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Histochemical insights into polysaccharide distribution during anther development in *Swietenia macrophylla* King.

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Abstract

Carbohydrates are essential for anther development, serving as the primary energy source and facilitating the differentiation of the anther wall, microsporogenesis, and pollen maturation. In this study we have examined histochemical distribution of polysaccharides during successive stages of anther development in *Swietenia macrophylla* King. using Periodic acid–Schiff (PAS) reagent. Results of the study revealed that young anther primordia exhibited uniformly rich PAS-positive reaction. During archesporial differentiation, connective cells contained starch grains, which later redistributed in anther wall layers at the sporogenous stage. Microspore mother cells were moderately PAS-positive and surrounded by an intensely PAS-positive callose wall. Microspores in tetrads and young microspores exhibited moderate PAS staining in cytoplasm while nuclei and cell walls were richly PAS-positive. The tapetum showed strong PAS-positive reaction at tetrads and young microspore stage which later declined gradually during anther dehiscence. Vacuolated microspores and bicellular pollen grains exhibited intense PAS positivity with progressive accumulation of starch grains. Mature pollen grains contained abundant starch grains. Secretory cells of anther connective exhibited intense PAS-positive reaction throughout anther development. However, the polysaccharide reserves of these cells gradually depleted during anther dehiscence. Endothecium developed fibrious thickenings which showed PAS-positive reaction. Polysaccharide dynamics in *S. macrophylla* anthers corresponded with physiological activities occurring at successive stages of anther ontogeny, supporting the formation of functional pollen grains.

Introduction

Proper development of pollen within anther is a key factor for successful sexual reproduction in angiosperms. The anther is a specialized structure that encompasses microsporocytes which undergo meiosis and subsequent differentiation to generate viable pollen grains (Goldberg *et al*., 1993; Scott *et al*., 2004). The generation of a

functional male gametophyte requires coordinated molecular interactions between sporophytic and gametophytic tissues of anther (Yang *et al*., 2018) particularly biosynthesis, distribution, and utilization of essential nutritional substances such as carbohydrates, lipids and proteins, which serve as structural constituents as well as temporary storage reserves during pollen development (Song *et al*., 2014; Konyar, 2018). Distribution of these biomolecules in anther tissues is not static, undergo dynamic changes in terms of their form and amount according to the physiological changes occurring during anther ontogeny. However, the distribution pattern of these biomolecules across the progressive stages of anther development differs from species to species (Wei *et al*., 2015).

Carbohydrates play a critical role during the anther ontogeny. These are the primary source of energy (Yang *et al*., 2017) and play a significant role in the differentiation of the anther wall, microsporogenesis and pollen maturation. Apart from this, carbohydrates regulate the hydration status of pollen and prevent it from desiccation, thereby helping proper pollen-stigma communication during pollination and fertilization (Lora *et al*., 2022). Research studies have revealed that perturbation in carbohydrate metabolism affects the pollen development which ultimately results in male sterility (Goetz *et al*., 2001; Castro and Clement, 2007; Yang *et al*., 2017). Hence, proper carbohydrate metabolism is a key factor for the successful development of a viable pollen grain. Histochemistry is a valuable technique to study the biochemical composition of cells and tissues in the developing organs using specific stains and indicators with the help of microscopes (Badria and Aboelmaty, 2019). Histochemical analysis of anther and pollen development enables the precise localization of biomolecules within specific tissues at a particular stage of development, thereby helping in the understanding of the dynamic changes of metabolites and their correlation with structural differentiation. Moreover, this technique also provides comprehensive information regarding the developmental physiology of the anther and fertility control in plants. In view of this, numerous research studies on the histochemistry of anther development in angiosperms have been reported, including Gupta and Nanda 1972; Panchaksharappa and Rudramuniyappa 1974; Chauhan and Kinoshita 1980; Rudramuniyappa and Annigeri 1984; Delvallee and Dumas 1988; Detchepare *et al*. 1989; Franchi *et al*. 1996; Zhang and Fernando 2005; Yeung *et al*. 2011; Agadi 2012; Agadi and Negalur 2014; Lin *et al*. 2014; Oliveira *et al*. 2015; Sharma *et al*. 2015; Dogan and Vardar 2023; Chang *et al*. 2024. The Periodic acid-schiff (PAS) reaction is a dependable histochemical tool for visualizing the in-situ spatiotemporal distribution of insoluble polysaccharides and gives critical insight into carbohydrate dynamics during anther and pollen development. However, studies on the histochemistry of anther development are limited for many species of angiosperms. Moreover, detailed histochemical localization during anther ontogeny improves knowledge about biochemical regulation of pollen fertility, species-specific strategies for nutrient allocation, and contributes to understanding reproductive efficiency in plants (Yun and Huiqiao, 2015; Wei *et al*., 2015; Tang *et al*., 2018).

Swietenia macrophylla King. is a large, deciduous tree of the family Meliaceae commonly known as big-leaf mahogany. This species is indigenous to Central and South America and widely distributed in the tropical regions of the world, including India, Bangladesh, Indonesia, China and Malaysia (Lamb, 1966; Pennington *et al.,* 1981; Tareq and Ali, 2026). *S.*

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macrophylla produces premium-grade timber which is highly valued throughout the world (Mayhew and Newton, 1998; Grogan *et al.,* 2010). In addition, different parts of this plant are known to be rich in phytochemical compounds, which have been used traditionally in the treatment of various human diseases (Moghadamtousi *et al.,* 2013; Tareq and Ali, 2026). Previous studies on this plant have focused primarily on phytochemical analysis and pharmacological applications (Arumugasamy *et al*., 2004; Telrandhe *et al*., 2022; Divakar *et al.,* 2023); tissue culture (Maruyama and Ishii, 1999; Rocha and Quoirin, 2004; Collado *et al*., 2006; Quiala *et al.,* 2022); ecology and management (Gullison *et al.,* 1996); and growth performance of this species in different climatic conditions (Shono and Snook, 2006). However, no research studies so far have been reported about histochemical aspects of anther development in this species. Therefore, the present study was undertaken to examine the histochemical distribution of polysaccharides during successive stages of anther development in *S. macrophylla*.

Materials and methods

Fresh flower buds of *S. macrophylla* were collected from the Botanical garden of Karnatak University, Dharwad, India, and fixed in FAA (Formalin Acetic acid Alcohol) fixative for 24 hrs. After fixation, flower buds were washed with distilled water and preserved in 70% alcohol. Following the routine plant microtechnique procedure of Khasim (2002), materials were dehydrated in a graded alcohol-butanol series and then embedded in paraffin wax. Later, transverse sections of flower buds were obtained at 6 µm thickness using a Leica rotary microtome (Model-RM2145). Serial sections were then mounted on microscope slides using gelatin adhesive. Prepared slides with anther sections were stained with Periodic acid-Schiff (PAS) reagent for the localization of polysaccharides by following the staining protocol described by Feder and O'Brien (1968). Stained sections were examined under Olympus CX23 light microscope and photomicrographed using Capture 3.0 digital microscope camera. PAS-positive regions were stained magenta-red.

Results and discussion

Histochemical analysis of anther ontogeny using light microscopy provides critical insight into biochemical mechanisms involved in tissue and organ differentiation. Differentiation of cells and tissues in anther largely depends on biosynthesis, accumulation, and transformation of macromolecules such as carbohydrates, lipids, proteins, enzymes and nucleic acids (Auti, 2015). The present study provides dynamic, stage-specific distribution of insoluble polysaccharides during anther and pollen grain development in *Swietenia macrophylla* King, indicating coordinated metabolic and structural variations ensuring normal microsporogenesis and pollen maturation.

Anther primordia and archesporial stage

During the early stage of differentiation, the young anther primordium of *S. macrophylla* was composed of a homogenous mass of meristematic cells with dense cytoplasm and prominent nuclei which exhibited a uniformly rich PAS-positive reaction in cell walls as well as cytoplasm (Fig. 1A–B). At the archesporial cell stage, no significant change was observed in polysaccharide content of anther cells. However, archesporial cells displayed relatively high polysaccharide concentration in the nucleus and cytoplasm. Starch grains did not appear at these stages (Fig. 1C). Uniformly rich PAS-positive staining in primordial cells indicates substantial

accumulation of polysaccharides, which forms a source of energy during morphophysiological activities of the anther. In addition to this, accumulation of high polysaccharide concentration at this stage signifies high metabolic and biosynthetic activity of meristematic cells for rapid cell division and early differentiation of anther tissues. Similar results have also been described in *Melia azedarach* (Talawar and Agadi, 2019). Whereas, in *Azardirachta indica* (Talawar and Agadi, 2018) a moderate PAS-positive reaction in primordial cells was reported. Likewise, in *Zea mays* (Panchaksharappa and Rudramuniyappa, 1974), the cytoplasm of primordial cells was faintly PAS-positive, while the cell walls exhibited an intense PAS-positive reaction, suggesting the presence of polysaccharides as a structural component in the cell wall. In the subsequent stage of anther development in *S. macrophylla*, as the archesporial cell divides into primary and secondary parietal layers as well as primary sporogenous tissue, distribution of small PAS-positive starch granules was observed at the connective region and in parietal layers as well (Fig. 1D–F). These findings are consistent with the previous histochemical observations of *Dyckia racinae* and *Aechmea recurvata* (Oliveira *et al.,* 2015), *Tecoma stans* (Gupta and Nanda, 1978), and *Melia azedarach* (Talawar and Agadi, 2019).

Sporogenous tissue and microspore mother cell (MMC) stage

At this stage, anthers of *S. macrophylla* were completely differentiated into four locules with sporogenous cells at the centre, and anther wall which is composed of five layers of cells, namely epidermis, endothecium, two middle layers and single layered glandular tapetum (Fig. 1G–H). When the anther attained the sporogenous stage, starch grains from anther connective cells disappeared and accumulated in endothecium and middle layers, whereas sporogenous and tapetal cells were devoid of starch grains and exhibited faint PAS staining in cytoplasm with PAS-positive cell walls (Fig. 1H). Concurrently, some of the parenchymatous cells at the connective region enlarged and differentiated into secretary cells with dense cytoplasm and showed an intense PAS-positive reaction (Fig. 1I). These observations are consistent with those of *Campsis radicans*, where at the early sporogenous stage starch grains were present in the anther wall layers and were later declined during the meiocytes stage (Konyar *et al., 2*013). Early deposition of starch grains at the connective and their subsequent redistribution in the anther wall layers of *S. macrophylla* reflect the metabolic demands of anther wall differentiation, development of sporogenous cells, and formation of callose wall around the microspore mother cells. A similar pattern of polysaccharide distribution was observed in tomato anthers (Yun and Huiqiao, 2015). In addition, poor PAS reaction in sporogenous cells and tapetum of *S. macrophylla* anthers at this stage suggests that sporogenous cells are metabolically active tissues that generally do not accumulate polysaccharide reserves. This is a characteristic feature of many flowering plant species (Rudramuniyappa, 1985; Xu *et al.,* 2006). Likewise, in *Bauhinia blakeana* (Zheng *et al.,* 2017), no starch grains were detected in sporogenous cells as well as anther wall layers, but connective cells had rich starch granules. On the other hand, PAS-positive starch granules in sporogenous tissue have been reported in *Ipomoea cairica* (Liu *et al.,* 2011), *Euphorbia pulcherrima* (Rudramuniyappa and Annigeri, 1985) and *Calanthe masuca* (Hegde and Rudramuniyappa, 1986). Occurrence of secretary cells at the connective region of *S. macrophylla* anther is a distinct feature that was previously reported in Meliaceae species such as *Azadirachta indica* (Talawar and Agadi, 2018) and *Melia*

azedarach (Talawar and Agadi, 2019). An intense PAS-positive reaction in secretory cells indicates accumulation of storage polysaccharides from nearby vascular tissue. At late sporogenous tissue stage of *S. macrophylla*, prior to transforming into meiocytes, the cell walls of sporogenous cells became thickened and showed a strong PAS-positive reaction, suggesting an accumulation of cell wall carbohydrates (Fig. 2A–B). In addition, tapetal cells at this stage enlarged slightly and became highly vacuolated (Fig. 2A–B). Likewise, in *Bauhinia blakeana* Zheng *et al.* (2017) reported pronounced tapetal vacuolation at the sporogenous stage and were later decomposed during microspore development. Vacuolation in tapetal cells at sporogenous stage is an unusual phenomenon observed in flowering plant species. At connective, secretory cells increased in number with consistent intense PAS-positive staining (Fig. 2C). Progressive vacuolation of the tapetal cytoplasm is a common cytological feature during microsporogenesis and is generally considered as an early sign of programd cell death that leads to the release of nutrients and precursors of the pollen wall into the locule (Parish and Li, 2010; Gotelli *et al.,* 2023).

At microspore mother cell stage of *S. macrophylla*, starch grains from the anther wall layers disappeared while the cytoplasm of the endothecium and middle layers showed a rich PAS-positive reaction. MMCs were moderately PAS-positive and surrounded by a thick callose wall which exhibited an intense PAS-positive reaction. Tapetal cells were highly vacuolated with scanty cytoplasm which showed a faint PAS reaction (Fig. 2D). Numerous secretory cells are distributed throughout the connective region and remain richly PAS-positive (Fig. 2E). Similarly, in *Pancratium maritimum* (Konyar, 2018) abundant starch grains were present in the anther wall at the pre-meiotic stage but later during meiosis, the amount of starch grains in anther wall layers decreased gradually and simultaneously increased in the MMCs, indicating that the stored starch in these layers was perhaps mobilized and hydrolyzed into soluble sugars to meet the high energy demand for meiosis and callose synthesis (Panchaksharappa and Rudramuniyappa, 1974; Yun and Huiqiao, 2015). On the other hand, in *Azadirachta indica* (Talawar and Agadi, 2018) and *Melia azedarach* (Talawar and Agadi, 2019) anthers, MMCs were moderately PAS positive and were bounded by PAS-positive callose wall, but anther wall layers were rich in starch grains. Development of a thick PAS-positive additional wall around MMCs is a common feature in angiosperms, which acts as molecular filter that separates the meiocytes from sporophytic tissues and provides a base for pollen exine development. This layer is a temporary isolation barrier, made of callose (β-1,3-glucan) and reacts positively for PAS staining (Panchaksharappa *et al.,* 1985). These observations also support the view that starch reserves in the anther wall layers during anther development act as a temporary storage form of anther sugars, which are partly mobilized to developing microspores through the tapetum while remaining utilized by somatic cells for their growth and differentiation (Clement *et al.,* 1994).

Microspore tetrads and young microspores

The MMCs of *S. macrophylla* anther underwent simultaneous cytokinesis during meiosis and produced tetrahedral microspore tetrads (Fig. 2F). Microspores in tetrads and young microspores which are just freed from the callose wall showed moderate PAS staining in the cytoplasm while the nucleus and cell wall of microspores reacted strongly with the PAS stain. In contrast, the tapetum at this stage appeared to be metabolically hyperactive

with significantly increased cytoplasmic density that displayed an intense PAS-positive reaction without starch grains (Fig. 2G, I). Furthermore, secretory cells at connective tissue are even larger in size than before with a persistent intense PAS-positive reaction (Fig. 2H). These results are consistent with those of *Melia azedarach* (Talawar and Agadi, 2019). Similarly, in *Parthenium hysterophorus* (Rudramuniyappa, 1985), the cytoplasm of young microspores showed poor PAS staining, while the cell walls of microspores were strongly PAS-positive, indicating the presence of structural carbohydrates in developing intine. In *Ricinus communis* (Wei *et al.,* 2015), the cytoplasm of young microspores was poor in polysaccharides, while nucleus and intine of the microspore wall showed strong PAS reaction, and also the amount of starch grains increased in the tapetum. Contrastingly, in *Campsis radicans* (Konyar *et al.,* 2013), microspores in tetrads and the tapetum displayed rich PAS-positive reaction along with few starch grains. However, the concentration of cytoplasmic polysaccharide declined during the young microspore stage, but cell wall of microspores exhibited a rich PAS-positive reaction. On the other hand, Rudramuniyappa and Annigeri (1985) observed accumulation of starch granules in the cytoplasm of young microspores of *Euphorbia pulcherrima* anther. In *Garcinia dulcis*, the tapetum at tetrad stage becomes denser and starts secreting lipid droplets in the anther locule, suggesting that carbohydrates from the staminal envelope were transported to the tapetum and transformed into lipid molecules which were later conveyed to developing pollen grains via locular fluid for synthesis of pollen exine (Sutthinon *et al.,* 2024). Moderate PAS positivity in young microspores of *S. macrophylla* anthers can be attributed to rapid consumption of sugars during microsporogenesis. Whereas, increased cytoplasmic density of tapetal cells with an intense PAS-positive reaction at tetrads and young microspore stage indicates peak metabolic activity of the tapetum at this phase with active synthesis and accumulation of carbohydrate metabolites as well as nutrients which are mobilized to locular fluid where these biochemical substances are utilized in microspore development and sporoderm formation (Castro and Clement, 2007).

Vacuolated microspores and young pollen grain stage

At vacuolated microspore stage, cytoplasm, nucleus and intine of microspores exhibited intense PAS positivity. Concomitantly, polysaccharide in the tapetum declined compared to the previous young microspore stage (Fig. 3A). In the subsequent stage, microspores underwent unequal mitotic division to form a large vegetative cell and a small generative cell (bicellular pollen grain), mean while vacuole from microspores disappeared and cytoplasm with intense PAS positivity restored at the centre and started the accumulation of starch grains. Similarly, in *Ricinus communis*, polysaccharide content was significantly increased in the cytoplasm of bicellular pollen grains (Wei *et al.,* 2015). On the other hand, tapetum of *S. macrophylla* at this stage remained moderately PAS-positive as it was in the previous stage. Additionally, cells of the endothecium elongated radially and started developing fibrous thickening which showed a PAS-positive reaction (Fig. 3B–C). Increased PAS-positivity in the microspores and reduction in polysaccharide content of the tapetum signifiy that some amount of polysaccharide catabolism from the anther wall tissues probably mobilised to the microspores as a source of energy required for vacuolation in the microspore, synthesis of DNA for unequal mitotic division of the microspore, formation of endothecial thickening and synthesis of

cellulosic intine layer, which characteristically shows an intense PAS reaction (Panchaksharappa and Rudramuniyappa, 1974; Clement *et al.,* 1994).

Mature pollen grain and anther dehiscence

At the maturation stage, the cytoplasm of pollen grains was richly filled with starch grains, while the tapetum layer had scanty cytoplasm with weak PAS staining and showed sign of degeneration. Endothecial cells were contained profuse fibrous thickenings which showed PAS-positive reaction (Fig. 3D–E). As the anther reached the phase of dehiscence, the tapetum disintegrated progressively, and finally a thin layer of its cellular debris with a moderate PAS-positive reaction remained around pollen grains. Pollen grains contained plentiful starch grains in cytoplasm (Fig. 3I). In addition, vascular cells at connective tissue were prominent with rich PAS-positive cell walls. Reserved carbohydrates in the secretory cells of connective decreased progressively and nearly exhausted during the anther dehiscence. Dehiscence of anther was longitudinal, dispersion of pollen grains occurred through stomium (Fig. 3F–H). Progressive reduction of polysaccharides from secretory cells of connective and its simultaneous increase in pollen grains indicates active mobilization of carbohydrates from somatic tissues to pollen grains via tapetum (Wang *et al.,* 2022). Present observations also support the views of earlier researchers who proposed that progressive decline in polysaccharide reserves from the staminal envelope and their subsequent accumulation in developing pollen grains is evidence of active mobilization of carbohydrates for pollen maturation, synthesis of pollen wall precursors, and as a source of energy for germination and pollen tube growth (Pacini and Franchi, 1983; Pacini, 1996; Konyar, 2018; Wang *et al.,* 2022).

The results of the present study showed that tannin ideoblasts were predominantly distributed in the connective region and epidermis of *S. macrophylla* anther. Initially, these cells appeared in the epidermis and connective region of the young anther, and later in the subsequent stages of anther development, these cells increased in number and distributed in the entire connective region extending up to the anther locule and persisted until the dehiscence of anther (Figs. 1C–I, 2C–F, H, and 3A, E–H). Vijayaraghavan *et al.* (1987) formerly reported the occurrence of tannin ideoblast cells in the epidermis and connective region of *Saxifraga ciliata* anther and proposed that starch grains from other parts of the plant might have been transported to the connective cells and stored in the form of tannin. Ideoblast cells containing tannins have been reported to occur in diverse vegetative as well as reproductive organs of numerous flowering plant species. These are specialized cells involved in various eco-physiological functions including anti-herbivory, protection against UV radiations and associated antioxidant activity, and pathogen resistance (Peter Constabel *et al.,* 2014; da Cunha Neto *et al.,* 2017; Molino *et al.,* 2023).

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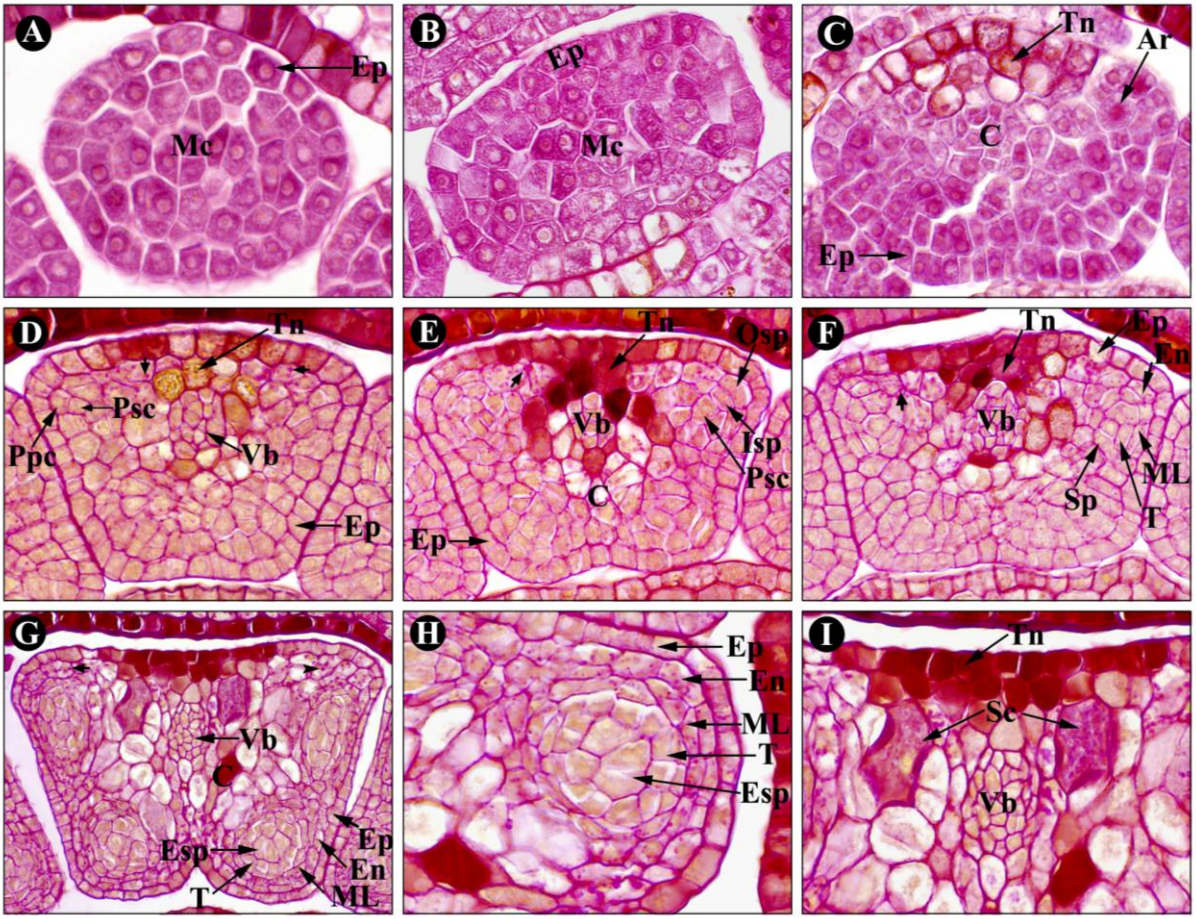


Figure 1. Histochemical distribution of polysaccharides during early anther development in *Swietenia macrophylla* King. **(A–B)** Undifferentiated anther primordia showing uniformly intense PAS-positive reaction. **(C)** Young anther at archesporial stage. Note: Archesporial cell is relatively larger with richly PAS-positive nucleus at the centre, and tannin ideoblast cells are started appearing at connective and epidermis. **(D)** Differentiation of archesporial cell into primary parietal cell and primary sporogenous cell. Note: distribution of small starch granules at connective (arrow head). **(E)** Anther showing division of primary parietal cell into outer and inner secondary parietal layers. Note: some starch granules are evident at connective cells (arrow head). **(F)** Anther during early anther wall differentiation showing distribution of starch granules in connective and secondary parietal layeres (arrow head). **(G)** Fully differentiated tetra-locular anther at early sporogenous stage. **(H)** Close-up view of anther locule at early sporogenous stage. **(I)** Enlarged view of anther connective at early sporogenous stage showing secretory cells with intense PAS-positive reaction. **Abbreviations:** Ar-Archesporial cell; C-Connective; En-Endothecium; Ep-Epidermis; Esp-Early sporogenous tissue; Isp-Inner secondary parietal layer; Mc-Mass of cells; ML-Middle layers; Osp-Outer secondary parietal layer; Ppc-Primary parietal cell; Psc-Primary sporogenous cell; Sc-Secretory cell; Sp-Sporogenous tissue; T-Tapetum; Tn-Tannin ideoblasts; Vb-Vascular bundle.

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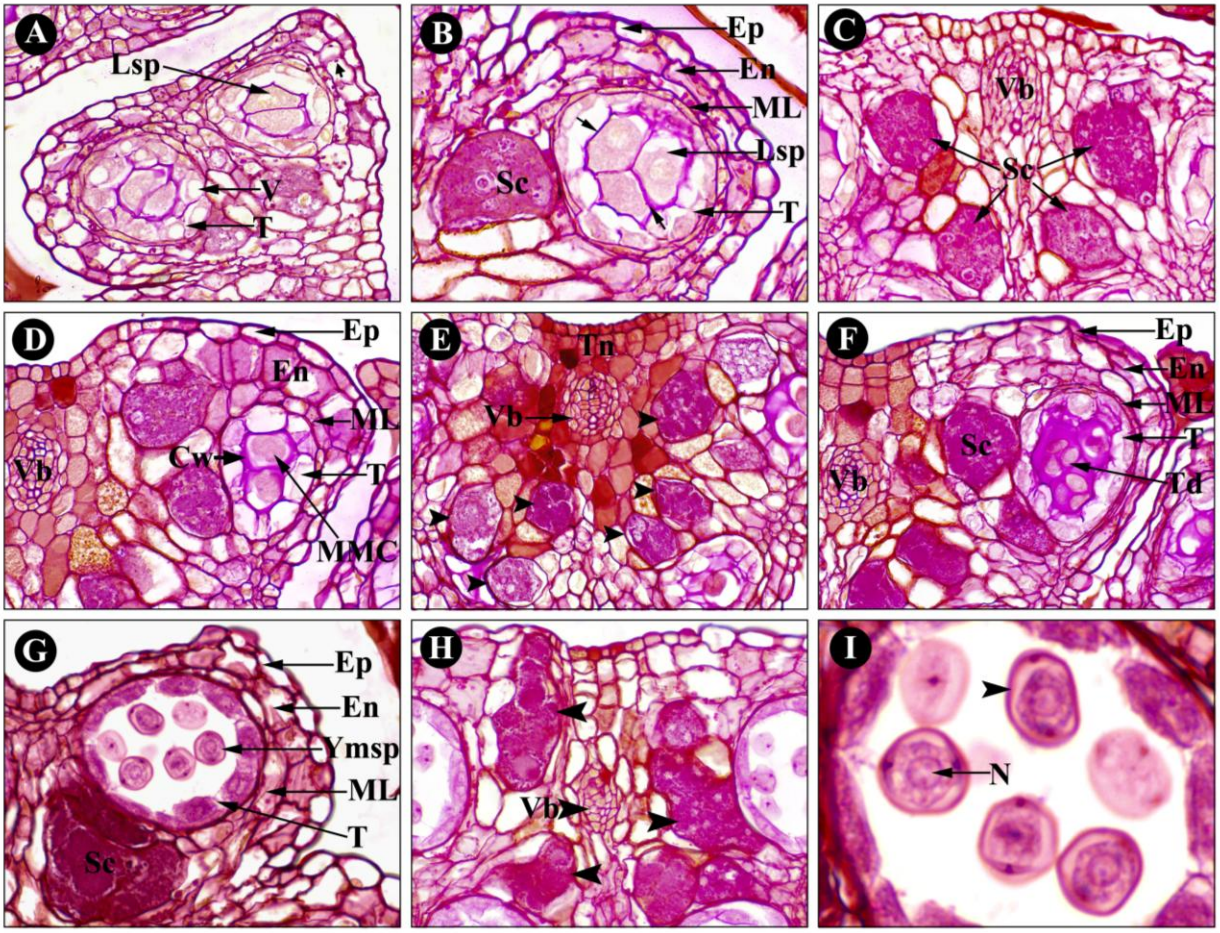


Figure 2. Histochemical distribution of polysaccharides during anther development in *Swietenia macrophylla* King. **(A–B)** Anther at late sporogenous stage showing starch grains in anther wall. Sporogenous cells and tapetum are moderately PAS-positive surrounded by thick PAS-positive wall (arrow head). Note: tapetum is highly vacuolated. **(C)** Connective at late sporogenous stage showing large secretory cells with a rich PAS-positive reaction. **(D)** Anther at microspore mother cell (MMC) stage. **(E)** Anther connective at MMC stage containing enlarged secretory cells with rich polysaccharide content (arrow heads). Note: tannin ideoblast cells besieged vascular bundle. **(F)** Anther at microspore tetrad stage. **(G)** Anther locule at young microspore stage. **(H)** Details of connective tissue at young microspore stage. **(I)** Close-up view of young microspores showing strong PAS staining in nuclei and cell wall (arrow head). **Abbreviations:** Cw-Callose wall; En-Endothecium; Ep-Epidermis; Lsp-Late sporogenous tissue; ML-Middle layers; MMC-Microspore mother cell; Sc-Secretory cell; T-Tapetum; Td-Tetrads; Tn-Tannin ideoblasts; V-Vacuole; Vb-Vascular bundle; Ymsp-Young microspores.

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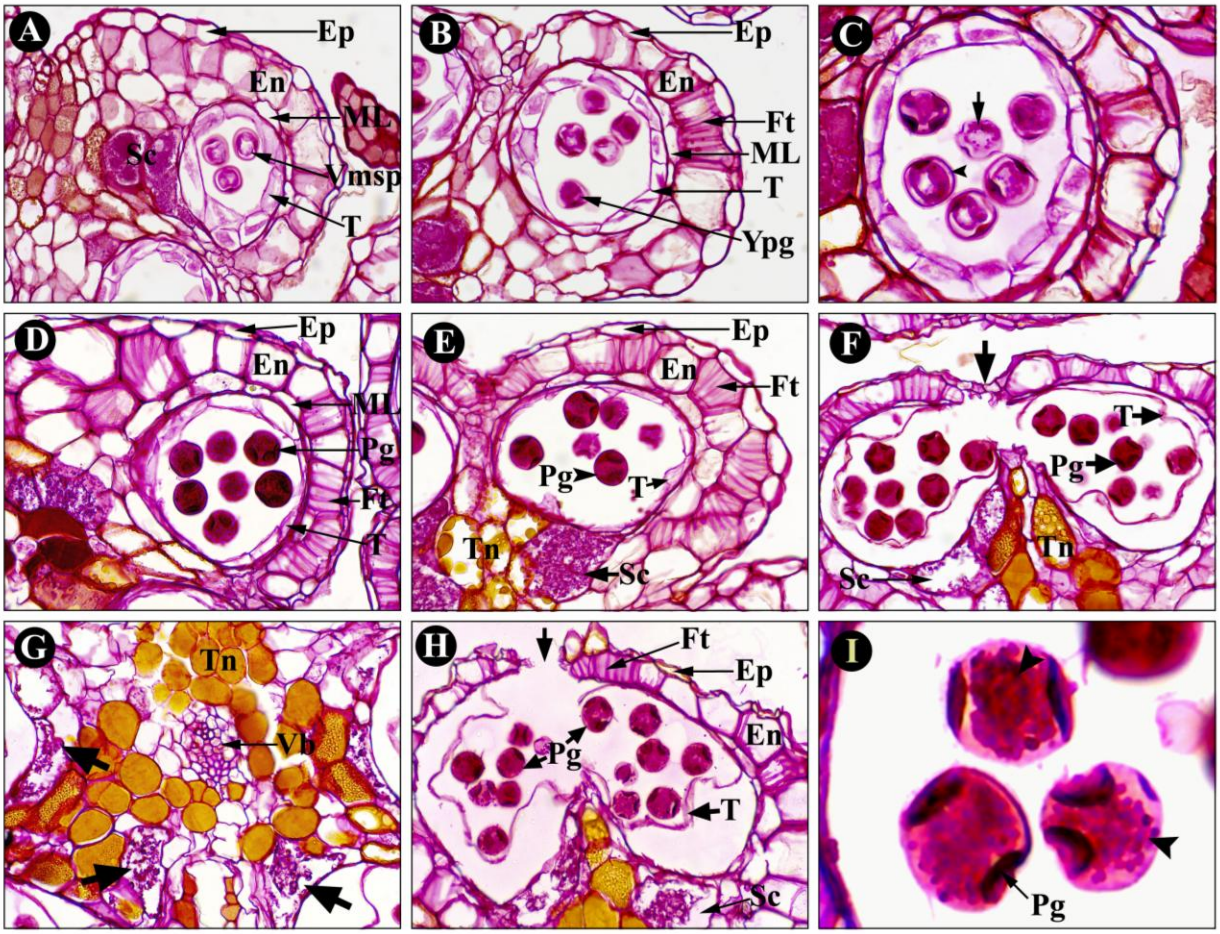


Figure 3. Histochemical distribution of polysaccharides during anther development in *Swietenia macrophylla* King. **(A)** Anther at vacuolated microspore stage. **(B)** Anther locule at young pollen grain stage. Note: formation of PAS-positive fibrous thickenings in endothecial cells. **(C)** Magnified view of anther locule at young pollen grain stage. Note pollen wall is intensely PAS-positive (arrow head). **(D–E)** Anther at mature pollen grain stage showing intense PAS staining in pollen grains, secretory cells and endothecial thickenings. **(F)** Portion of the anther during dehiscence showing formation of stomium (arrow head). Tapetum is completely degenerated. **(G)** Details of connective during anther dehiscence showing reduction of polysaccharide reserves in secretory cells (arrow heads), and tannin ideoblast cells extending up to anther locule. **(H)** Dehiscent anther. **(I)** Mature pollen grains engorged with starch grains (arrow head). **Abbreviations:** En-Endothecium; Ep-Epidermis; Ft-Fibrous thickenings; ML-Middle layers; Pg-Pollen grains; Sc-Secretory cell; T-Tapetum; Tn-Tannin ideoblasts; Vb-Vascular bundle; Vmsp-Vacuolated microspores; Ypg-Young pollen grains.

Conclusion

The present study reports the stage-specific distribution and dynamic redistribution of polysaccharides during anther development in *Swietenia macrophylla* King. Polysaccharides showed distinct localization patterns in anther tissues, such as the connective region, anther wall layers, sporogenous cells, microspore mother cells, developing microspores, tapetum, and mature pollen grains. The progressive redistribution of polysaccharides from the layers of the

anther wall and secretory cells of the connective region to the developing pollen grains suggests their involvement in the differentiation of anther tissues, microsporogenesis, pollen wall formation and pollen maturation. The strong PAS-positive reaction in the tapetum at the tetrad and young microspore stages with a gradual decline during further development suggests its role in supporting the microspore development. The deposits of starch grains in mature pollen grains suggest the importance of carbohydrate reserves for pollen metabolism and post-germination. PAS-positive fibrous thickenings in the endothecium also indicate the presence of structural polysaccharides involved in anther wall differentiation. These results provide histochemical insights into the distribution of polysaccharides during anther ontogeny and pollen development in *S. macrophylla* and enhance understanding of the biochemical changes involved in male reproductive development in Meliaceae.

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Conflict of interest

The authors declare no conflict of interest.

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