose is degraded by β-1,3-glucanase.

In ferns, callose performs multiple roles during stomatal development and function. Callose, in cooperation with the cytoskeleton, is involved in stomatal pore formation, in the mechanism of pore opening and closure and wall thickenings of guard cells [110].

It is now generally recognized that the sieve plate of phloem is one of the several sporophytic locations of callose in higher plants (1). Barratt *et al.* [111] suggest that the callose coating of sieve plates pores is essential for normal phloem transport because it confers favorable flow characteristics on the pores. Callose is synthesized in functioning sieve elements in response to damage and other stresses, such as mechanical situmulation and high temperatures. The wound callose is deposited in the sieve elements of surrounding intact tissue. As the sieve elements recover from damage, the callose disappears from these pores. Callose is also found in sieve elements under cases other than wounding, although its function always seems to be sealing. Definitive callose is deposited in dying cells or sieve elements undergoing elimination due to the formation of secondary tissues. Callose associated with dormancy is found in many perennial plants which have become dormant in the winter. Such dormancy callose is redissolved in the spring in preperation for resumption of transport and growth [112].

Biotic and abiotic stresses induce K^+ efflux and Ca^{2+} influx into the cell. Plasma membrane depolarization may result because of changes in ion fluxes. It has been reported that salicylic acid activates callose synthesis due to the induction of calcium influx into the cell which increases its concentration in the cortical cytoplasm layer [113-115]. In *Arabidopsis,* two hours treatment with salicylic acid increased the content of *AtGSL5* gene that encodes a protein homologous to the catalytic subunit of β-1,3-glucan synthase [116].

Although the mechanisms behind the rapid callose synthesis are not well understood, it has been proposed that callose synthase may be activated by perturbed conditions, leading to some loss of membrane permeability [114, 117]. The membrane perturbation results in membrane leakage and the apoplastic Ca^{2+} leaks into the cytosol. The increment of the local Ca^{2+}concentration activates callose synthase. It is reported that several annexin-type molecules that are known to respond to Ca^{2+} levels interact with callose synthase [118]; Callose synthase may be activated by annexin interaction. After wounding, the membrane lipids may change and affect the activity of callose synthase [119].

Wounding or pathogen invasion can induce reversible callose synthesis in plants. This may ameliorate the results of wounding or stop the pathogen from spreading to other cells or tissues. Synthesis of callose within the sieve pores can help to seal off damage or prepare the cells for developmental changes [69]. Iglesias *et al.* [120] indicated that a silencing mutant of β-1,3-glucanase decrease the plant sensitivity to viruses, after the invasion, the plasmodesmata are found to be smaller than in wild-type plants, because of the accumulation of callose in the plasmodesmata, which is degraded in the wild-type plants.

During the fungal infections, callose is deposited to form beneath infection sites and thought to provide a physical barrier to penetration. However there is little knowledge about the signaling pathway leading to callose synthesis during plant-microbe interaction. Although the induction mechanism is not known, it has been reported that callose is induced in carrot (*Daucus carota* L.) cell suspensions treated with a spirostanol saponin from *Yucca* [121].

Furthermore over-expression of the tomato disease resistance gene *PTO* induces callose deposition [122]. Kohler and Blatt [123] reported that *Arabidopsis* plants treated with the synthetic acquired resistance (SAR) inducer benzothiadiazole (BTH) also increase callose deposition, as well as the expression of resistance genes.

After the powdery mildew *Erysiphe cichoracearum* penetration, callose is deposited along the whole cell margin determined by an intense aniline blue fluorochrome staining in wild-type plants, whereas cells in *CalS12* mutants showed only a punctuate callose staining pattern at the cell periphery. It has been suggested that the punctuate staining pattern in *CalS12* plants may be plasmadesmata callose, because callose is typically deposited in the cell wall area immediately surrounding the orifice of a plasmadesmata, particularly during wounding or aldehyde fixation [25, 124, 125].

Luna *et al.* [126] examined the robustness of callose deposition under different growth conditions and in response to two different pathogen-associated molecular patterns, the flagellin epitope Flg22 and the polysaccharide chitosan on *Arabidopsis*. Based on a commonly used hydroponic culture system, the resarchers found that variations in growth conditions have a major impact on the plant's overall capacity to deposit callose.

The constitutive capacity to quickly synthesize callose on wounding provides cells with the ability to generate a new physical barrier, that seals the injured plant tissue. The physiological machinery involved in the induction and maintenance of callose deposition can be triggered also by metal toxicity, without conferring any apparent protection against metal toxicity. Aluminum-induced callose formation has been studied in detail and used for the secreening of plant genotypes for Al sensitivity, because it is a sensitive and reliable indicator and measure of the level of stress perceived by the plant tissue provided the dynamics of callose turnover, and constitutive synthesis capacity are taken into account [112]. For instance, Vardar *et al.* [127] reported time and dose dependent callose accumulation after Al treatment in the root tips of *Zea mays* (Figure 8).

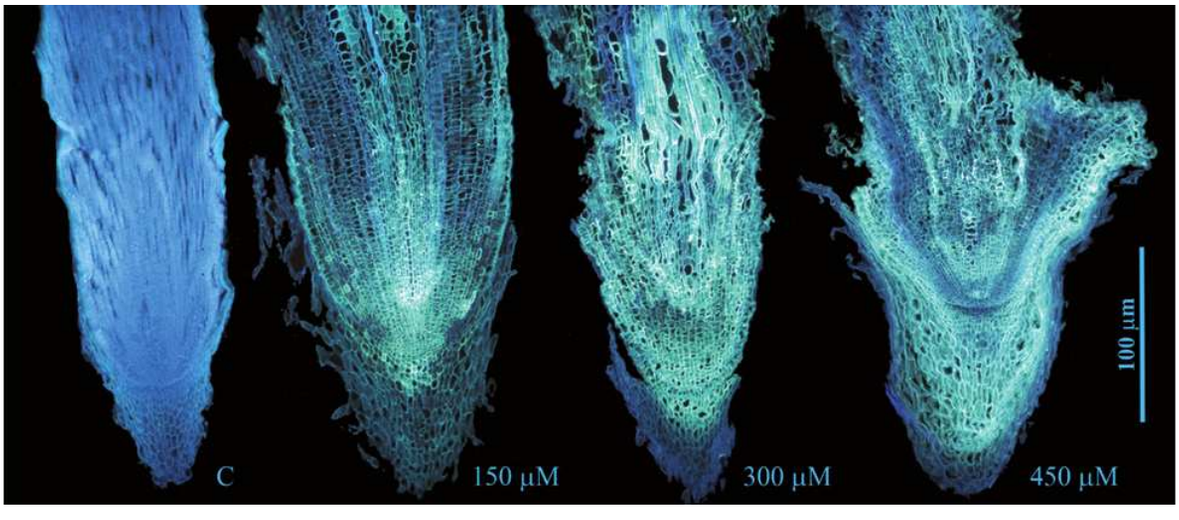

Figure 8. Aluminum-induced root callose deposition (yellowish-green) in maize roots. The seedlings were exposed to aluminum concentrations of 150, 300 and 450 µM AlCl3 (pH 4.5) for 96 h [127].

Among other metals inducing callose formation, only Mn has been studied in some detail [128]. The potential of metal toxicity-induced callose formation to increase understanding of the dynamics and spatial perception of stress within plant tissues has not yet been exploited [112].

4. Conclusion

Callose, which is a 1,3- β- glucan polymer with some 1,6 branches, is involved in diverse biological processes associated with plant development, biotic and abiotic stress responses. Callose plays important roles in the reproductive biology of angiosperms. It appears around microsporocytes and megasporocytes during meiosis. It can be suggested possible that callose is involved in some aspects of meiosis in higher plants. Furthermore it is also involved in plasmodesmata regulation, cell plate formation, in response to multiple biotic and abiotic stresses. Although remarkable progress has been performed, there are still some unexplained cases, such as the biochemical pathway of callose synthesis, functional components of callose synthase complex and signal pathway of callose synthesis. The future perspectives in biochemistry, cell biology, genetics and molecular biology will be helpful improving our knowledge

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