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Organelle aggregations during microsporogenesis with simultaneous cytokinesis in species from the family Malvaceae (*Gossypium arboreum*, *Alcea rosea*, *Lavatera thuringiaca*)

Przemieszczanie się organelli komórkowych podczas mikrosporogenezy z cytokinezą równoczesną u gatunków z rodziny Malvaceae (*Gossypium arboreum*, *Alcea rosea*, *Lavatera thuringiaca*)

ABSTRACT

During meiosis in microsporogenesis in spermatophytes and in sporogenesis in bryophytes and ferns, regular rearrangement of cytoplasmic organelles (chondriokinesis) occurs. In the present paper, the course of chondriokinesis has been analysed in several representatives of the family Malvaceae (*Gossypium arboreum, Alcea rosea* and *Lavatera thuringiaca*). It was revealed that cell organelles in all the species analysed aggregated around the nucleus at the end of prophase I, and next they surrounded two nuclei in telophase I. This position persisted not only until the end of meiosis, but also in post-meiotic cells after formation of microspore sporoderm on mononuclear pollen grains. Currently, this type of cell organelle aggregation has not been reported from other plant groups, and it seems to be characteristic of the representatives of the family Malvaceae only. The role of this type of cell organelle rearrangement still requires elucidation. The current theories are concerned with dividing cells, whereas the cell organelle aggregation described in the present work was observed in post-meiotic cells as well, i.e. in mononuclear pollen grains.

Keywords: Malvaceae, microsporogenesis, organelle aggregations

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STRESZCZENIE

W mikrosporogenezie u roślin nasiennych oraz sporogenezie mszaków i paprotników zachodzi mejoza, podczas której następuje regularne przemieszczanie się organelli komórkowych (chondriokineza). W niniejszej pracy analizowaliśmy przebieg chondriokinezy u kilku przedstawicieli rodziny Malvaceae (*Gossypium arboreum, Alcea rosea* i *Lavatera thuringiaca*). Okazuje się, że u wszystkich badanych gatunków, pod koniec profazy I organella komórkowe grupowały się w formie otoczki wokół jądra, a następnie w telofazie I wokół 2 jąder. Takie położenie utrzymywało się nie tylko do końca mejozy, ale także po jej zakończeniu gdy 1-jądrowe ziarna pyłku miały już uformowaną sporodermę. Taki typ grupowania się organelli komórkowych nie był dotychczas opisywany u innych grup roślin i wydaje się charakterystyczny jedynie dla przedstawicieli rodziny Malvaceae. Wyjaśnienia wymaga natomiast rola tego rodzaju przemieszczeń organelli komórkowych. Dotychczasowe teorie dotyczą komórek podczas podziału, natomiast przedstawione w niniejszej pracy zgrupowanie organelli komórkowych obserwowane było także w komórkach po mejozie – 1-jądrowych ziarnach pyłku.

Słowa kluczowe: Malvaceae, mikrosporogeneza, grupowanie się organelli komórkowych

INTRODUCTION

The family Malvaceae comprises ca. 1,000 species, including both wild-living plant species (*Alcea rosea*, *Lavatera thuringiaca*) and economically important species, e.g. cotton (*Gossypium arboreum*). Since sterility of male reproductive cells is a common phenomenon in plants (60), the microsporogenesis process yielding viable pollen has a fundamental role in the evolutional development of organisms.

In microsporogenesis of spermatophytes and in sporogenesis in bryophytes and ferns, meiosis takes place, during which, besides karyokinesis, regular rearrangement of cytoplasmic organelles (chondriokinesis) occurs. Chondriokinesis occurring in microsporogenesis has been reported since the 30s of the last century (4–8, 15, 21, 22, 37–44, 53).

Regular rearrangement of cytoplasmic organelles, primarily plastids and mitochondria, during meiotic division in microsporogenesis and sporogenesis proceeds in a few ways. In young archesporial cells and early-prophase meiocytes, plastids and mitochondria are irregularly scattered throughout the cytoplasm. In the leptotene stage, organelles are aggregated in one site next to the nucleus, which was observed in *Equisetum* (24, 28, 33), *Marsilia quadrifolia* (34), *Tetraclinis articulata* (46), *Aucuba japonica* (4), *Ribes rubrum* (21, 22), and in *Larix* (8). In some species, e.g. in *Ceratozamia mexicana*, plastids and mitochondria in the leptotene-zygotene stage are aggregated on one side of the nucleus, but some mitochondria are rearranged towards its opposite side (2). In turn, in *Stangeria eriopus* (39, 40, 42) and *Nymphaea alba* (39, 40), cell organelles are arranged on one side of the nucleus, but some mitochondria surround it.

Besides all the types of rearrangement of cytoplasmic organelles, rearrangement of the cytoplasm takes place. At the beginning of the leptotene stage, the cytoplasm contains a small number of ER canals, spherical mitochondria, and small proplastids devoid of inner membranes. In the zygotene stage, a large proportion of proplastids take the form of cup-like bodies, which is accompanied by a distinct decrease in the number of ribosomes in the cytoplasm; however, the number of vesicle-like vacuoles is increased and the smooth ER canals expand, which was reported from *Stellaria media* (9), *Lilium,* and *Trillium* (30).

Aggregation of plastids and mitochondria next to the meiocyte nucleus does not persist for a long time; at the end of the zygotene stage, ER cisterns disappear and become vacuoles or vesicles (8). Next, mitochondria and, subsequently, plastids are scattered throughout the cytoplasm (43).

During late prophase I cytoplasmic organelle aggregation recurs.

Organelles are most commonly arranged in:

– two groups on the opposite sides of the nucleus, e.g. in *Equisetum* (5, 7) and *Impatiens* (5),

– one large group next to the nucleus, e.g. in *Nymphaea* (43).

During metaphase I, single or double aggregations of cell organelles move to the region of metaphase chromosomes towards the cell equatorial plane. In microsporogenesis with simultaneous cytokinesis, cytoplasmic organelles in telophase meiocytes migrate between the daughter nuclei, thereby forming the so-called equatorial plate. Such an arrangement of organelles was observed in sporocytes of ferns *Equisetum palustre* (28), *Nephridium molle* (47), *Equisetum limosum* (24), *Adiantum hispidum* (32), *Pteridium aquilinum* (48), *Dryopteris borreri* (49), and *Psilotum nudum* (20, 27, 53, 55), and in microsporocytes of *Helleborus foetidus* (35), *Chamaedorea karwinskyana* (50), *Tropaeolum perignum* (51), *Stangeria paradoxa* (1), *Ginkgo biloba* (31, 59, 61), *Lycopersicon peruvianum* (36), *Lysimachia thyrsiflora*, and *Clarkia elegans* (38).

The second meiotic division proceeds in the binuclear meiocyte. The organelle equatorial plate separates regions, in which karyokinesis takes place in metaphase II. In telophase II, the mitochondrial-plastid plate changes its shape and gradually moves between the telophase nuclei, thereby dividing the tetranuclear cell into four parts at the end of the telophase. In this cell, the organelles are located at the exact site of future primary septa. In some plants, e.g. *Equisetum* (6) and *Psilotum* (53), a characteristic arrangement of organelles in the plate is then visible: the mitochondria are located towards the centre of the plate, and the elongated, longitudinally arranged plastids form outer layers. Finally, the cytoplasmic organelles are scattered throughout the cytoplasm of the microspores formed after meiosis.

In both sporogenesis and microsporogenesis, plastids and mitochondria are evenly distributed in the four newly formed cells (11, 23). Geneves (21, 22) suggests that, during cell division, organelles are distributed in daughter cells as precisely as chromosomes are.

A highly dissimilar pattern of cell organelle rearrangement has been described in *Alcea* (41, 43, 25), *Lavatera* (25, 54), and *Gossypium* (57), in which the cell organelles aggregate around the nucleus and form a characteristic envelope only at the end of prophase I. Both the first and second meiotic division takes place within the single or double envelope composed of cell organelles, in particular plastids and mitochondria.

In the present study, we have analysed the course of chondriokinesis during the complex process of microsporogenesis in some representatives of the family Malvaceae (*Alcea rosea*, *Lavatera thuringiaca* and *Gossypium arboreum*). We have also analysed the arrangement of cell organelles in post-meiotic cells in the stage with visible sporoderm. It was shown that cell organelles, in all the species analysed, formed an envelope around the nucleus at the end of prophase I and karyokinesis took place within the envelope composed of cell organelles. Such an arrangement of organelles persisted not only during microsporogenesis, but also after formation of microspore sporoderm.

MATERIAL AND METHODS

Plant materials

Differently sized anthers of *Gossypium arboreum* plants were collected from the greenhouse at the Department of Plant Anatomy and Cytology, Maria Curie-Skłodowska University, Lublin. Anthers of *Alcea rosea* and *Lavatera thuringiaca* plants were collected from the Botanical Garden of Maria Curie-Skłodowska University in Lublin, Poland.

Light microscopy and transmission electron microscopy (TEM)

Pieces of anthers were fixed for 24 h in 2.5% paraformaldehyde and 2.5% glutaraldehyde in phosphate buffer (pH 7.0), at room temperature. The specimens were washed three times in

phosphate buffer and postfixed in 1% osmium tetroxide. The anthers were then dehydrated in a graded ethanol series, diluted with distilled water, and embedded in London Resin White Medium (Sigma). Semi-thin sections (2 µm thick) for light microscopy were stained with 2% toluidine blue. Ultrathin sections (60 nm thick) for TEM were stained with uranyl acetate (5 min) and lead citrate (10 min). The sections were observed with a JEM 100B transmission electron microscope.

Fluorescence microscopy

For fluorescence microscopy, anthers were fixed for 24 h in 4% paraformaldehyde and 0.25% gutaraldehyde in MT stabilizing buffer (MSB) (3), pH 6.7, at room temperature. They were then rinsed in MSB buffer, dehydrated, embedded in polyethylene glycol and sectioned according to the method of van Lammeren et al. (26). Sections, 2 µm thick, were mounted on slides coated with 2% organosilan (Sigma) and the slides were rinsed in phosphate-buffered saline (PBS). In order to stain DNA in the nuclei and organelles, 4',6-diamidino-2-phenylindole dihydrochloride (DAPI) was added to the sections. The sections were observed with a fluorescence microscope (Nikon Optiphot II). Images of microspores were recorded on Kodak TMAX-400 film.

RESULTS AND DISCUSSION

The species described in this paper have hermaphrodite flowers with stamens and pistils which are placed on a convex receptacle above the perianth base. In *Alcea rosea*, *Lavatera thuringiaca,* and *Gossypium arboreum*, filaments of stamens are fused into a tube and they surround a single pistil (Fig. 1, 2, 3). Most Malvaceae species, including *A. rosea* and *L. thuringiaca*, are characterised by presence of mucilage in the flower (52). Lack of mucilage in flowers is the distinguishing feature of *Gossypium arboreum*.

Early prophase meiocytes in the stamens of the species studied adhered tightly to each other and the tapetal cells. The cell wall of the meiocytes was thin and had a thin callose envelope. Dense cytoplasm contained evenly dispersed cell organelles and centrally located nucleus with a visible nucleolus (Fig. 4). Transmission electron microscope images showed that the cytoplasm of prophase meiocytes in the leptotene stage contained numerous ribosomes, small vacuoles, and multi-layered ER canals distributed around the cell perimeter and around the nucleus. Both the mitochondria and proplastids were evenly distributed throughout the cytoplasm. A centrally located nucleus had a continuous nuclear membrane and spiralized chromatin (Fig. 5). In the zygotene stage, DAPI-stained *A. rosea* meiocytes observed under a fluorescence microscope exhibited plastids and mitochondria scattered homogeneously throughout the cytoplasm, whereas the cell nucleus was located asymmetrically on one side of the cell. Strongly spiralized chromatin and a nucleolus were visible in the nucleus (Fig. 6). In late prophase, gradual rearrangement of cell organelles proceeded towards the cell centre; thus at the end of prophase I plastids and mitochondria formed a relatively compact envelope around the cell nucleus (Fig. 7–8).

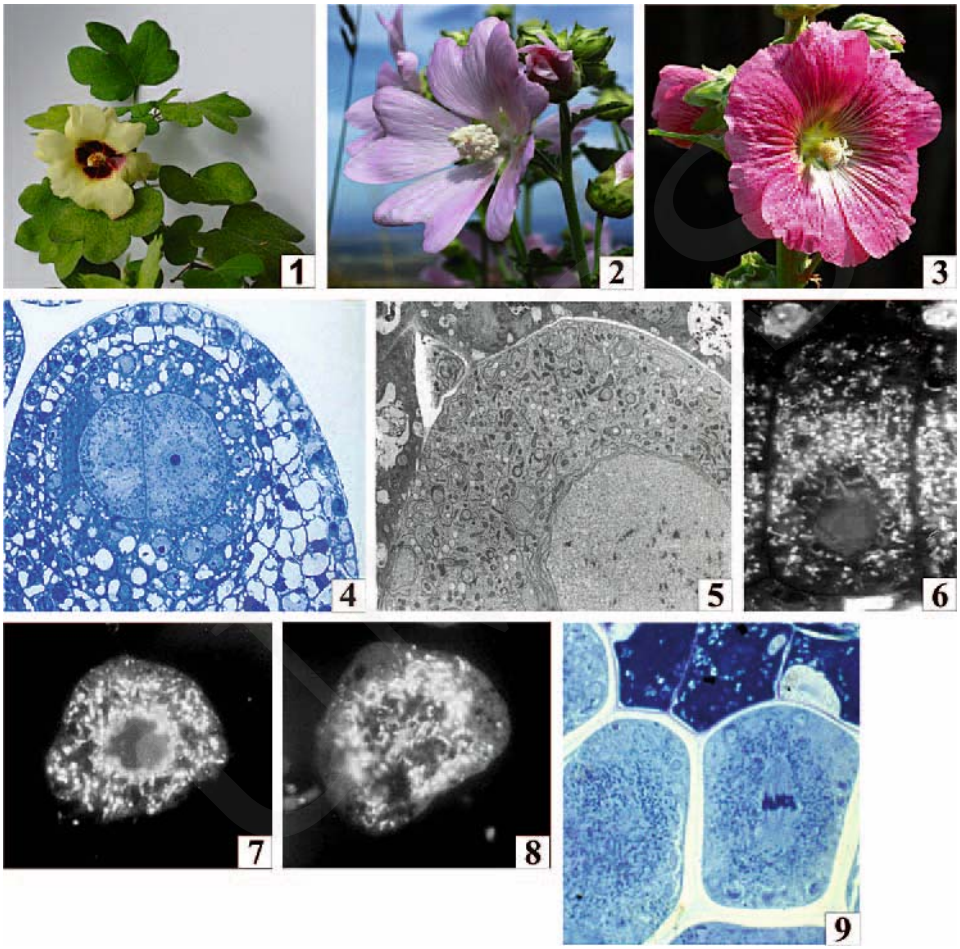

Fig. 1, 2, 3. Shoots with flowers: 1. *Gossypium arboreum*, 2. *Lavatera thuringiaca*, 3. *Alcea rosea*.

Fig. 4. Cross-section of a *G. arboreum* anther head; visible early-prophase meiocytes in the pollen sac. Toluidine-blue staining. Magn. 250x.

Fig. 5. Fragment of *L. thuringiaca* meiocyte in the leptotene stage of prophase I. Magn. 2400x

Fig. 6, 7, 8. *A. rosea* meiocytes stained with DAPI. 6. Zygotene stage. Magn. 500x. 7, 8 Diakinesis. Magn. 350x

Fig. 9. *L. thuringiaca* meiocyte in metaphase I. Toluidine-blue staining. Magn. 400x

This type of chondriokinesis was described in many Malvaceae species at the beginning of the 20th century (18, 19, 58). However, based on observation of the nuclear envelope, some authors reported that it emerged as a fixation artefact (29). Periodic organelle aggregation is common and seems to have biological importance. As reported by some authors, it is related to organelle division. Plastid

division is known to occur in prophase meiocytes, which has been described in detail in monoplastid species (12, 13, 14, 16). Yet, the physiological function of organelle aggregation at the cell nucleus has not been fully elucidated. Interesting investigations have been conducted by Bush et al. (17), who observed mesophyll chloroplast aggregation in C_3 plants. They have reported that a continuous layer of chloroplasts covering the portion of the mesophyll cell periphery that is exposed to the intercellular air space creates a diffusion barrier for CO_2 exiting the cell. This facilitates the capture and re-assimilation of photorespired CO_2 in the chloroplast stroma (17).

In the species studied herein, after disappearance of nucleus membrane in metaphase meiocytes, cell organelles formed a compact envelope around the karyokinetic spindle with metaphase chromosomes. Only few concentrically arranged ER canals were visible in the peripheral cytoplasm devoid of organelles. The callose layer in the meiocyte wall was distinctly thicker (Fig. 9). In anaphase I when metaphase chromosomes moved towards the opposite poles, cell organelles became slightly dispersed, while in telophase I two groups of chromosomes were surrounded by two relatively compact cell organelle aggregations (Fig. 10). TEM observation of meiocytes in metaphase II showed two compact envelopes composed of cell organelles around the chromosome plates. Relatively numerous concentric or elongated ER canals were visible in the peripheral cytoplasm (Fig. 11). Similarly as in anaphase I, the organelle aggregations became loose in the subsequent phase of meiosis, and in telophase II each of the emerging 4 nuclei had its own envelope consisting of cell organelles. TEM observation of meiocytes in late metaphase II revealed daughter nuclei with a reconstructed nuclear envelope and nucleolus. Radially arranged, elongated plastids surrounded the nuclei (Fig. 12).

In the analysed species, simultaneous cytokinesis occurs in meiosis. Formation of a cell wall among the 4 nuclei was visible at the end of telophase II. Despite the on-going cytokinesis, the cell organelle envelopes still surrounded the nuclei. The post-meiotic microspore tetrad was encased by a thick callose wall. In a later stadium, in microspores with a formed cell nucleus, the organelles still persisted as a compact envelope around the nucleus (Fig. 13). It was also observed that the cell organelle envelope still surrounded the cell nucleus in mononuclear pollen grains with complete sporoderm (Fig. 14, 15).

In many species described in literature, chondriokinesis both in sporogenesis and in microsporogenesis with simultaneous cytokinesis proceeds differently than in Malvaceae species. In telophase I, cell organelles form a characteristic equatorial plate. The second meiotic division takes place within two regions separated by the plate (20, 24, 27, 28, 32, 35, 38, 47, 48, 50, 51). The equatorial plate composed of cell organelles is thought to separate regions of the cytoplasm with dividing chromosomes, thereby substituting the still inexistent cell wall. This

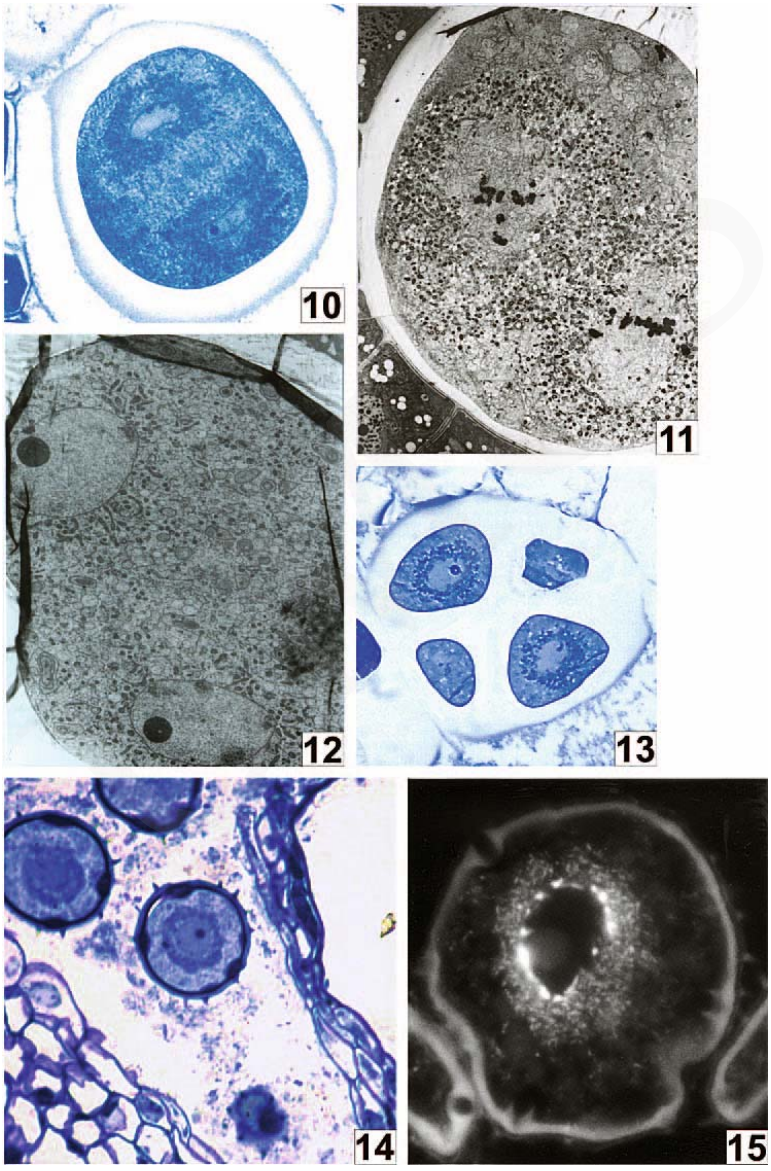

Fig. 10. G. arboreum in late telophase I. Cell organelles form two envelopes around telophase nuclei. Magn. 450x.

Fig. 11, 12. *L. thuringiaca* meiocyte in TEM. Magn. 1950x. 11. Metaphase II, cell organelles form two envelopes around the metaphase chromosomes. 12. Telophase II, cell organelles form two envelopes around nuclei.

Fig. 13. Microspore tetrad in *G. arboreum* within the callose envelope. Magn. 450x.

Fig. 14, 15. Mononuclear pollen grain. 14. *G. arboretum*. Magn. 250x. 15. *L. thuringiaca*. Magn. 700x

is confirmed by the fact that when the primary septum and wall are formed after the first division in meiosis with successive cytokinesis, cell organelles do not form an equatorial plate, but they are scattered in the cytoplasm or aggregate close to the nucleus (8, 37, 45, 56).

The characteristic cell organelle envelope found in Malvaceae, which functions from late prophase I to the end of meiosis, seems to play the same role as the equatorial plate in other species characterised by simultaneous cytokinesis. Nevertheless, its further role in post-meiotic cells is not clear, as the observations reported herein show that cell organelles in mononuclear pollen grains with complete sporoderm still make up compact aggregations around the nucleus.

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