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Polarity during sporogenesis and gametogenesis in plants

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In this article the importance of polarity during sporogenesis and gametogenesis in plants is discussed. Polarity is one of the important processes during cell differentiation. Many studies have been done about this subject but it does not become clear how or why polarity is taken place during cell differentiation. The aim of this article is to bring together the knowledge about polarity from the past and recently done studies.

Key words: polarity, microsporogenesis, megasporogenesis, megagametogenesis, cell differentiation.

Polarity

Polarity is the state of morphological and functional difference of macromolecules, organelles, cells, embryos, organs and organisms from the others. It has been derived from the word polos (axis) in Greek. Polarity can be considered as a stratification or a distinct composition of a cell or tissue along a particular axis (Willemse, 1981).

Some of the cell organelles have polar structures. These organelles are Golgi apparatus and microtubules (Lodish et al., 1995). Golgi apparatus has a structural and functional polarity in many cells. The region that face towards the granular endoplasmic reticulum (ER) is named as forming face or external face (cis-face) and the opposite concave side of this region is named as maturating face or internal face (trans face).

Microtubules are constituted by gathering dimers which consist of α-tubulin and β-tubulin units. The end that gathers rapidly is named as positive (+) end, and slowly gathering end is named the negative (–) end.

Polarity during sporogenesis and gametogenesis in plants

Polarity of cells and tissues is one of the important characteristics of differentiating systems. Studies with polarity during sporogenesis in plants had started in 1921 and still continue today. Table 1 provides a summary of references mentioning aspects of locular polarity during microsporogenesis in *Gramineae*. In addition to locular polarity, specific protoplasmic polarity has been observed within individual microspores and pollen grains. These examples, including distinctive patterns of cytoplasmic vacuolation, engorgement and nuclear migrations, have also been summarized in Table 1 (Christensen & Horner, 1974).

During sporogenesis and gametogenesis in plants, there are several factors that cause polarity. We basically separate these factors into two groups as external and internal factors (Halac & Harte, 1985).

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Table 1. Summary of polarities reported during microsporogenesis in grasses. [a,b]

Type of polarity observed	Polarity within anther locule						Polarity within microspores & pollen	
Species	PMCs distinctly arranged	Callose in the center of locule, PMCs adjacent to tapetum	Tetrad partition walls – to tapetum	Tetrads retained against tapetum	Microspores/pollen at locule periphery	Pore oriented to tapetum at maturity	Nuclear migrations	Polar vacuolation and/or engorgement
Festucoideae								
Avena sativa	O,(G)	O	O	O	G,M,O	M	(G)	
Avenastrum decorum					C	C		
Poa annua					J	J		
Secale cereale	O	M,O	O	O	M,O	C,M	N	
Sesleria heufleriana					C			
Triticum spp.	A,O	O	A,O	A,O	A,M,O	M	K,L,M,Q,U	A,K,L,Q,U
Panicoideae								
Pennisetum typhoideum	E							
Setaria italica	F					(F)		
Sorghum bicolor	T,V	R,T,V	R,V	R,V	V	V	V	V
Zea mays	B,D,H	B,D,H	B	H,M,N,(S)	M,N,P,(S)	I,N,U	I,N,U	

[a] Author key: A. Percival, 1921; B. Reeves, 1928; C. Drahowzal, 1936; D. Kiesselbach, 1949; E. Narayanaswami, 1953; F. Narayanaswami, 1956; G. Bonnett, 1961; H. Carniel, 1961; I. Korobova, 1961; J. Rowley, 1962; K. Batygina, 1962; L. Watanabe, 1961; M. Romanov, 1966; N. Oryol,1969; O. Romanov, 1970; P. Banerjee & Barghoorn, 1970; Q. Romanov, 1971; R. Christensen, Horner & Lersten, 1972; S. Troughton & Donaldson, 1972; T. Warmke & Overman, 1972; U. Oryol,1972; V. Christensen & Horner, 1974.
[b] Parentheses indicate that the article contained pictures showing polarity but did not mention it in the text (Christensen & Horner, 1974).

External factors

The generation of polarity in the cells of eukaryotes in most cases requires an external asymmetrical input (Cove, 2000). In developing cells (especially at the tip), polarity is firstly caused by gravity and also external factors like pH, ions, electrical potential gradients and light cause polarity (Halac & Harte, 1985).

Internal factors

Internal factors that cause polarity during sporogenesis and gametogenesis can be categorized into three groupes. These groupes are as follows: 1) cellular factors: formation of vacuoles, migration of nucleus, dispersion of starch, distribution of organelles and formation of callose; 2) tissual interactions; and 3) molecular factors.

Cellular factors

During sporogenesis and gametogenesis in plants, some alterations can be observed in volume, dimension and distribution of some cell organelles in spores and gametes. Therefore cell gains polar aspect. These factors are explained below with patterns.

Formation of vacuoles and polarity. Vacuolation is a part of cellular organization that determines cell polarity. Ovule is full of cytoplasm, while it was growing, it expands and many vacuoles generate. Egg cell shows a clear polarity. In many plants, cytoplasm that contains nucleus and organelles locate in the chalazal region; in the micropylar region it includes a large vacuole. Polarity continues in zygote; for this reason polarity in egg cell is important (Cass & Karas, 1974). In *Peperomia blanda*, the embryo sac development is *Peperomia* type. In the egg cell of *Peperomia blanda*, as due to

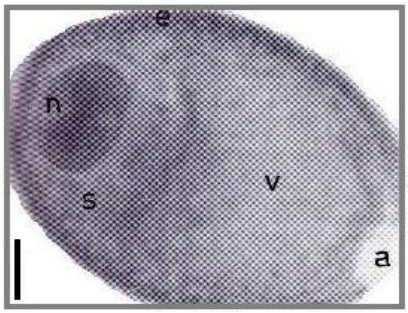

Fig. 1. Hexaploid *Bellevalia edirnensis* microspore; prepared for pollen mitosis and polarized (DANE, 1999); a – aperture, n – nucleus, v – vacuole, s – cytoplasm, e – exine. Bar = 10 μm.

large vacuole, polarity has been occurred. (BANNIKOVA et al., 1987).

At the beginning of microspore development, microspores had a nucleus and abundant cytoplasm in the centre. A microspore absorbed the fluid in the locus, rapidly enlarged its volume (two or three fold) and then is released from the tetrad. Several vacuoles are occurred in the cytoplasm. Then, these vacuoles are fused and one large vacuole is occurred (Fig. 1) (DANE, 1999).

Migration of nucleus and polarity. During megagametogenesis the number of mitotic divisions, the type of vacuolization, nuclear migration, nuclear fusion and again the orientation of the spindle are the main factors responsible for different types of embryo sac development (WILLEMSE, 1981).

Embryo sac development in *Polygonum* type can be considered as a pattern of polarity influenced by migration of nucleus. In *Polygonum* type, embryo sac development is generally due to a position of the nucleus in the cell, orientation of spindles, development of cell wall, degeneration of megaspore cells, position of the vacuole, migration and fusion of nucleus.

Embryo sac of *Paeonia tenuifolia* is monosporic *Polygonum* type with eight nucleus (Fig. 2). Functional chalazal megaspore volume increases before mitosis initiates. Functional megaspore undergoes three consecutive mitoses and became eight nucleated stage. Three of the four nucleus go towards micropyle constituting the egg apparatus, the fourth nucleus goes towards the centre of the embryo sac. Thus, eight nucleated embryo sac developed. Polar nuclei come from micropylar and chalazal side. Chalazal polar nucleus is bigger than the micropylar one. Polar nuclei are surrounded

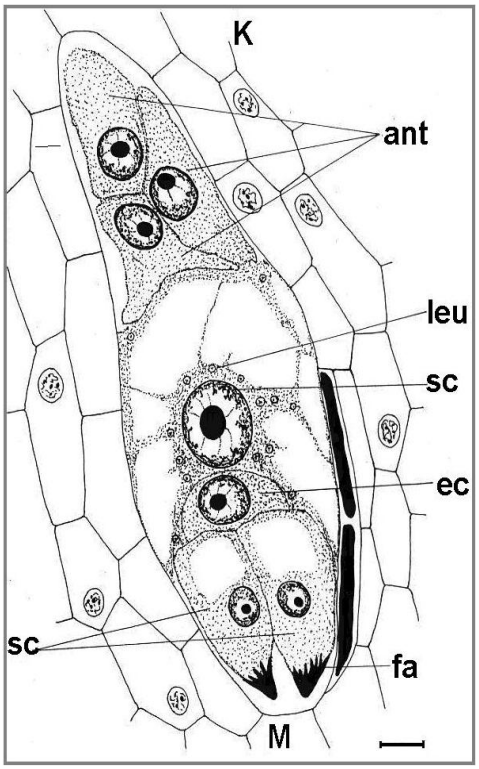

Fig. 2. Mature embryo sac of *Paeonia tenuifolia* (DANE, 1997); ant – antipode cells, sn – secondary nucleus, ec – egg cell, sc – synergid cells, leu – leucoplasts, fa – filiform apparatus, K – chalaza, M – micropyle. Bar = 10 μm.

by dense cytoplasm and embryo sac contains numerous large and small vacuoles. Polar nuclei fuse before fertilization and constitutes secondary nucleus (DANE, 1997).

During microgametogenesis, before pollen mitosis, two different events occur in pollen protoplasm.

a) Nucleus migrates to one side from the centre of the cell (Fig. 3). Migration is always towards one certain direction and determines the generative cell position. The position of generative cell is under genetic control and fixed for each species.

b) Cytoplasm became vacuolated. When chromosomes became visible, polarization is observed in the cytoplasm due to distribution of organelles.

In *Cypripedium fasciculatum* prior to pollen mitosis, the microspore nucleus migrates to a proximal position opposite the aperture, as is typical for monocotyledons (BROWN & LEMMON, 1994).

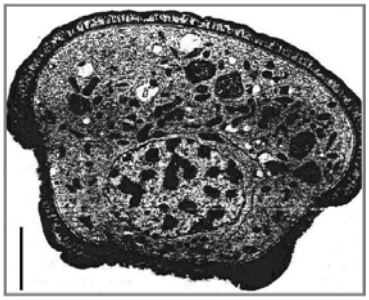

Fig. 3. TEM. In *Cypripedium fasciculatum* organelles are concentrated in the generative hemisphere (Brown & Lemmon, 1994). Bar = 4 μm.

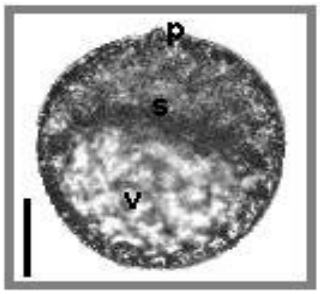

Fig. 5. *Sorghum bicolor* one-half engorged pollen; vacuole retained at end opposite pore (Christensen & Horner, 1974). P – pore, S – starch, V – vacuole. Bar = 5 μm.

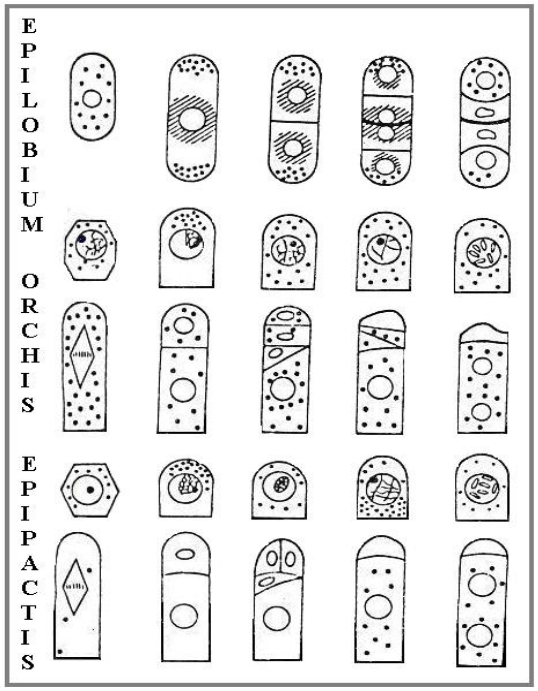

Fig. 4. Dispersion of starch during megasporogenesis. In *Epilobium palustre* plastids contained starch accumulated near micropylar or chalazal pole of the megaspore mother cell. Diad cells and functional megaspore at micropyle side contains more starch. During metaphase, in megaspore mother cell of *Epipactis palustris*, starch almost disappears and appears again only in the chalazal megaspore (Kapil & Bhatnagar, 1981).

Dispersion of starch and polarity. During megasporogenesis different distribution of cytoplasmic organelles is closely related with embryo sac ontogeny. In *Epilobium palustre* most of the plastids accumulated near micropylar or chalazal pole of the megaspore mother cell (Fig. 4). Functional micropylar megaspore contains more plastids and mitochondria after meiosis (Kapil & Bhatnagar, 1981).

In *Epilobium* megaspore tetrads, the plastids are preferentially located in the terminal cells of both poles at the chalazal end of the cells, independent of which one is going to be functional megaspore. The presence of plastids with starch in the micropylar functional megaspore of the tetrad may show importance as first sign of polarity. This could mean that starch has a function similar to statholytes in root tip graviperception (Halac & Harte, 1985). Starch dispersion is also observed with PAS method in *Equisetum* microsporocytes (Rudramuniyappa, 1991).

In *Sorghum bicolor*, generative nucleus near the pore can not be seen because of starch accumulation (Fig. 5) (Christensen & Horner, 1974).

In the microsporocyte of *Stangeria eriopus*, when meiosis began plastids were loosely scattered around the nucleus (Fig. 6A). During late leptotene or zygotene, their deposition changes when all plastids and many mitochondria are aggregated around the nucleus (Fig. 6B,C). In late prophase I, plastids and mitochondria are again situated around the nucleus (Fig. 6D,E). During metaphase I, plastids indicated by starch grains are situated along the meiotic spindle fibers and later in a wide ring around the chromosome plate (Fig. 6F,G). At post telophase I, all plastids and mitochondria are placed in an equatorial space inside a ring (Fig. 6H) (Rodkiewicz et al., 1988).

Distribution of organelles and polarity. During

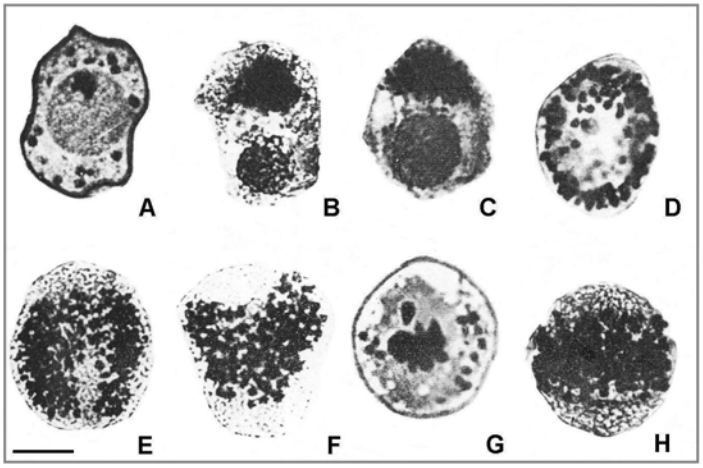

Fig. 6. Microsporocytes of *Stangeria* (RODKIEWICZ et al., 1988). (**B–F, H**) PAS stained squash preparations, bar = 10 μm. (**A,G**) Semithin sections, toluidine blue. (**A**) Early prophase I, plastids around the nucleus. (**B,C**) Aggregation of plastids with starch grains, chromosomes at the bouquet stage in the lower part of the picture. (**D**) Prophase I, plastids probably mitochondria are situated around the nucleus. (**E**) Late prophase I, plastids along the meiotic spindle. (**F,G**). Metaphase I, plastids grouped in a ring, around the chromosome plate. (**H**) Post-telophase I meiocyte, plastids between the nuclei.

sporogenesis and gametogenesis some organelles such as plastids, mithocondria, dictyosomes and ER show polar distribution.

Plastids and mitochondria are described in several species from a morphological and developmental point of view. In most of the investigated species the morphology of organelles is simplified during meiosis. Plastids as well as mitochondria are covered by two membranes at the beginning of meiosis. During megagametogenesis, they redifferentiate by developing internal membranes and starch is become visible in the plastids. During the microsporogenesis and microgametogenesis, some species have a constant number of organelles. Disappearance of organelles, especially mitochondria, during megasporogenesis and their reappearance during megagametogenesis has also been observed. It is not clear even now, whether these organelles are formed *de novo* or by division from the existing ones. The distribution of organelles in the growing systems and the relation between different cell structures are important.

Polarity of ER is noticed in several plants. During megasporocyte differentiation, *Ginkgo biloba* shows concentration of ER and vacuoles towards the micropylar end while plastids and mitochondria were concentrating towards the chalazal end. In *Epidendron scutella* and *Zea mays*, ER concentrated towards the micropylar end of megasporocytes and megagametophytes. Concentration of ER towards the micropyle of the ovule may be an evidence of the secretory function of this part of the structures which could be important during pollen tube growth (HALAC & HARTE, 1985).

Based on quantitative data of cell organelles, different localization of plastids and dictyosomes was noticed in a distinct cytoplasmic area of *Gasteria*. In this approach the cell in different stages of development is divided into sixteen radial parts with the cell centre as a fixed point. By comparing the data, a preferential distribution of organelles is observed. Before meiosis I, no preference exists. During telophase, plastids and dictyosomes prefer the cell centre, as a result of the nuclear division. In the tetrad stage, the organelles are located on the periphery of the cytoplasm, besides the nucleus. Above the nucleus, a sheet of ER indicates the future colpal region. This situation continues till the first mitosis, just before the increase of cell organelles, and also after the migration of the nucleus to the side opposite to the colpus (WILLEMSE, 1981).

In *Cypripedium fasciculatum* before the pollen mitosis has begun plastids, mitochondria and lipid bodies move towards the cytoplasm of the pollen where the vegetative cell will be originated (BROWN & LEMMON, 1994).

Microsporocytes of *Stangeria eriopus* become polarized during early prophase I; plastids and mitochondria aggregate at one side of the nucleus (Fig. 7) (RODKIEWICZ et al., 1988). Another example of organelle polarization can be given in *Glycine max* microsporocytes (Fig. 8) (ALBERTSEN & PALMER, 1979).

Formation of callose and polarity. Callose is seen in megaspore mother cell wall and it is related with the polarity in the cell. Callose formation starts at the beginning of meiosis, only at the functional megaspore side, then surrounded whole cell and isolated it for a short period. This pe-

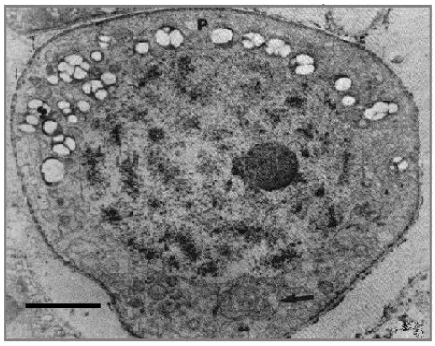

Fig. 7. Pachytene microsporocyte of *Stangeria eriopus* (Rodkiewicz et al., 1988). Plastids with starch grains spread at one side of the nucleus, a whorl of ER on the opposite side (arrow). Bar = 4 μm.

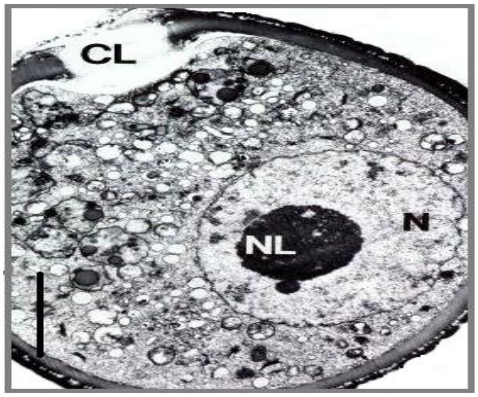

Fig. 8. *Glycine max* microsporocyte during microsporogenesis (Albertsen & Palmer, 1979). CL -colpus, NL – nucleolus, N – nucleus. Organelles aggregated around the colpus in opposite direction to nucleus. Bar = 4 μm.

riod is essential for the independent differentiation that causes development of megaspore mother cell to female gametophyte. Then callose disappears partly or completely from the cell wall where functional megaspore is found. Thus, permeability of this region is better than that of the other side and this causes convenient nutrient flow. So callose has an important role in differentiation of metabolic conditions in the cell and finally in development of the cell specific type (Kapil & Bhatnagar, 1981).

During megasporogenesis, development of callose wall is investigated in three orchid species. *Orchis incarnata* L., *Epipactis latifolia* All. and *Cephalanthera alba* Cranz. At prophase, meiocyte is wholly enveloped by a wall showing callose fluorescence, which is strong especially in the chalazal wall (Fig. 9A-E). The cell walls of dyads and tetrads continue to display strong fluorescence (Fig. 9F-G). Although the fluorescence of the side walls in *Orchis* dyads and tetrads becomes weaker (Fig. 9B-C). Fluorescence is gradually disappeared when the meiotic division is accomplished (Fig. 9D) (Rodkiewicz & Bednara, 1976).

Embryo sac development in *Gasteria verrucosa* is the *Polygonum* type. A callose wall be-

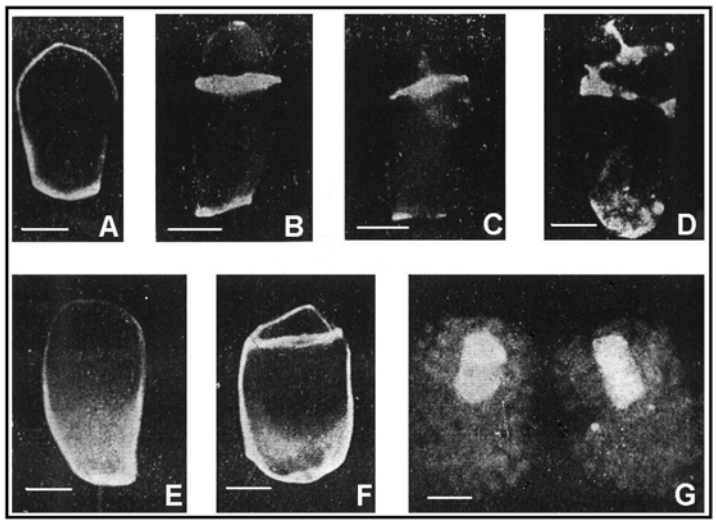

Fig. 9. Callose fluorescence in the cell walls (Rodkiewicz & Bednara, 1976). (**A**–**D**) *Orchis incarnata*, megasporogenesis, chalazal megaspore is functional. (**E**–**G**) *Epipactis latifolia*. (**E,F**) Meiocyte and dyad. (**G**) Ovules with megaspore tetrads. (**A**–**F**) bar = 10 μm; (**G**) – bar = 30 μm.

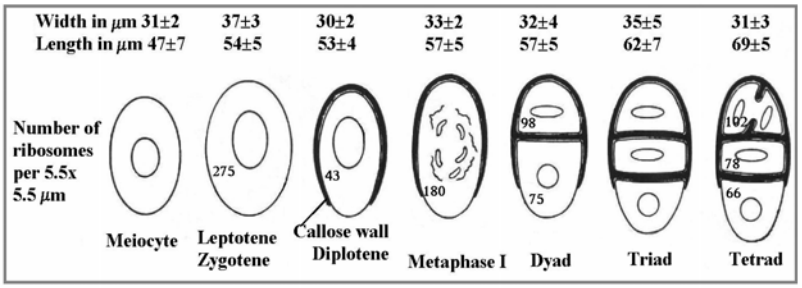

Fig. 10. Cell dimensions and change in number of ribosomes (Willemse & Bednara, 1979).

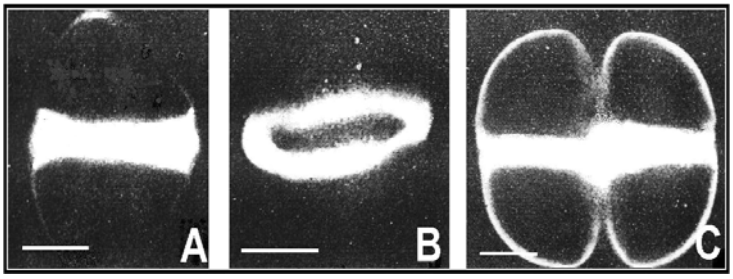

Fig. 11. (**A,B**) Microsporocytes of *Stangeria*. (**C**) Tetrad, callose fluorescence. (**A**–**C**) Anilin blue callose fluorescence in post-telophase cells; bar = 10 μm (Rodkiewicz et al., 1988).

gins to appear at the micropylar end of the cell and thickens continuously (Fig. 10). At diakinesis the callose wall surrounds the entire cell but it is thicker at micropylar side. At basal end of the cell the wall is very thin or sometimes absent. During dyad stage, the callose wall at chalazal end disappears but envelops the micropylar cell completely. In the tetrad, all cells are surrounded by a callose wall except the megaspore, which has only a cap of callose at micropylar end (Willemse & Bednara, 1979).

During microsporogenesis, formation of callose is observed and microspores gain polar appearance. After telophase I in *Stangeria eriopus* organelles become aggregated in the equatorial plate of a dyad. At this stage, callose begins to accumulate at the inner side of the cell wall (Rodkiewicz et al., 1988).

During pachytene, in microsporocyte of *Stangeria eriopus* the inner layer of cell wall is formed by deposition of osmiophilic granules. It becomes continuous at late prophase I. The equatorial strip of this layer grows out, in a form of a ring, and extends into the cell. After telophase I, this ring gives strong callose fluorescence (Fig. 11) (Rodkiewicz et al., 1988).

Tissual interactions

During microsporogenesis and megasporogenesis an interaction occurs between developing spores and surrounding tissues. Some structural differences are occurred in nucellar tissue that surrounds megaspores and also in tapetum that surrounds microspores.

The chalazal part of the nucellar tissue near the *Gasteria* megasporocyte is still meristematic. In this part of the nucellar tissue and megaspore a specific localization of proteins, amino acids, lipids, peroxidase and phosphatase is observed. These factors in and around the megasporocyte have an important role for the future behavior of the megaspore. A cytologic or tissue structural components which can be related with nutrition and regulation and probably originating from the chalazal nucellar tissue, are the most important parts of the determination of polarity after the induction of meiosis.

The scheme in Figure 12 presents the polarity during megasporogenesis in relation with the nucellar tissue. In the megasporocyte of *Gasteria* the elements in relation with polarity as well as the future position of the functional megaspore are noticed. Before the meiotic divisions these are the presence of the clear regions in the cytoplasm at the chalazal end of the cell, the position and shape of the nucleus, the localization of the plasmodesmata and the irregular shape of the callose wall. During the formation of the megaspore the volume of the chalazal dyad cell increases and the number of ribosomes is unequal (Willemse & Bednara, 1979).

In anther, microsporocytes are surrounded by

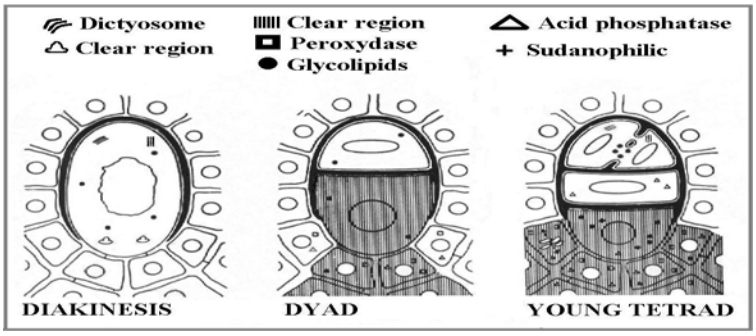

Fig. 12. Polarity during megasporogenesis of *Gasteria* sp. Survey of polar localization of some organelles and organic components (Willemse & Bednara, 1979).

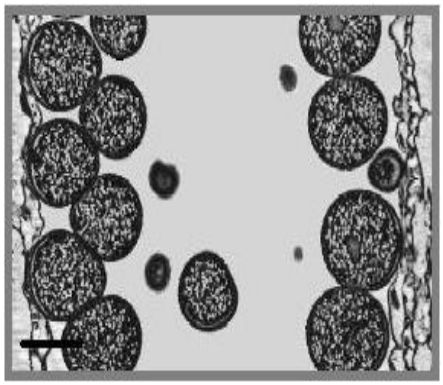

Fig. 13. Engorged pollen stage of *Sorghum* (Christensen et al., 1972). Near-median section. Mature exine and intine surround the starch-engorged cytoplasm. Tapetal protoplasts are gone, but orbicular wall remains. Bar = 30 μm.

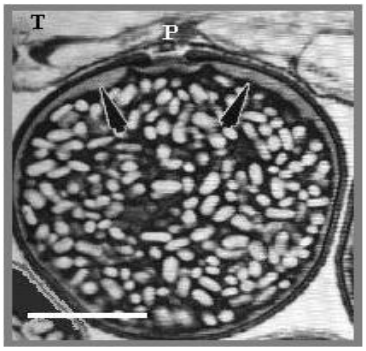

Fig. 14. Fully engorged pollen grain of *Sorghum* with pore adjacent to tapetum. Intine (arrows) under pollen wall adjacent to tapetum is thicker than elsewhere (Christensen & Horner, 1974). Bar = 10 μm.

single cell layered, secretive or ameboidal tapetum. Tapetum participates in three different events in pollen development. Nourishment of microspores, formation of exine, synthesis and secretion of materials function as storage of substances like triphin and pollenkit.

By the early tetrad stage, the tapetal cell walls, especially those bordering the sporangial cavity, increase their thickness and appear to be composed of two layers of different texture. Simultaneously, the dictyosome activity slightly increases and dense osmiophilic globules are formed against and outside the plasmalemma: They are named as pro-orbicules. (Audran, 1979).

Pro-orbicules pass through tapetal cell wall that face to anther locule. They secreted from tapetal cytoplasm to area between plasma membrane and cell wall and they become covered with sporopollenin and after that they named as orbicules. Orbicules are several micron diametered, spherical bodies they unite to form greater heaps. They join the external exine thickness and are able to constitute the exine without spore's aid (Echlin & Godwin, 1968).

Studies with *Gramineae*, *Sorghum bicolor* during microspore development showed that microspores settle at adjacent to tapetum. This coincides after vacuolate microspore stage in pollen development (Fig. 13) (Christensen et al., 1972).

Sorghum bicolor pollen grains have only one pore. During all developmental stages, each sporogenous cell and its derivatives lie continuously adjacent to the tapetum. The microspores and pollen grains form depressions in the tapetal orbicular wall. When the single pore of each microspore is initiated as a gap in the primexine, it lies adjacent to tapetum, too, and remains tightly appressed there until pollen maturation (Figs. 14, 15). The tapetal cytoplasm completely degenerates at the beginning of pollen engorgement, and its degradation products are believed to be avail-

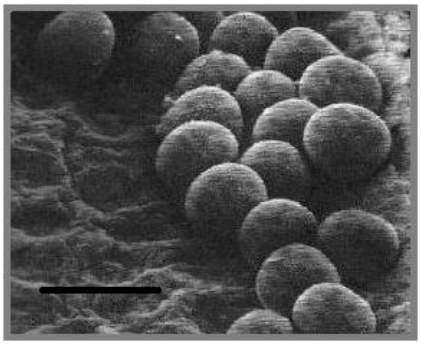

Fig. 15. SEM of anther split of *Sorghum* longitudinally to expose locular surface (tapetal orbicular wall). Vacuolate pollen grains are nestled into depressions in this surface. No pores are visible; they are all oriented towards tapetum (CHRISTENSEN & HORNER, 1974). Bar = 20 μm.

able for uptake at this time by the pollen (CHRISTENSEN & HORNER, 1974).

Molecular factors

During sporogenesis and gametogenesis in plants, external factors (such as gravity, light) and internal factors (such as cellular events, tissual interactions) effect polarity depending on genetic characteristics of a plant.

During microsporogenesis, on the basis of differences in chromatin composition between the generative and vegetative nuclei, a model is proposed to account for the nuclear differentiation and different cell fates of the generative and vegetative cells. In this model, it is postulated that chromatin is significantly modified at the end of the mitotic phase (telophase) by cytoplasmic factors which are synthesized during the last interphase.

During microspore development, two kinds of regulatory molecules are synthesized and accumulate in the cytoplasm. One is a gametophytic factor (GF), as proposed by EADY et al. (1995). The other is a gametic factor (gf). They are oppositely polarized in the microspores prior to microspore mitosis, but the GF is more abundant and predominant than the gf. The gfs are present only near the generative pole. Just after the asymmetric nuclear division, which is controlled by the microtubule system, one telophase nucleus located near the cell center is modified by surrounding GFs that function in the removal of histone H1 from the chromatin. This promotes chromatin diffusion and induces large-scale expression of genes, including the late pollen genes. This nucleus is the vegetative nucleus. The other sister nucleus, which is located near the generative pole, is not affected by GF and hence can maintain chromatin condensation. This nucleus is the generative nucleus. The chromatin of the generative nucleus is also modified by gf. This modified chromatin thereafter expresses the presumed generative cell-specific genes and begins to contain the specific histone variants during further chromatin condensation. In this model, the differentiation of the vegetative (gametophytic) cell has priority in pollen development, and the differentiation of the generative (gametic) cell is secondary (TANAKA, 1997).

A range of proteins that are either marked or involved in the establishment of a (polar) axis are now available, as many relevant mutants. These tools are likely to facilitate a dissection of the molecular mechanisms behind cell and organ polarity in the near future (GREBE et al., 2001).

Importance of polarity

Polarity of cells and tissues is one of the important manifestations of living systems during differentiation. Light and gravity seem to be very important in nature for the establishment of polarity, also pH, O_2 and CO_2 concentration, and biochemical gradients can be mentioned as external factors. Environmental factors determine the direction of the polarity axis, but the disposition for the reaction to polarizing influences is genetically fixed.

For the development of a definite polarity during sporogenesis and gametogenesis, several factors concerning cell structure can be stated as important: asynchronous and/or unequal cell division, heterogeneous distribution of cell organelles and cytomembranes between the haploid cells or in a single cell, development of differential cell to cell connections; plasmodesmatas, transfer structure, unequal callose wall, etc., perception of positional information (e.g. graviperception or light perception), development of biochemical gradients (nutritional, hormonal), genetic constitution of the haploid cells (chromosome balance, DNA type and quality) related or not related with incompatibility phenomena with the surrounding sporophyte (HALAC & HARTE, 1985).

In conclusion, polarity is a process in cell differentiation during sporogenesis and gametogenesis. Recently, the factors that are responsible for cell differentiation cannot be explained completely. Genetical researches besides cellular and histological studies about polarity allow us to understand the polarity in the cell clearly, with causes and results.

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