1. REVIEW OF LITERATURE

Unlike animals in which primordial germ cell development occurs early during embryonic development, the development of reproductive organs and their sporocytes occurs late in plant development. In higher plants the formation of male gametes occurs within the anther and the female gametes within the ovule. Periclinal divisions in several adjacent hypodermal cells within the anther primordium signal the formation of male gametes. RNA-protein rich archesporial cells differentiate at four corners of the anther primordium. The archesporial cells divide periclinaly to form inner primary sporogenous cell (PSC) and outer primary parietal cell (PPC). PSC undergoes number of divisions to form meiocytes (pollen mother cells).

1  **Scott et al. (2004)**: PSC sets up a radial field of signals that induce periclinal division of PPC to form outer endothelial cell and inner secondary parietal cell (SPC). SPC then executes the final division of the program, forming outer middle layer and inner tapetal cells.

2  **Hegde and Andrade, (1982)**: The anther wall layers (epidermis, endothecium, middle layer and tapetum) form concentric rings around the sporogenous cells. Sporogenous cells and tapetum, but not other wall layers and connective, are rich in RNA, proteins, ascorbic acid and array of oxidative and hydrolytic

3  **Hegde and Isaacs, (1992)**: The anther wall layers (epidermis, endothecium, middle layer and tapetum) form concentric rings around the sporogenous cells. Sporogenous cells and tapetum, but not other wall layers and connective, are rich in RNA, proteins, ascorbic acid and array of oxidative and hydrolytic enzymes

4  **Hegde et al., (1993)**. Histochemically and ultrastructurally premeiotic meiocytes closely resemble sporogenous cells

5  **Sheel and Bhandari, (1990)**: Periclinal divisions in several adjacent hypodermal cells within the anther primordium signal the formation of male gametes. RNA-protein rich archesporial cells differentiate at four corners of the anther primordium.

6  **Wilson and Yang 2004**: Periclinal divisions in several adjacent hypodermal cells within the anther primordium signal the formation of male gametes. RNA-protein rich archesporial cells differentiate at four corners of the anther primordium.

7  **Scott et al. 2004**: The archesporial cells divide periclinaly to form inner primary sporogenous cell (PSC) and outer primary parietal cell (PPC). PSC undergoes number of divisions to form meiocytes (pollen mother cells).
8 **Mackenzie et al.,** (1967), The growth rate of different cell types is not uniform. The meiocytes and tapetal cells develop rapidly while the endothelial layer remains underdeveloped till mature stage of anther. The expansion of meiocytes and tapetum crushes the narrow middle layer.

9 **Worrall et al.** (1992): Concomitant to meiosis rapid synthesis of meiocyte callose wall occurs. According to change in calcium ion concentration at plasmamembrane causes conversion of cellulose (β-1, 4-glucan) to callose (β-1, 3-glucan). Susequent to callose wall synthesis plasmadesmata severe links between the meiocytes and tapetum. Eventually meiocytes and tapetum develop into coenocytes. As meiosis proceeds meiocytes exchange their cytoplasm through now expanded plasmadesmata (cytomictic channels).

10 **Panchaksharappa et al.**(1985):, The event is believed to be essential to initiate synchrony within the meiocyte mass. Meanwhile the anticlinal walls of secretory tapetum become gelatinous and interconnecting plasadesmata enlarge to form irregular channels. The entire microsporangium becomes sealed within the lipid/sporopollenin peritapetal membrane.

11 **Knox et al.,** (1971): The premeiotic interaction between tapetum and meiocytes is insignificant as evidenced in exs/ems1 mutants of *Arabidopsis* where meiocytes develop into tetrads in the absence of tapetum. Later, tapetally-derived β-1, 3-glucanase causes dissolution of tetrad callose walls.

12 **Agadi and Hegde,** (2003), The onset of meiosis is associated with cytoplasmic reorganization in meiocytes. Plastids and mitochondria divide and differentiate. rRNA and mRNA become significantly.

13 **Bird et al.,** (1983): Except in the organelles, both DNA synthesis and expression of number of nuclear genes decline. This physical cleaning of sporophytic information from the meiocyte cytoplasm presumably facilitates gametophytic development after meiosis and freeing the germ line from detrimental RNA species such as viruses and silencing elements.

14 **Rodkiewicz et al.,** (1986): During prophase I of meiosis, meiocytes secrete callose wall (β-1, 3-glucan) between the plasmalemma and original cellulosic wall. At the end of meiosis callose wall extends as intersporal walls in tetrads. At the end of meiosis the external and intersporal walls of the tetrad are dissolved to release individual microspores by the secretion of a mixture of enzymes- the callase- by the tapetum.

15 **Dickinson,** (1987), Callase contains endoglucanases and exoglucanases. In addition, it might contain cellulases also needed to degrade the cellulosic primary walls of the
meiocytes. Male sterile mutants defective in temporal synthesis/dissolution of callose, produce sterile pollen grains

16 Izhar and Frankel, (1971). The formation of individual microspores depends on temporal synthesis and dissolution of the intersporal callose wall. In the members of Juncaceae, Ericaceae and Oenotheraceae, where microspores remain in permanent tetrads, there is little or no callose within the intersporal cross walls.

17 Blackmore and Crane, (1988). Although these microspores possess individual exine walls, they fuse along the line of intersporal walls thereby preventing separation of microspores. Interestingly, in the absence of intersporal callose wall, individual microspores are formed in *Pandanus*.

18 Periasamy and Amalathas, (1991). The absence of intersporal callose wall, individual microspores are formed in *Pandanus*. This suggests that for some species callose is not essential for exine formation.

19 Bhandari et al., (1981), Normal patterns of callose wall synthesis and dissolution will not ensure the formation of individual microspores in all plant species. Formation of permanent tetrads in quartet mutants of *Arabidopsis* is due to presence of persistent pectic components in the parent meiocyte wall surrounding tetrads. Persistent primary wall of meiocytes is also reported in *Allium tuberosum* and *Cyclamen persicum* and *Allium sativum*.

20 Gori, (1983). Persistent primary wall of meiocytes is also reported in *Allium tuberosum* and *Cyclamen persicum* and *Allium sativum*. Therefore, the degradation of pectin is also necessary for the liberation of microspores from tetrads.

21 Mandaron et al., (1990): Synthesis of RNA and total proteins regain in the microspores when they are still in tetrads. Conversion of chromosome-associated ribosomal RNA into residual RNA and restoration of ribosomal population are responsible for increase in cytoplasmic RNA and proteins in microspores.

22 Dickinson and Heslop-Harrison (1977): The development of free microspores includes the enlargement of spores, gradual accumulation of reserve substances in them, elaboration of exine, pollen mitosis that produces two celled pollen grains at the time of anther dehiscence.

23 Reznickova and Willemse (1980). In *Lilium*, increase in the microspore volume results from the water uptake, whereas according to in *Zea mays*, it is due to the removal of restraining influence of callosic wall. Presence of rich quantities of carbohydrates, RNA,
total proteins and ascorbic acid in the old microspores indicates that the increase in the volume of microspores is accompanied by the increase in the cytoplasmic contents.

24 **Moss and Heslop-Harrison (1967)**, Pollen development and maturation seem to require sugar supply during distinct growth phases. In early stages of *Arabidopsis* anther monosaccharide transporter AtSTP₂ facilitates the uptake of hexoses released during callose degradation.

25 **Schneidereit et al., (2003)**, At STP₆ expression is found only in the maturing pollen tubes, whereas transcript of AtSTP₉ is detected in pollen and AtSTP₉ protein is detected in pollen tubes.

26 **Preuss et al., (1994)**, The first mitotic division in microspore is asymmetric and establishes polarity within the pollen grain. The large vegetative cell accumulates a dense cytoplasm containing lipids, proteins and carbohydrates. This cell does not divide further, but provides storage compounds for pollen tube growth. The smaller generative cell has highly condensed chromatin. It divides to produce two germ cells.

27 **Rhee and Somerville, (1998)**, The tetrad period, although the briefest during the pollen grain maturation process, is the most complex with regard to the formation of pollen wall.

28 **Fernandez and Rodriguez-Garcia, (1988)**, The large vegetative cell accumulates a dense cytoplasm containing lipids, proteins and carbohydrates. This cell does not divide further, but provides storage compounds for pollen tube growth. The smaller generative cell has highly condensed chromatin. It divides to produce two germ cells.

29 **Chaudhary and Vijayaraghavan, (1996)**, Both gametophytic and sporophytic cells of anther contribute to the synthesis of pollen wall. The two major phases of exine ontogeny are template formation, which takes place when microspores are in callose-bound tetrads, and sporopollenin deposition, which takes place in free microspores.

30 **Kronstedt-Robards and Rowley (1989)**, The pollen wall is a multilayered structure consisting of a pecto-cellulosic intine surrounded by a sporopollenin-based exine. Exine itself consists of inner nexine and outer sexine. It is the sexine that provides species-specific variation in pollen wall patterning through its collumellae and tectum.

31 **McCormic, (1993)**, The callose wall may be regarded as the first deposition at the microspore surface. This is followed by the primexine, which acts as a precursor of the sexine.
Vijayaraghavan and Sudesh, (1994). Susequent to callose wall synthesis plasmadesmata severe links between the meiocytes and tapetum. Eventually meiocytes and tapetum develop into coenocytes. As meiosis proceeds meiocytes exchange their cytoplasm through now expanded plasmadesmata (cytomictic channels).


Katti et al., (1994). Persistence of callose causes the misleading the process of the development of microspores. The absence of secretion of callase enzyme leads to persistence of callose.

Waterkeyn and Beinfait, (1970). Deposition of nexine and finally the intine. The primexine is mainly composed of polysaccharides that directs the accumulation of sporopollenin.

Takahashi and Skavarla, (1991). Precocious dissolution of callose disrupts pollen wall formation in tobacco, deleting the tectum to leave only exposed columellae. This suggests that callose wall probably provides a solid surface against which the tectum forms.

Kaul and Sudha, (1990). Deficiency in these metabolites is known to cause a deleterious effect on anther development. The staining procedures for these substances are well established and dependable. The two major phases of exine ontogeny are template formation, which takes place when microspores are in callose-bound tetrads, and sporopollenin deposition, which takes place in free microspores.
