

Organelle Dynamics During Cell Division

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Abstract Many organelles in plant cells show a more or less random distribution in the interphase cell but assume very specific positions during mitosis and/or cytokinesis. Most prominent among these is the Golgi apparatus which is thought to provide the majority of raw materials for the assembly of the forming cell plate. However, the localization of other organelles also seems to indicate specific functions during cell division. In addition, organelle positioning mediated by the actin cytoskeleton has been implicated in equal inheritance of organelles by the daughter cells. This review summarizes the current knowledge of dynamic organelle positioning during mitosis and cytokinesis and discusses the mechanisms responsible for the observed localizations.

1

Introduction

Plant cells, like those of all eukaryotes, are compartmentalized into a number of membrane-bound organelles that carry out specialized functions within the cell (Lunn 2006). An important aspect of cell division is the distribution of these organelles into the daughter cells to ensure proper functioning of these progeny cells (Warren 1993). This concept is immediately obvious for organelles that originate from fission of preexisting organelles, such as mitochondria and plastids. Once a cell has lost either of these organelles, it cannot create new copies of them since their genetic information is lost.

However, the issue of organelle inheritance also applies to compartments that do not contain their own genome. For example, it is not clear how a cell would regenerate a new endoplasmic reticulum (ER) should it ever lose this important biosynthetic organelle. In other cases, an organelle may be crucial for the process of cell division itself and may be required in both daughter cells for its successful completion. The Golgi apparatus which provides the raw material for cell plate assembly can serve as an example for this class of organelles.

To ensure faithful inheritance of organelles during cell division, a number of different approaches can be envisioned that fall broadly into two categories: regulated and random (Warren and Wickner 1996). An extreme example for regulated inheritance is the mitotic division of the nucleus itself. In this case

individual chromosomes are tightly attached to a bipolar spindle to ensure that their duplicated products, the chromatids, are reliably partitioned into the two daughter cells. A similar approach also applies to those organelles that are present in small copy numbers such as chloroplasts and sometimes mitochondria in some algae. Many organelles of flowering plant cells, on the other hand, exist in high copy numbers and a random distribution throughout the cytoplasm should suffice to ensure inheritance of at least some copies by both daughters (Sheahan et al. 2004).

In reality, most organelle inheritance schemes fall somewhere between these extreme cases of total control and pure chance. In particular, those organelles that function in some aspect of cell division may not be randomly distributed in order to allow for efficient cell division to occur. As a result, any deviation from a purely random distribution of high copy number organelles can be used to infer that this organelle may play a role in mitosis or cytokinesis. This reasoning formed the basis of a number of studies that have examined the positioning of organelles during various stages of cell division. This work will review these studies and highlight some of the conclusions derived from these observations.

2

Organelle Positioning During Mitosis and Cytokinesis

2.1

Endoplasmic Reticulum

One of the first organelles to be examined in detail for its distribution during mitosis and cytokinesis was the ER. Staining of *Haemanthus* endosperm cells with chlorotetracycline, which marks high Ca^{2+} concentrations, revealed intense signals in the mitotic spindle (Wolniak et al. 1980). Since it is well known that the ER serves as an intracellular store of Ca^{2+} ions it was proposed that this staining represented the presence of ER in the mitotic spindle (Fig. 1). This conclusion was confirmed by electron microscopy (EM) of Os-FeCN stained barley and lettuce root tip cells (Hepler 1980, 1982). In both species a high density of ER elements was detected at the spindle poles as well as intermixed and associated with spindle microtubules (MTs). Newer studies employing ER-targeted GFP or immunofluorescence of HDEL-carrying proteins further confirmed these results for tobacco suspension cultured cells (Gupton et al. 2006; Nebenführ et al. 2000) and gymnosperms and pteridophytes (Zachariades et al. 2003). It has been proposed that the spindle ER plays a role in regulating local cytoplasmic Ca^{2+} concentrations that in turn are crucial for spindle function (Hepler 1980).

Prior to mitosis, the ER was found to align with the pre-prophase band (PPB) of MTs in *Pinus* (Zachariades et al. 2001). During cytokinesis, the

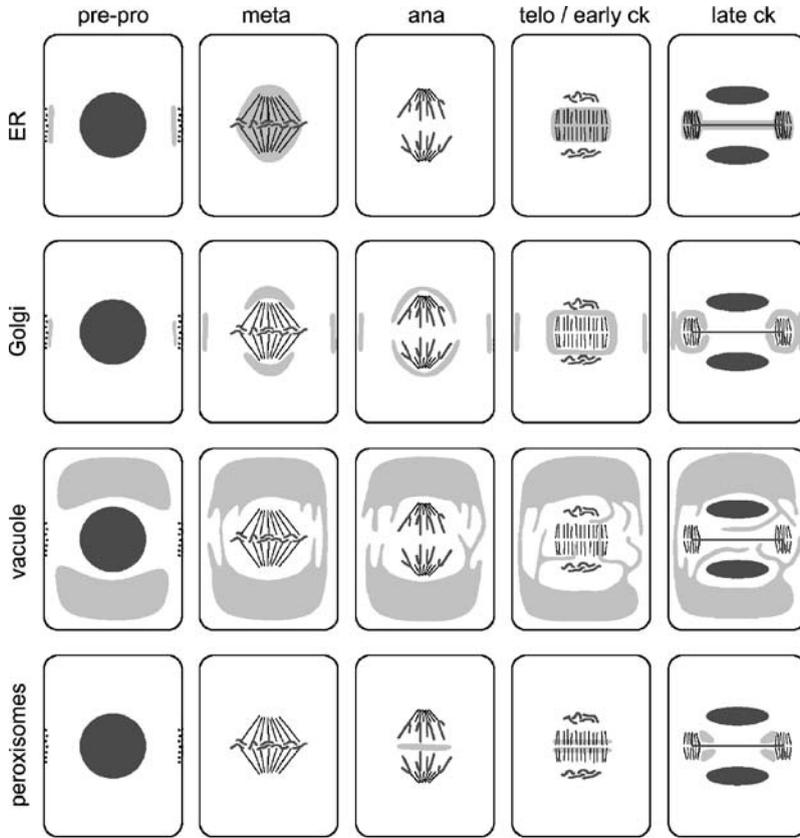


Fig. 1 Several organelles accumulate in specific regions during various stages of cell division. *Light gray* regions identify regions where ER, Golgi stacks, and peroxisomes preferentially accumulate at the given mitotic phase. The vacuole is largely confined to the periphery of the cell but sends tubular extensions into the phragmosome. For details see text. pre-pro, preprophase; meta, metaphase; ana, anaphase; telo/early ck, telophase to early cytokinesis; late ck, late cytokinesis

ER is prominently present within the phragmoplast where tubular elements seem to align with the MTs when viewed by fluorescence microscopy (Gupton et al. 2006; Nebenführ et al. 2000; Zachariades et al. 2003). ER also associates closely with the cell plate leading to the appearance of a brightly fluorescing line at the division plane (Gupton et al. 2006; Nebenführ et al. 2000; Zachariades et al. 2003). The function of this cell-plate associated ER is not fully established. Initially, it has been proposed that the ER may form a “cage” within which Golgi-derived vesicles fuse to form the cell plate (Hepler 1982). However, a more recent study employing three-dimensional EM tomography revealed that the ER is not present during the earliest stages of vesicle fusion

and approaches the cell plate only later (Seguí-Simarro et al. 2004). This study speculates that the close proximity of ER and cell plate is required to facilitate exchange of membrane lipids between these compartments during cell plate maturation (Seguí-Simarro et al. 2004).

2.2

Golgi Apparatus

The Golgi apparatus assumes a special position among the organelles of plant cells in that its activity is directly necessary for cell plate formation. This special function has been postulated for the first time based on the unusual arrangement of Golgi stacks in the vicinity of the growing cell plate in maize root tips (Whaley and Mollenhauer 1963). In fact, until recently it has been assumed that the cell plate is formed exclusively from Golgi-derived vesicles (e.g., Staehelin and Hepler 1996). However, recent evidence suggests that endocytosed material from the maternal plasma membrane may also contribute to the new dividing structure (Bolte et al. 2004; Dettmer et al. 2006; Dhonukshe et al. 2006). Irrespective of these new findings, it is clear that Golgi products are required for cell plate formation, a conclusion that is further supported by recent studies on Golgi stack partitioning.

Golgi stacks are randomly distributed throughout the cytoplasm during interphase (Nebenführ et al. 2000; Seguí-Simarro and Staehelin 2006) and double in number during G2 phase (Seguí-Simarro and Staehelin 2006). In larger cells that contain large numbers of Golgi stacks, such as the highly vacuolated tobacco BY-2 cells, these stacks start to accumulate in an equatorial ring underneath the thinning PPB (Dixit and Cyr 2002; Nebenführ et al. 2000). This accumulation, termed the “Golgi belt” (Fig. 1), fully develops during pro-metaphase and is specific for this organelle since mitochondria do not accumulate in this region (Nebenführ et al. 2000). The Golgi belt is not found in meristematic cells of the *Arabidopsis* shoot meristem (Seguí-Simarro and Staehelin 2006) which contain fewer stacks and may also impose spatial constraints on organelle distribution due to their smaller size. The Golgi belt continues to mark the future division site after disappearance of the PPB which has led to the speculation that these stacks are involved in preparing the cortical division site for insertion of the cell plate (Nebenführ et al. 2000). Contrary to this prediction it was found that disruption of Golgi stacks with brefeldin A (BFA) did not inhibit insertion of the cell plate in this area (Dixit and Cyr 2002). However, it has to be noted that cell-plate insertion is also possible at non-division sites (Mineyuki and Gunning 1990), in other words, secretion from Golgi stacks to the PM at the division site may not be necessary for cell division, but may only facilitate some aspect such as maturation of the division wall. The unusual positioning of Golgi stacks in the Golgi belt at this stage of cell division clearly deserves further study to elucidate its function.

During metaphase, another accumulation of Golgi stacks becomes evident at the opposing poles of the metaphase spindle (Nebenführ et al. 2000). The density of stacks in close proximity to the spindle of BY-2 cells is approximately twice as high as in the rest of the cytoplasm. The function of this accumulation is again unknown, but has been linked to the presence of Golgi vesicles and products in the metaphase spindle (Hepler 1980; Sonobe et al. 2000) and a priming of the division area with cell plate building blocks (Nebenführ et al. 2000). During anaphase, Golgi stacks begin to appear in the interzone between the separating chromosomes but are excluded from the forming phragmoplast (Nebenführ et al. 2000).

Golgi stacks are prominently associated with the growing cell plate and accumulate around the phragmoplast as demonstrated by conventional EM in root tips (Whaley and Mollenhauer 1963), fluorescence microscopy of GFP-labeled stacks in BY-2 cells (Nebenführ et al. 2000) and EM serial sections in shoot meristems (Seguí-Simarro and Staehelin 2006). These stacks do not display a preferred orientation relative to the phragmoplast (Seguí-Simarro and Staehelin 2006), but are most likely involved in the delivery of secretory products to the phragmoplast. This association of Golgi stacks with the phragmoplast is not static but allows dynamic repositioning of the organelle as the cell plate expands (Nebenführ et al. 2000). It is not clear how long individual stacks remain in close proximity to the cytokinetic machinery. Golgi stacks are also often seen close to the maturing cell plate in late stages of cytokinesis and following completion of the cell wall (Kawazu et al. 1995; Nebenführ et al. 2000).

Golgi products have been tracked with anti-xyloglucan antibodies to fluorescently label the presence of hemicelluloses within BY-2 cells (Sonobe et al. 2000). Although direct evidence from EM labeling is not available, it is assumed that the signals generated in this way represent post-Golgi secretory vesicles. The random distribution of small spots found in interphase cells is first broken in metaphase when a diffuse staining of the metaphase spindle is detected. During anaphase, the signal appears as a broad band in the interzone between the chromosomes that gradually narrows until it finally, in telophase, is confined to a narrow line that corresponds to the cell plate (Sonobe et al. 2000). This distribution is consistent with the expected movement of Golgi vesicles along phragmoplast MTs to the division plane. Notably, the presence of hemicelluloses in the metaphase spindle supports the idea that Golgi stacks already produce cell plate precursors prior to cytokinesis and deliver these precursors to the spindle region where they are available for cell plate assembly as soon as the phragmoplast forms (Nebenführ et al. 2000).

2.3

Endosomes and Prevacuolar Compartments

As mentioned above, there is recent evidence that endocytic membrane traffic may contribute to cell plate formation. This is mostly based on the endocytic

tracer FM4-64, a lipophilic dye that partitions into the plasma membrane and is thought to be endocytosed and eventually delivered to the vacuole (Aniento and Robinson 2005; Bolte et al. 2004). Interestingly, FM4-64 prominently labels the region of the forming cell plate in cytokinetic cells (Bolte et al. 2004; Dettmer et al. 2006; Dhonukshe et al. 2006) suggesting that endocytic traffic in these cells is redirected to the forming cell plate. This conclusion appears to be supported by immuno-labeling of PM proteins and cell wall polysaccharides in the cell plate as well as small punctate structures that seem to colocalize with FM4-64 spots (Dhonukshe et al. 2006).

Curiously, FM4-64 label is found not only in small spots that likely represent endosomes but also throughout the metaphase spindle (Dhonukshe et al. 2006). It is not clear which membrane compartment is labeled in this case, although the ER shows a similar distribution. Some of the FM4-64 spots were also labeled with GFP-RabF2b (= Ara7) near the cell plate (Dhonukshe et al. 2006), a Rab protein that has been implicated in Golgi-to-vacuole traffic and localizes to prevacuolar compartments (PVCs) (Kotzer et al. 2004). It is unclear whether this partial colocalization of FM4-64 with a PVC marker represents a bifurcation of the endocytic pathway between a vacuolar and a cell plate branch. This finding, however, would suggest that PM-to-vacuole traffic is not completely blocked in dividing cells. Interestingly, PVCs or more specifically GFP-RabF2b-positive structures were also labeled with a YFP-2xFYVE construct that binds to phosphatidylinositol-3-phosphate (PI3P) in membranes (Vermeer et al. 2006). In dividing BY-2 cells this marker was found in areas that correspond to the phragmoplast (Vermeer et al. 2006).

Multi-vesicular bodies (MVBs) have been identified previously as PVCs (Tse et al. 2004), although it is not clear whether all MVBs are PVCs, or whether all PVCs are MVBs. However, their unique morphology makes it possible to identify MVBs unambiguously in the EM and this was exploited in a 3D reconstruction from serial sections of *Arabidopsis* meristem cells (Seguí-Simarro and Staehelin 2006). It was found that during interphase MVBs often are located in small clusters near Golgi stacks and during cytokinesis are also associated with the cell plate. The size of MVBs increases during cell division such that their volume quadruples. This volume increase coincides with the appearance of clathrin coated buds and vesicles on the cell plate, suggesting that these cell-plate associated MVBs are involved in targeting excess membrane to the lytic vacuole (Seguí-Simarro and Staehelin 2006).

It should be cautioned that the identity of fluorescently labeled compartments is not always known but only inferred from colocalization data at the LM level. Similarly, the composition and function of membrane compartments identified in the EM is often unclear and only predicted based on morphological similarity to known structures. An additional difficulty in this part of the endomembrane system is that all compartments are only temporary containers and can change their composition and hence identity as they mature. A better understanding of the endocytic/post-Golgi/pre-vacuolar

trafficking pathways is needed before we can assign definitive functions to any of these labeled structures and come to final conclusions about their role in cell plate formation.

2.4

Vacuole

The vacuole is, by volume, the largest organelle in mature plant cells and at the same time displays an enormous variability in shapes and structures (Higaki et al. 2006). In most dividing cells, the vacuole is much smaller and even decreases in volume during division (Seguí-Simarro and Staehelin 2006), but nevertheless is a prominent component of the cell. In effect, the absence of the vacuole from the center of the cell defines the “phragmosome”, the continuous cytoplasmic domain within which mitosis and cytokinesis occurs. Two recent studies have pursued complementary approaches to follow vacuole dynamics in two very different dividing cells. In the first study, fluorescent labeling of the tonoplast, the vacuolar membrane, was used to visualize vacuoles in 3D confocal reconstructions (Kutsuna et al. 2003). The second study used EM serial sections to visualize vacuole structure in *Arabidopsis* shoot meristem cells (Seguí-Simarro and Staehelin 2006).

Interestingly, both cell types displayed the formation of tubular extensions of the vacuole that surrounded the mitotic apparatus and connected the two parts of the vacuole across the phragmosome (Kutsuna et al. 2003; Seguí-Simarro and Staehelin 2006; Fig. 1). In meristematic cells the vacuole breaks down into smaller units around metaphase (Seguí-Simarro and Staehelin 2006), a feature that was not evident in BY-2 cells presumably due to the higher degree of vacuolation in the latter. However, during telophase the vacuoles of both cell types projected tubular extensions into the region surrounding the cell plate. These parts of the vacuole may be participating in the degradation of material that was removed from the maturing cell plate (see above).

2.5

Other Organelles: Peroxisomes, Mitochondria, and Plastids

Organelles outside the endomembrane system have received relatively little attention with respect to their dynamics during cell division. The most thorough study was conducted on immuno-labeled peroxisomes in dividing cells of the onion root tip and leek leaf epidermis (Collings et al. 2003). In this case it was found that peroxisomes, which are randomly distributed during interphase and up to metaphase, start to accumulate in the division plane in anaphase (Fig. 1). Interestingly, this accumulation preceded formation of a clear phragmoplast but coincided with an accumulation of actin filaments (Collings et al. 2003). This cluster of peroxisomes is then split into two layers

by the forming cell plate. As the ring-phragmoplast expands outward, the peroxisome clusters seem to trail behind and continue to remain closely associated with the maturing cell plate (Collings et al. 2003). The authors speculate that this localization of peroxisomes indicates the production of hydrogen peroxide radicals in the cell plate or a role of these organelles in membrane lipid recycling (Collings et al. 2003). However, it has to be cautioned that not all species accumulate peroxisomes near the cell plate to the same extent as onions and leek. In particular, the peroxisome accumulation is not as prominent in BY-2 cells and not detectable at all in *Arabidopsis* root tip cells (Collings et al. 2003). This suggests that organelle accumulations during cell division may reflect species-specific adaptations.

The distribution of mitochondria and plastids in dividing cells has not been studied in detail. Staining of these organelles with a fluorescent dye in tobacco BY-2 cells revealed that they accumulate in the phragmosome but largely are relegated to the periphery and don't approach the spindle apparatus closely (Nebenführ et al. 2000). This is particularly true for the larger plastids which are found mostly close to the vacuolar membrane. This pattern persists also during cytokinesis when some mitochondria can be found in close proximity of the phragmoplast but plastids are mostly confined to the area behind the re-forming daughter nuclei (Nebenführ et al. 2000). This pattern is also seen in EM images of the dividing cell (e.g., Seguí-Simarro and Staehelin 2006). The proximity of mitochondria to the cytokinetic apparatus may reflect the energy requirements of this machinery, while the plastids (at least in the non-photoautotrophic BY-2 cells) do not contribute to the cell division process.

3 Mechanisms of Organelle Positioning

While considerable attention has been paid to the role of the cytoskeleton in moving cell plate precursors through the phragmoplast to the division plane (Vanstraelen et al. 2006), relatively little information has been garnered on the mechanisms that lead to the specific positioning of organelles surrounding the mitotic and cytokinetic machinery. It is reasonable to assume that the cytoskeleton plays a major role in getting the organelles to their correct positions. In interphase cells, all organelles discussed so far can move along the actin cytoskeleton with the help of myosin motor proteins (Collings et al. 2002; Higaki et al. 2006; Kwok and Hanson 2003; Nebenführ et al. 1999; Runions et al. 2006; Ruthardt et al. 2005; van Gestel et al. 2002). However, all these rapid, saltatory motions come to a standstill during mitosis and all movements in dividing cells are much slower (Mineyuki et al. 1984). In addition, MTs have been found to bind organelles in interphase (Sonobe et al. 2000; van Gestel et al. 2002) and MT-based motors are known to be associated

with various organelles (e.g., Lu et al. 2005; Romagnoli et al. 2003). Thus, it is not possible to a priori predict which cytoskeletal system is being used to mediate the observed distribution of the different organelles.

The presence of tubular ER elements in the metaphase spindle and the phragmoplast is suggestive of an interaction of this organelle with MTs. Close apposition of ER membranes with spindle MTs (Hepler 1980) seems to support this notion. Disruption of MTs with oryzalin, unlike cytochalasin D treatment, does indeed lead to a redistribution of the ER in mitotic cells (Zachariades et al. 2003) but in addition leads to a dramatic rearrangement of cellular elements that make interpretation difficult.

The specific accumulation of Golgi stacks in certain regions of metaphase cells could not be disrupted by actin depolymerizing drugs (Nebenführ et al. 2000) suggesting that the actin cytoskeleton is not involved in anchoring them in specific areas. However, it should be pointed out that this kind of experiment does not rule out a role for actin tracks during delivery of Golgi stacks to these positions. Disruption of MTs with propyzamide also did not result in a loss of Golgi accumulation, although the segregation of mitochondria and plastids from Golgi stacks could be disrupted by additional mechanical force, i.e. by shaking of the treated cells (Nebenführ et al. 2000). This might indicate that MTs provide anchoring points for Golgi stacks. As for the ER, these results are difficult to interpret since removal of the metaphase spindle leads to a complete loss of normal cell architecture and structural integrity of the phragmosome.

A clear involvement of the actin cytoskeleton has been found for the positioning of two organelles, the vacuole and peroxisomes. In these cases, treatment with various actin-disrupting drugs (bistheonellide A, latrunculin B, or cytochalasin D) broke up the tubular extensions of the vacuoles seen during mitosis (Kutsuna et al. 2003) and prevented accumulation of peroxisomes in the division plane (Collings et al. 2003), respectively. In the latter case, the same result was obtained with the myosin inhibitor 2,3-butanedione monoxime (BDM) indicating that the accumulation of peroxisomes at the cell plate depends on myosin-driven movements (Collings et al. 2003).

The actin cytoskeleton also seems to play a role on a global scale in ensuring even distribution of organelles into the two daughter cells. Inheritance of mitochondria, chloroplasts, and ER is normally very even in cells derived from tobacco mesophyll protoplasts (Sheahan et al. 2004). However, disruption of actin filaments with latrunculin B resulted in many cells receiving only a small fraction of some organelles while disruption of MTs with oryzalin did not yield this effect (Sheahan et al. 2004). Thus, the actin cytoskeleton seems to be needed to position roughly equal numbers of organelles on both sides of the division plane. A complementary interpretation could be that actin is required for proper positioning of the division plane so that the cells are divided evenly. This interpretation is supported by the observation that alignment of the forming cell plate with the cortical division site in *Tradescatia* stamen

hair cells depends on the acto-myosin system (Molchan et al. 2002). Current data seem to suggest that both effects occur at the same time (Sheahan et al. 2004). However, a detailed spatio-temporal analysis of organelle distributions in actively dividing cells in the presence and absence of latrunculin B will be required to determine their relative contributions.

4

Outlook

Progress in recent years has demonstrated that many organelles assume non-random positions during cell division in a wide variety of plant cells. These specific accumulations indicate that these organelles are performing specific functions at these positions, which in some cases has led to new insights in the process of cell division. For example, the proximity of peroxisomes, multivesicular bodies, and vacuolar elements near the forming cell plate has resulted in new hypotheses that can now be tested experimentally. More research will also be necessary to elucidate the mechanisms that mediate this organelle positioning. In particular, precise surgical interventions will be required since the wholesale disruption of all MTs or all actin filaments have often proven too crude to identify specific localization mechanisms. Knowledge of these mechanisms then should allow us to disrupt positioning of specific organelles which in turn will directly address the function of these organelles during cell division.

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