ORIGINAL ARTICLE

An ultrastructural study of cytomixis in tobacco pollen mother cells

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Abstract Intercellular chromatin migration (cytomixis) in the pollen mother cells of two tobacco (*Nicotiana tabacum* L.) lines was analyzed by electron microscopy during the first meiotic prophase. The maximal manifestation of cytomixis was observed in the pachytene. As a rule, several cells connected with one another by cytomictic channels wherein the nuclei migrated were observable at this stage. In the majority of cases, nuclei passed from cell to cell concurrently through several closely located cytomictic channels. Chromatin migrated between cells within the nuclear envelope, and its disintegration was unobservable. The nucleus, after passing through cytomictic channels into another cell, can be divided into individual micronuclei or, in the case of a direct contact with another nucleus, can form a nuclear bridge. It has been demonstrated that the chromatin structure after intracellular migration visually matches the chromatin structure before it passed through the cytomictic channel. No signs of pyknosis were observable in the chromatin of the micronuclei formed after cytomixis, and the synaptonemal complex was distinctly seen. The dynamics of changes in the nucleoli during cytomixis was for the first time monitored on an ultrastructural level. Possible mechanisms determining cytomixis are discussed and the significance of this process in plant development is considered.

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Introduction

It is known that specialized channels spanning the cell wall, the plasmodesmata (McLean et al. 1997), play the main role in the interaction between plant cells. However, plasmodesmata are not the only type of intercellular channels present in plant tissues. During development of the male gametophyte and in several other cases, plant cells can be connected with one another by the channels considerably exceeding plasmodesmata in their size and differing from them in their structure. Such channels are referred to as cytomictic channels, and the cell contents migrate through these channels during the cytomixis.

Cytomixis is the migration of nuclei as well as other organelles and cytoplasm between cells through the cytomictic channels. This phenomenon was first described by Arnoldy (1900) in reproductive organs of gymnosperms, then by Koernicke (1901) in the microsporogenesis of *Crocus vernus* and Miehe (1901) in the leaf epidermis of *Allium cepa*. The term *cytomixis* was proposed by Gates (1911), who observed this phenomenon in the microsporogenesis of *Oenothera gigas*.

Cytomixis is a widespread phenomenon for higher plants; it has been so far discovered in over a hundred angiosperm (Heslop-Harrison 1966; Falistocco et al. 1995; De Souza and Pagliarini 1997; Bellucci et al. 2003; Ghaffari 2006) and gymnosperm (Guzicka and Wozny 2005) species. Cytomixis is most frequently met in pollen mother cells (PMCs) (Heslop-Harrison 1966; Falistocco et al. 1995; Singhall and Kumar 2008); however, the cases of intercellular migration of nuclei have been also observed in

plant vegetative tissues (Zhang et al. 1990; Wang et al. 2004; Guzicka and Wozny 2005).

Cytomixis commences from formation of cytomictic channels between cells; the size of these channels allows cell organelles, including nuclei (Heslop-Harrison 1966), to migrate from one cell to another. The role of these channels is still questionable. Some researchers associate the formation of cytomictic channels with the need in exchange with certain substances between the cells for a synchronous pollen development (Heslop-Harrison 1966). However, the predominant opinion is that cytomictic channels are the pathways for migration of nuclear material between cells (Falistocco et al. 1995; Lattoo et al. 2006; Singhall and Kumar 2008).

The results of studies into cytomixis suggest that the migration of nuclear fragments and in some cases whole nuclei between cells can lead to changes in the plant karyotype emergence of polyploid and aneuploid plants and plants with B chromosomes (Patra et al. 1988; Falistocco et al. 1995; Ghaffari 2006). In some plant species, a high rate of cytomixis in PMCs correlates with production of aneuploid and polyploid pollen (Falistocco et al. 1995; Ghaffari 2006; Lattoo et al. 2006; Negron-Ortiz 2007; Singhall and Kumar 2008). However, note that there is yet no evidence the development of polyploid and aneuploid gametes in these plant species is a direct consequence of nuclear migration between PMCs during cytomixis.

Although cytomixis attracts attention of researchers for already over a hundred years, many details, mechanisms, and consequences of this enigmatic phenomenon are still to be clarified. In part, this is connected with the absence of convenient models for studying this phenomenon, i.e., the plants with a constantly high level of cytomixis. It is also important that the majority of results on cytomixis have been obtained by light microscopy, while ultrastructural studies of cytomixis are yet few (Heslop-Harrison 1966; Feijo and Paris 1989; Zhang et al. 1990; Wang et al. 1998; Yu et al. 2004; Mursalimov et al. 2010).

Among the transgenic tobacco plants obtained from SR1 line, we have earlier isolated the lines with mutant phenotype (changed flower structure and decreased pollen fertility) displaying a high level of cytomixis (Zagorskaya et al. 2001; Sidorchuk et al. 2004). The level of cytomixis in the nontransgenic tobacco line SR1 was about 4% versus the transgenic plants of several lines produced involving this line, where the level of cytomixis in some cases increased to 50% and retained in the selfed progeny (Zagorskaya et al. 2001; Sidorchuk et al. 2004, 2007a). This specific feature of the isolated lines allowed them to be used as models for a comprehensive cytological analysis of cytomixis, including an ultrastructural examination.

In this work, we describe the results on the specific ultrastructural features of cytomixis in tobacco PMCs; in particular, it has been demonstrated that the nuclear envelope and chromatin display no visible signs of damage during cytomixis. After passing through cytomictic channels, nuclei can separate into micronuclei or from nuclear bridges. The dynamics of changes in the nucleoli when passing through cytomictic channels within the nucleus is described for the first time.

Materials and methods

Plant material

Two tobacco (*Nicotiana tabacum* L.) lines were used in the work: line SR1 was represented by nontransgenic plants and line Res79 by the transgenic plants obtained from line SR1 via agrobacterial transformation (Zagorskaya et al. 2001; Sidorchuk et al. 2004). The rate of cytomixis in line SR1 was about 4% versus about 15% in line Res79 (Sidorchuk et al. 2004, 2007a). Line Res79 is a spontaneous polyploid ($2n=96$) and displays an altered flower structure and decreased pollen fertility (Sidorchuk et al. 2004, 2007a).

All plants were grown in a hydroponic greenhouse with a photoperiod of 16/8 h (day/night) at a temperature of 22/18°C (day/night).

Preparation of material for ultrastructural analysis

Tobacco anthers containing PMCs were picked at various meiotic stages, and their developmental stage was determined by light microscopy; then anthers were cut into pieces of 2–3 mm and fixed with 2.5% glutaraldehyde (Serva, Germany) in phosphate buffer (pH 7.2–7.4) for 4 h at room temperature. Then the material was washed three times for 10 min with phosphate buffer followed by postfixation with 1% osmium tetroxide (Azurite, Russia) for 2 h at room temperature, washed with phosphate buffer two times for 15 min, and dehydrated with ethanol solutions of increasing concentrations. The samples were placed into acetone for 1 h and embedded into araldite epoxy resin (Fluka, Switzerland).

Ultrathin sections with a thickness of about 80 nm were made using an Ultracut UCT (Leica, Switzerland) ultramicrotome and stained with lead citrate and uranyl acetate (Serva, Germany). The stained sections were examined using a JEM 100S (Jeol, Japan) or a Libra120 (Carl Zeiss, Germany) transmission electron microscope at an accelerating voltage of 60 kV. Microscopic examination was performed at the joint access center for microscopic analysis of biological objects with the Siberian branch of the Russian Academy of Sciences.

Results

Cytomixis in tobacco PMCs

Figure 1 shows the overall picture of cytomixis at an ultrastructural level in the tobacco PMCs during meiotic prophase I. This is the particular meiotic stage when the frequency of nuclear migration between cells is maximal. Since the observed cytomixis pattern at an ultrastructural level was similar for both the transgenic (Res79) and nontransgenic (SR1) lines, the microphotographs for illustrating individual specific features of cytomixis simultaneously detectable in both studied lines were chosen according to better quality independently of particular line.

Figure 1a shows two neighboring cells connected with cytomictic channels with one another and adjacent cells (shown with arrows). It is evident that nuclei migrate between cells through these channels. The nuclear migration is unidirectional: the nuclei of all cells cross the cell wall only in one direction, and no migration of nuclei in opposite directions towards one another is observed. Thus, a sort of chains of cells connected with migrating nuclei is formed. It is well seen that the chromatin of all four PMCs is at the same stage of compaction and displays no abnormalities associated with desynchronization in PMCs or pathological changes in cell structure.

Figure 1a shows that each individual nucleus concurrently migrates from one cell to another through several closely located channels. When passing through a cytomictic channel, the nuclear envelope extends and forms projections with chromatin observable in them. The extension of the nuclear envelope in the direction of nucleus movement is likely to be caused by cell cytoskeleton structures, which are assumed to provide for the nuclear migration during cytomixis. Presumably, the nuclear envelope upon entering the recipient cell carries with it the chromatin attached to its inner surface (Fig. 1a).

Figure 1b shows a nucleus passing through a cytomictic channel into another cell at a high magnification. It is evident that the nuclear envelope retains its integrity before
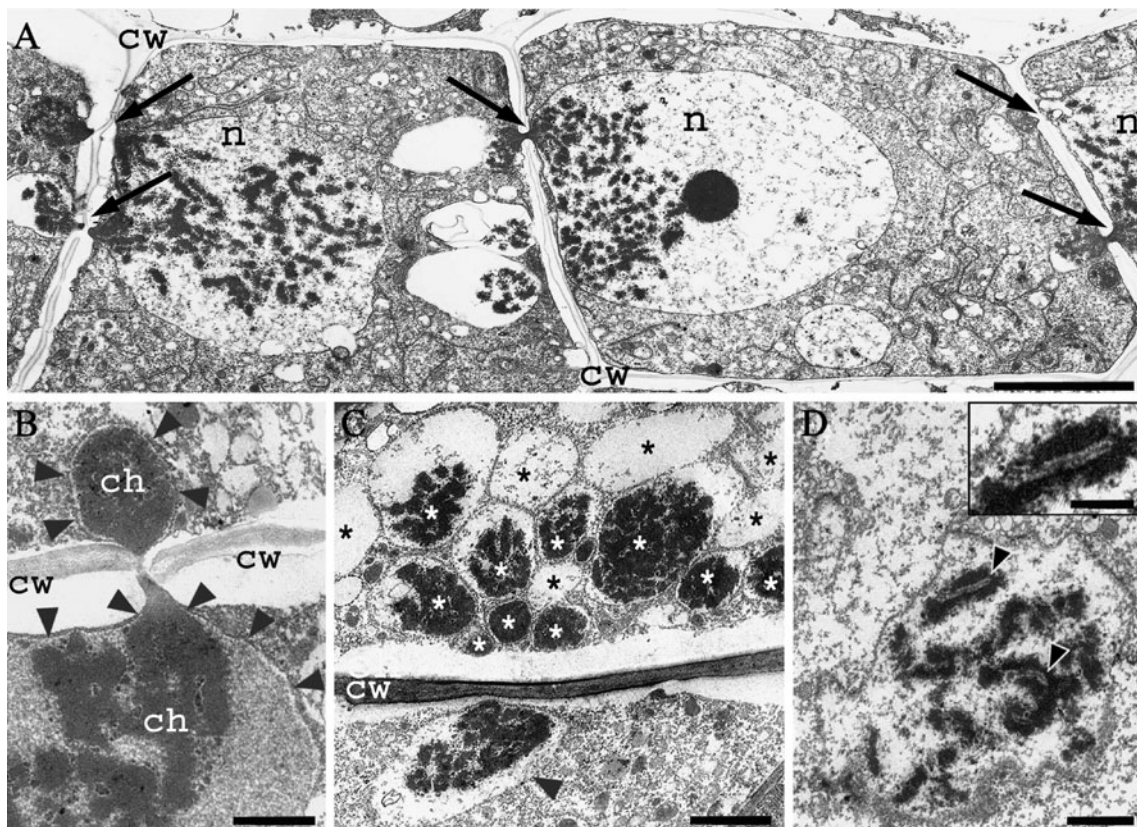

Fig. 1 Cytomixis and its consequences in the PMCs of tobacco lines. **a** SR1 and **b**–**d** Res79 in the pachytene. **a** The cytomixis in tobacco PMCs with successive unidirectional nuclear migration from cell to cell in a rightward direction. Cytomictic channels are shown (*arrows*); part of the channels is beyond the section plane; *cw* cell wall, *n* nucleus. **b** Nuclear migration through cytomictic channel. Integrity of the nuclear envelope (*arrows*) is shown; in this case, the migration direction is from bottom upwards; *cw* cell wall, *ch* chromatin. **c** Micronuclei formed as a result of cytomixis (*asterisks*). Initial cell contains a fragment of the nucleus that remained after nuclear migration to another cell (*arrow*); *cw* cell wall. **d** Micronucleus formed as a result of cytomixis. Synaptonemal complex (*arrows*) is seen in chromosome structures. Inset shows upscaled synaptonemal complex. *Bars* represent 5 μm in **a**, 1 μm in **b**, 2 μm in **c**, 1 μm in **d** and 500 μm in the insert

and after migration through cytomictic channel (denoted by arrows). Note that the chromatin displays the structure characteristic of the pachytene before approaching the cytomictic channel (Fig. 1b); however, when already approaching it, inside the channel, and after exiting, chromatin looks as a uniform dark-colored mass (Fig. 1b). Despite this, chromatin restores its initial structure after a certain time period, and any visible changes in its structure are undetectable (Fig. 1a, c, d).

According to our observations, cytomixis, as a rule, leads to formation of micronuclei from a migrating nucleus. Figure 1c demonstrates formation of over ten micronuclei containing chromatin as a result of cytomixis; in this case, the initial cell still contains a remaining part of the migrating nucleus (denoted by arrow). Note that the chromatin structure looks identical both in all the micronuclei formed as a result of cytomixis and in the nuclear fragment that remained in the initial cell (Fig. 1c).

Moreover, a native chromosomal structure, a synaptonemal complex, is distinctly seen in the micronuclei formed after cytomixis (Fig. 1d; denoted by arrows), which demonstrates the preservation of normal chromosomal organization after passing through the cytomictic channel. The fact that, according to our observations, the nuclear envelope retains its integrity during cytomixis and chromatin is constantly surrounded by nuclear envelope both during migration through the cytomictic channel and in the recipient cell (Fig. 1b) also favor the assumption that chromatin remains undamaged during cytomixis.

Figure 2 shows a more complex picture of cytomixis between three PMCs (cells 1–3 with their nuclei denoted as n_1, n_2, and n_3). We propose the following interpretation for this picture. Five cytomictic channels (denoted by arrows) are formed between these cells; three of them are involved in nuclear migration. Nucleus n_2 migrates from cell 2 to cell 1 concurrently through two cytomictic channels (denoted by arrows). Micronuclei (white asterisks) are seen at the opposite pole of cell 2; presumably, they migrated from the cell located to the right, which suggests that these cells form a chain with the nuclei migrating in the same direction. Cell 3 is not involved in this chain, and its nucleus n_3 migrates in the opposite direction to enter cell 2 (this cytomictic channel is beyond the section plane; however, an elongated shape of nucleus n_3, the chromatin orientation within this nucleus towards the site of putative channel, and a small nuclear fragment with chromatin in cell 2 located near the site of putative channel (dark asterisk), definitely suggest that nucleus n_3 migrates into cell 2). A concurrent migration of the nuclei from several cells into one cell is also typical of the cytomixis in tobacco PMCs along with a unidirectional nuclear migration (Sidorchuk et al. 2007a).

However, the most interesting detail in this picture of cytomixis is formation of a direct contact between nuclei n_1 and n_2 (denoted by a white arrow and upscaled in the inset). Such interaction between the nuclei in neighboring cells during cytomixis is described for the first time. The contact between n_1 and n_2 is provided by a nuclear bridge, which is presumably formed via a fusion of the nuclear envelopes of two contacting nuclei after passing of part of one of the nucleus through cytomictic channel. Once two nuclei have contacted, a channel is formed, a nuclear bridge with a

Fig. 2 Cytomixis with nuclear bridge formation in the pachytene in tobacco line SR1 PMCs. Cytomictic channels (*arrows*), nuclear bridge (*white arrow*), micronuclei (*white asterisks*), and a fragment of n_3 nucleus that migrated to cell 2 (*black asterisk*) are shown; *1–3* cell numbers, n_1–n_3 the nuclei of the corresponding cells; *cw* cell wall. *Bar* represents 2 μm. Inset shows an upscaled nuclear bridge; integrity of the nuclear envelope in the nuclear bridge (*arrows*) is shown; *ch* chromatin. *Bar* represents 500 nm
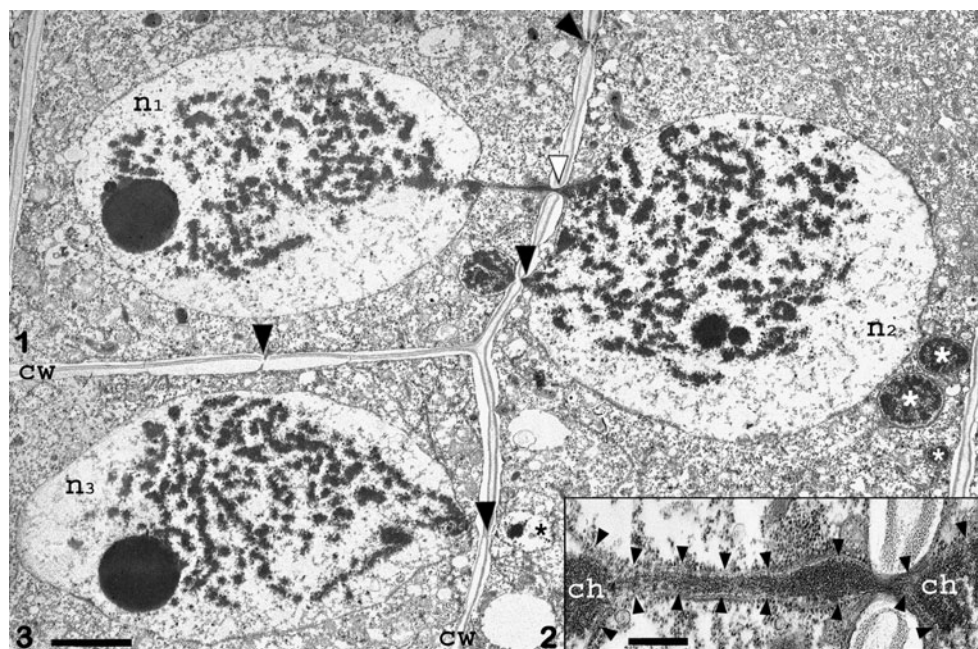
diameter of about 250 nm, which is limited by the nuclear envelope and directly connects the nuclei of two cells (Fig. 2).

We have observed such structures during cytomixis in few cases in SR1 line. It is not impossible that such structures are formed between PMCs of the second tobacco line; however, their small size, specific features of their formation, and a random character of the ultratome sections could interfere with their detection. Furthermore, nuclear bridges appeared to be very unstable structures which could easily be disrupted during material preparation.

Note that no regions of disrupted integrity of the nuclear envelope are observed over the whole nuclear bridge (Fig. 2, inset). Chromatin is detectable inside the nuclear bridge; presumably, chromatin migrates from one nucleus to another. Since nucleus n_2 migrates to cell 1, this suggests that if chromatin moves inside the nuclear bridge, this movement is directed from nucleus n_2 to nucleus n_1.

In addition to that nucleus n_2 is involved in formation of a nuclear bridge; it forms one more projection, which spans the cell wall through the cytomictic channel (Fig. 2; denoted by arrows and located below the nuclear bridge). We can only assume whether this projection of nucleus n_2 will form an additional nuclear bridge or it will be involved in formation of micronuclei.

Figure 3 shows the microphotographs that allow us to postulate one of the possible ways in to form nuclear bridges. In this case, nucleus n_1 migrates to the cell located below through at least two cytomictic channels (the whole channels are beyond the section plane; however, projections of the nuclear envelopes localized to the other cell and containing chromatin demonstrate that this is an event of cytomixis).

We assume that nucleus n_1 when passing through cytomictic channels forms two projections, one of which directly contacts nucleus n_2; it is also likely that the nuclear envelopes dissolve in the contact zone (shown with black arrows). Consequently, such contact accompanied by dissolution of nuclear envelopes may result in nuclear bridge formation. Interestingly, a sort of interaction is assumed between nucleus n_2 and the second projection of nucleus n_1, located below and filled with chromatin (shown with a white arrow in Fig. 3b). In this case, a group of vesicles is detectable between the membranes of two nuclei, which, presumably, are involved in the formation of contacts between the nuclei; however, their origin is unclear.

Note also that the chromatin in nucleus n_2 concentrates at the pole opposite to the site of formed internuclear contacts (Fig. 3a), thereby suggesting a cytomictic migration of this chromatin along the chain into the next cell.

Note that the formation of direct contacts between nuclei of different cells via cytomictic channels was observed in a few cases and the conclusions made based on these data are preliminary. However, these data allow for certain interesting assumptions, for example, on the chromatin that is involved in this process. The migration of chromatin along a nuclear bridge between two cells can be regarded as its movement within a single nucleus, since the chromatin is within a closed space limited by the nuclear envelope and finds itself in another nucleus without leaving this space (Fig. 2). Presumably, the chromatin involved in this process is not subject to the action of any damaging factors, and, thus, its migration can have certain genetic consequences. Note that no pyknosis in the chromatin is observable in the cells when nuclear bridges are formed as well as no vacuolation in the cytoplasm or any other signs of cell pathology.

These phenomena can be differently estimated from the standpoint of chromatin migration between cells as well as the genetic consequences of these events; however, the mere fact that nuclei from different cells can contact with one another during tobacco microsporogenesis is intriguing enough.

Fig. 3 A contact of two nuclei during cytomixis in the pachytene in tobacco line SR1 PMCs. **a** Two cells connected by cytomixis. Nucleus n_1 migrates to the cell located below and contacts nucleus n_2. **b** The site of contact between two cells, upscaled. Putative fusion region of the nuclear envelopes (*black arrow*) and the group of vesicles contacting the surface of both nuclei (*white arrow*) are shown; *cw* cell wall, *ch* chromatin, n_1 and n_2 are the nuclei of the corresponding cells. *Bars* represent 2 μm in **a** and 1 μm in **b**
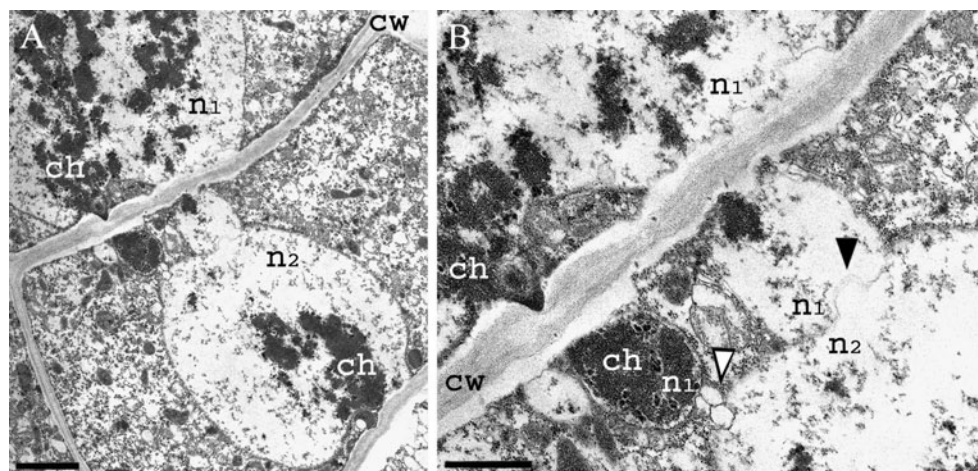
The nucleolus during cytomixis

When using the tobacco line displaying a high rate of cytomixis (Res79), we pioneered in monitoring the dynamics of changes in the nucleolus during the nuclear migration through cytomictic channels at an ultrastructural level (Fig. 4). The maximal size of cytomictic channel in tobacco PMCs is about 600 nm (Mursalimov et al. 2010), while the diameter of the nucleolus in tobacco PMCs is on the average about 2 μm. Correspondingly, the nucleolus changes its shape when migrating through cytomictic channels because the size of the nucleolus is at least threefold larger than the maximal size of cytomictic channels. The nucleolus in tobacco PMC meiotic prophase I is dense, dark-colored, and round-shaped (Fig. 4a). When passing through a cytomictic channel, the nucleolus changes its shape—it elongates and becomes oval (Fig. 4b; shown by an arrow). The initially round shape of the nucleolus is restored in the recipient cell after migration through the cytomictic channel. Having passed through a cytomictic channel, the nucleolus can enter the formed micronucleus as a whole or can be divided into several parts. In some cases, the nucleolus can be present in the recipient cell as a "nucleolar micronucleus," which is covered by a nuclear envelope and contains minimal amounts of the nuclear chromatin (Fig. 4c; shown by an arrow).

Discussion

So far cytomixis has been discovered in microsporogenesis of many higher plant families growing under diverse conditions and represented by both herbal and woody forms (Bedi 1990; Falistocco et al. 1995; Lattoo et al. 2006; Negron-Ortiz 2007). A wide abundance of cytomixis in various distant species suggests that this phenomenon can be characteristic of microsporogenesis in all higher plants; however, this phenomenon is difficult to discover and study, which yet prevents such general conclusion.

Undoubtedly, cytomictic channels play a key role in cytomixis. It has been demonstrated that cytomictic channels can be formed by several ways, namely, joining of several closely located plasmodesmata (Wang et al. 2004), enlargement of individual plasmodesmata (Mursalimov et al. 2010), or de novo formation in the case of cell wall dissolution (Wang et al. 1998; Yu et al. 2004). Evidently, the goal of these channels is to provide for exchange of cell contents between PMCs in an anther. However, the functioning of cytomictic channels is still unclear. It is also unknown for transportation of which substances or organelles they are intended. Similarly, unclear what signal induces formation of cytomictic channels and initiates nuclear migration. Moreover, there is still no common opinion on whether cytomixis is a norm or a result of mutational changes in individual genes involved into the control of a complex process, plant microsporogenesis.

Cytomixis can be a useful tool for studying the mechanisms of nuclear migration both in the cell and between cells. Usually, the nucleus in the cell occupies a fixed position; however, it can migrate in some cases for performing certain tasks. For example, the growth of root is accompanied by migration of nuclei from epidermal cells into the body of root hair (Chytilova et al. 1999) or the nuclei migrate along a growing hypha of filamentous fungi, evenly spreading over its space (Suelmann et al. 1997). Such migration of nuclei is provided by the interaction between cytoskeleton and motor proteins (Suelmann et al. 1997; Fischer 1999; Liu et al. 2003). It is logical to assume that the nuclear migration from one cell into another during
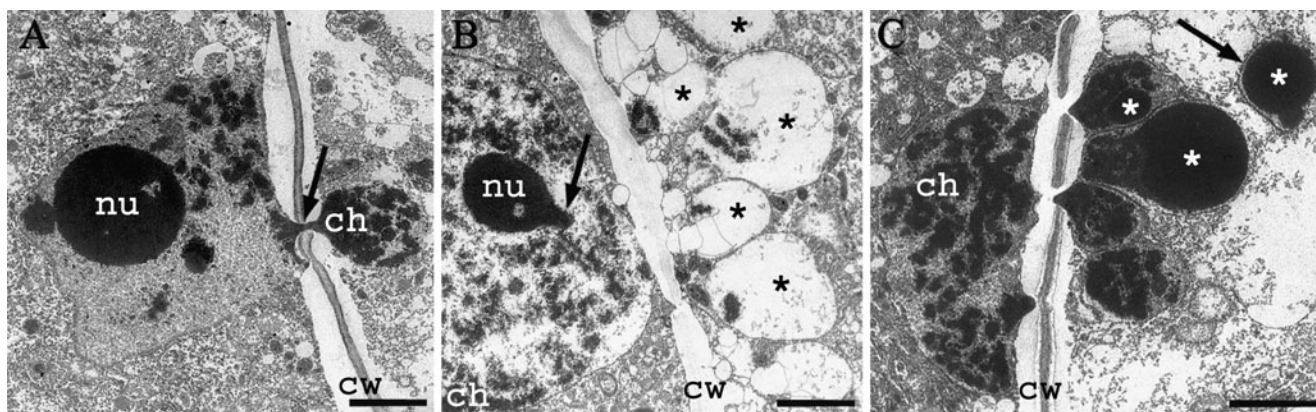

Fig. 4 Behavior of the nucleolus in tobacco line Res79 PMCs in the pachytene (in **a**–**c**, the nuclei migrate from cell to cell from left to right). **a** The initial shape of the nucleolus before migration through the cytomictic channel. The nucleus migrates through the cytomictic channel (*arrow*). **b** Change in the shape of the nucleolus (*arrow*) immediately before the migration through cytomictic channel. After the migration into another cell, the nucleus divided into micronuclei (*asterisks*). **c** Separation of the nucleolus into several fragments after migration through the cytomictic channel with formation of micronuclei. The nucleolar material is denoted by *asterisks*. One of the formed micronuclei is almost completely filled with nucleolar material (*arrow*); *cw* cell wall, *ch* chromatin, *s* nucleolus. *Bars* represent 2 μm

cytomixis is performed in a similar manner. As we have found earlier, the microtubular cytoskeleton is not involved in the cytomictic nuclear migration (Sidorchuk et al. 2007b). Presumably, the cell actin cytoskeleton is the main player in the nuclear migration during cytomixis. The fact that the migration of cell contents through cytomictic channels is halted in the presence of cytochalasin B, which prevents the growth of actin filaments (Zhang et al. 1985), also favors this hypothesis. Moreover, it has been demonstrated that the movement of cell contents through cytomictic channels is also stopped in the presence of KCN and at a decreased temperature, which suggests that this is an energy-dependent process (Zhang et al. 1985).

Discovery of particular motor proteins responsible for migration of individual cell organelles through cytomictic channels as well as various molecular mechanisms associated with cytomixis is the problem to be studied in the future. The tobacco lines with a high rate of cytomixis that we have obtained can be a useful model object for such studies.

Our data on the change in the shape of nucleolus during its migration through the cytomictic channels reflects the general migration pattern of the cell nucleus during cytomixis. The change in the shape of nucleolus (Fig. 4b) is most likely determined by migration of the chromosomes with the nucleolar organizer regions being drawn by the nuclear envelope to which they are attached. Since the S10 and T3 chromosomes from the S and T subgenomes in the karyotype of tobacco line SR1 ($2n=48$) display a secondary constriction and are involved in formation of the nucleolus (Moscone et al. 1996), the plants of line Res79 ($2n=96$) can have double the number of such chromosomes. Since the nucleolus-forming chromosomes are attached to the cell membrane at different sites, they can migrate through different channels during cytomixis. Correspondingly, the nucleolus can be divided into several fragments, and each nucleolar-forming chromosome brings with it part of the nucleolar material (Fig. 4c). Presumably, the nucleolar micronucleus shown in Fig. 4c contains only one nucleolus-forming bivalent and can be presumably identified as one of the copies of bivalents S10 or T3.

The observed cases of intercellular migration of nuclei suggest that the migrating nucleus during the cytomixis in tobacco PMCs is most frequently divided into micronuclei after entering another cell (Figs. 1c, d and 4b, c). However, when two nuclei contact during cytomixis, this can lead to development of nuclear bridges (Figs. 2 and 3). Figure 5 shows the schemes of formation of micronuclei (left) and nuclear bridges (right) during cytomixis.

The migration of chromatin of one PMC into another either via nuclear bridges or as micronuclei implies the transfer of part of the genetic material between the cells involved in cytomixis. Moreover, our ultrastructural studies of microsporogenesis in two tobacco lines suggest that the
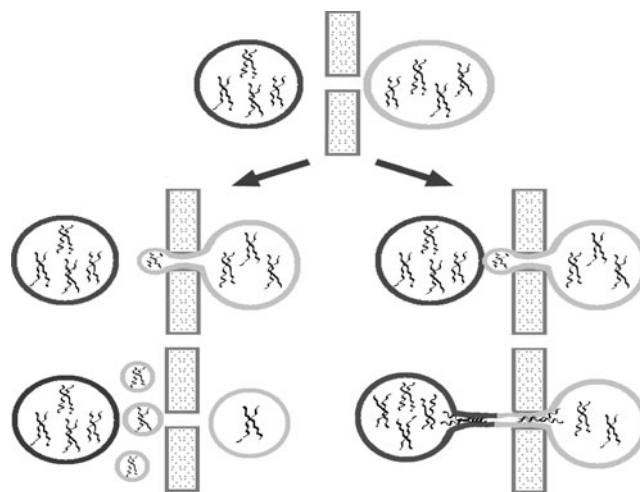

Fig. 5 Hypothetical schemes for two possible variants of nucleus behavior during cytomixis (the nuclei migrate from right to left). The *left panel* shows formation of micronuclei (in the case when the nuclei of two cells do not contact during cytomixis). The *right panel* shows a less frequent case of nuclear bridge formation (a direct contact between nuclei during cytomixis)

chromatin structure after migration through cytomictic channels does not change. This allows cytomixis to be regarded as a normal process in the cell rather than a pathology. However, the preservation of chromatin structure after its migration into another cell does not guarantee its inclusion into the nucleus as additional chromosomes because it can be later eliminated. Even the migration of chromatin into another nucleus via a nuclear bridge does not guarantee that this chromatin will not be later eliminated from the nucleus. So far, there is no direct evidence of emergence of aneuploid or polyploid plants as a result of cytomixis; however, numerous indirect data suggest a correlation between cytomixis and the pollen with different ploidy levels (Falistocco et al. 1995; Ghaffari 2006; Lattoo et al. 2006; Negron-Ortiz 2007; Singhall and Kumar 2008).

Thus, insufficient experimental data so far prevent from an unambiguous conclusion that cytomixis in the plant microsporogenesis is the mechanism that increases genetic diversity of the formed gametes; however, we believe that it is difficult to interpret in any other way the reason for formation of cytomictic channels, which provide for the nuclear migration between cells. Additional studies of the further "fate" of the genetic material migrating between PMCs during cytomixis using specific molecular probes are necessary to get a more comprehensive picture of these processes.

Conflict of interest The authors declare that they have no conflict of interest.

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