Dynamics of the Plant Nuclear Envelope and Nuclear Pore[1]

The nucleus is the most prominent compartment of any eukaryotic cell and home to its genetic information. The nucleoplasm is surrounded by a double membrane system, the nuclear envelope (NE). The outer nuclear membrane (ONM) and the inner nuclear membrane (INM) are separated by the perinuclear space (or periplasmic space; Hetzer et al., 2005). The lipid bilayer of the ONM is continuous with the endoplasmic reticulum (ER), thus allowing for direct insertion of NE membrane proteins and translocation of proteins into the perinuclear space (Hetzer and Wente, 2009); however, the ONM protein composition differs from the ER (Hetzer et al., 2005). The INM has a distinct protein composition and specialized functions.

The INM and ONM are fused at specific sites to form aqueous pores. Inserted at these sites are the nuclear pore complexes (NPCs), large protein conglomerates responsible for the selective nuclear import and export of macromolecules (D'Angelo and Hetzer, 2008; Brohawn et al., 2009). Chromatin association with the nuclear pores and the NE is involved in gene activation and repression, respectively (Akhtar and Gasser, 2007; Kalverda et al., 2008; Capelson and Hetzer, 2009). In higher organisms, the NE plays a role in the dissociation and reformation of the nucleus during cell division (Kutay and Hetzer, 2008). Proteins that interact in the perinuclear space connect the nucleoplasm and cytoplasm through the NE, thereby transmitting information from the cytoskeleton and giving rise to nuclear mobility (Burke and Roux, 2009). Like the ER, the NE lumen acts as a repository of calcium, and ion transporters in both the ONM and INM are involved in signal transduction (Erickson et al., 2006; Bootman et al., 2009).

Together, the NE and NPCs are at the crossroad of communication between the nucleus and cytoplasm. Recent reviews have discussed the mechanism and relevance of nuclear import and export in plants (Merkle, 2009), the regulation of plant nuclear import in the context of signal transduction (Meier and Somers, 2011), and the plant NE during the cell cycle (Evans et al., 2011). Here, we focus on the dynamic organization of the NE and nuclear pore in quiescent and dividing plant cells.

COMPONENTS OF THE NUCLEAR PERIPHERY

The Nuclear Lamina

A mesh of intermediate filament proteins, the nuclear lamina, lines the mammalian INM. Lamins mediate the attachment of chromatin to the NE during interphase and chromatin detachment during mitosis (Gant and Wilson, 1997; Dechat et al., 2010). Lamin mutations cause a variety of human diseases that are collectively termed laminopathies (Andrés and González, 2009). Lamins have not been found outside the metazoan lineage; however, early electron microscopy and immunohistochemistry suggested a nuclear lamina and lamin-like proteins in plants (Galcheva-Gargova and Stateva, 1988; Li and Roux, 1992; McNulty and Saunders, 1992; Mínguez and Moreno Díaz de la Espina, 1993). In contrast, no lamin-coding genes were found in the complete plant genome sequences (Meier, 2007).

New ultrastructural studies now suggest that a lamina-like structure does indeed exist in plants. A meshwork of filaments underlying the inner NE in tobacco (*Nicotiana tabacum*) BY-2 cells was recently revealed, closely resembling the animal nuclear lamina both in terms of organization and filament thickness (Fiserova et al., 2009). The best candidates for plant lamin-like proteins are currently a family of coiled-coil proteins about twice the size of lamins but with similar overall structure. First identified as Nuclear Matrix Constituent Protein1 (NMCP1) in carrot (*Daucus carota*; Masuda et al., 1997), NMCP1-like proteins have been found in many plant species, and some localize exclusively to the nuclear periphery (Moriguchi et al., 2005; Fig. 1A). Mutants in two NMCP1-related proteins in Arabidopsis (*Arabidopsis thaliana*), LITTLE NUCLEI1 (LINC1) and LINC2, have reduced nuclear size and changes in nuclear morphology, suggesting an involvement in plant nuclear organization (Dittmer et al., 2007).

It is conceivable that NMCP1-like proteins or other, unknown proteins form a lamina-like protein meshwork underneath the plant NE. It will be well worth unraveling the function of plant lamin-like proteins, given the exciting emerging connection between the animal nuclear lamina and gene regulation (see below).

Nuclear Envelope Proteins

Proteins of the animal INM have been related to several human genetic diseases (Ellis, 2006; Worman

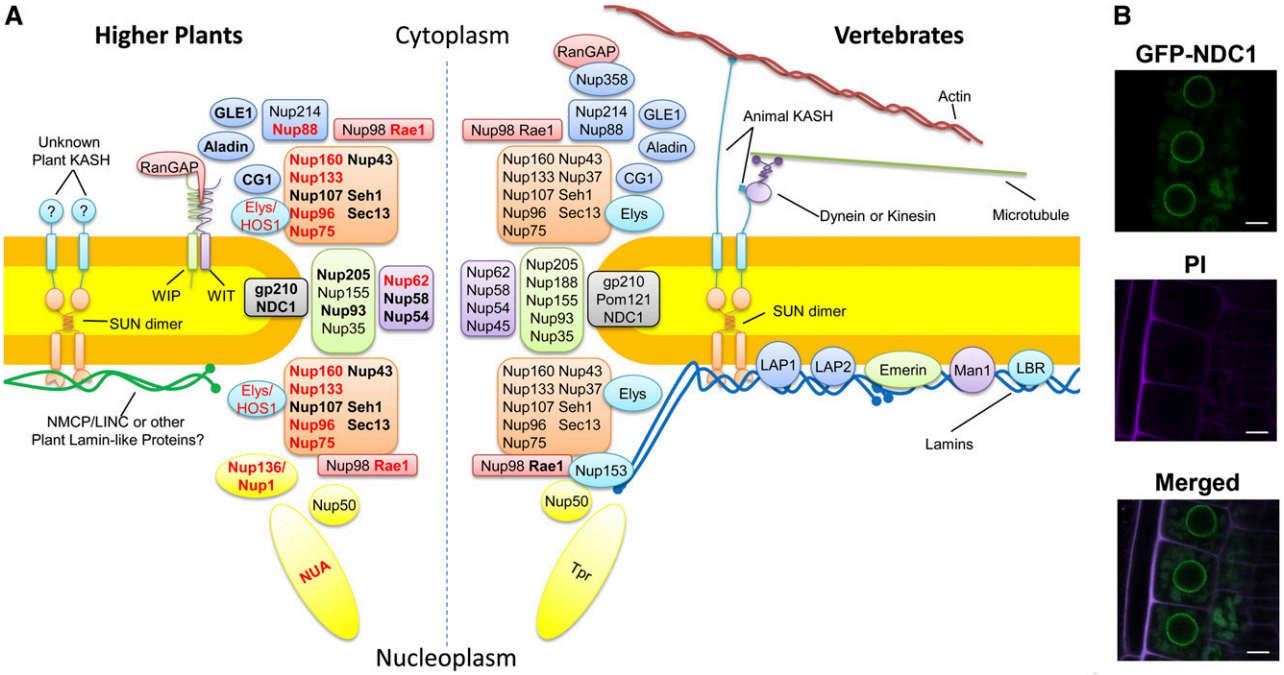

Figure 1. Identified NE and NPC components in higher plants and vertebrates. A, Comparison of the NE and NPC components between higher plants and vertebrates. Subcomplexes are grouped in single units. Units in contact indicate confirmed interactions. The NPC organization is modified after Tamura et al. (2010). In the higher plant NPC, boldface protein names indicate confirmed NE localization. Mutant phenotypes have been reported for the plant Nups indicated in red. Mammalian Nups, Nup358, Nup188, Nup37, Nup97, Nup45, and Pom121, appear to have no counterparts in plants. The positioning of plant Nups is based on their vertebrate counterparts. B, NE localization of putative Arabidopsis NDC1 in Arabidopsis root tip cells. Cell walls were counterstained with propidium iodide (PI). Bars = 5 μm.

and Bonne, 2007; Wheeler and Ellis, 2008). They include Lamin B Receptor (LBR), Lamina-Associated Polypeptide1 (LAP1), the LEM (for LAP2, Emerin, MAN1) domain protein family, as well as the Spindle Architecture Defective1/UNC84 (SUN) domain proteins (Wilson, 2010). Proteome analyses have added more proteins that have not yet been functionally investigated (Schirmer and Gerace, 2005). Surprisingly, very few INM proteins have homologs in plants.

There is no plant LBR, but a GFP-LBR fusion protein is located at the plant INM, suggesting that the INM targeting signal is conserved (Irons et al., 2003). The first bona fide plant INM proteins have recently been reported in Arabidopsis and maize (*Zea mays*; Graumann et al., 2010; Murphy et al., 2010; Graumann and Evans, 2011; Oda and Fukuda, 2011). While the maize genome encodes at least five different SUN domain proteins, there are only two of them in the Arabidopsis genome. AtSUN1 and AtSUN2 are the Arabidopsis homologs of animal and yeast INM proteins containing a conserved SUN domain. In animals, SUN proteins interact in the perinuclear space with KASH domain proteins (located at the outer NE) to form protein bridges that connect the nucleus to the cytoplasmic cytoskeleton. SUN-KASH protein bridges are involved in attaching centrosomes to the nuclear periphery, the alignment of homologous chromosomes, and their pairing and recombination in meiosis. They have been implicated in the regulation of apoptosis, the maturation and survival of the germline, nuclear location, and human diseases such as laminopathies and Emery-Dreifuss muscular dystrophy (Burke and Roux, 2009; Fridkin et al., 2009; Hiraoka and Dernburg, 2009).

AtSUN1 and AtSUN2 form dimers and are located at the INM in tobacco BY-2 cells (Graumann et al., 2010) and at the NE in different cell types of Arabidopsis plants (Oda and Fukuda, 2011). Their only currently known in planta role is an involvement in root hair nuclear shape. Nuclei in mature root hairs, which are normally elongated, appear round in the mutant, suggesting an involvement of plant SUN proteins in nuclear morphology. No KASH proteins are known in plants; thus, it is of great interest to identify plant interaction partners of SUN proteins.

There are now a significant number of proteins available to serve as markers for NE dynamics in plants: NMCP1/2 (LINC1/2), SUN1/2, WPP DOMAIN-INTERACTING PROTEIN1 (WIP1)/2/3, WPP DOMAIN-INTERACTING TAIL-ANCHORED PROTEIN1 (WIT1)/2, and Nuclear Pore Anchor (NUA; Dittmer et al., 2007; Jacob et al., 2007; Xu et al., 2007a, 2007b; Zhao et al., 2008; Graumann et al., 2010; Fig. 1A). Together with the nucleoporins (see below), this should allow for the first thorough investigation of the order of disassembly/reassembly of plant NE/NPC components, similar to the impressive studies performed in

other model organisms (Onischenko et al., 2009). In addition to dual and multicolor labeling for real-time imaging, the requirement of individual proteins, protein families, and protein domains for the dynamic behavior of other NE/NPC components can now be tested.

NPCs

NPCs are 40- to 60-MD multiprotein complexes embedded in the NE and involved in the nucleocytoplasmic trafficking of macromolecules. They consist of multiple copies of about 30 different nucleoporins (Nups) organized in a structure of 8-fold symmetry (Brohawn et al., 2009; Brohawn and Schwartz, 2009; Elad et al., 2009). The actual transport barrier in the core is composed of unfolded, hydrophobic repeat regions (FG repeats) of FG-Nups, which bind to shuttling transport receptors moving through the NPC (Frey et al., 2006; Frey and Görlich, 2007; Jovanovic-Talisman et al., 2009). For recent reviews on the different models of passage through the nuclear pore, see Wälde and Kehlenbach (2010) and Kahms et al. (2011).

For many years, plant biologists have relied on high-resolution images of yeast and vertebrate NPCs and on one early study of the plant NPC (Roberts and Northcote, 1970). An in-depth view of the tobacco BY-2 cell and onion (*Allium cepa*) NPC structure and organization has recently been provided, demonstrating that the plant NPC closely resembles the known yeast and vertebrate NPCs (Fiserova et al., 2009). Plant NPCs appear to be surprisingly densely spaced (approximately 50 NPCs μm^{-2} compared with 60 NPCs μm^{-2} for *Xenopus laevis* oocytes, considered very rich in NPCs). Interestingly, the NPCs are not randomly distributed but rather aligned in rows, similar to other higher eukaryotes but different from yeast (Belgareh and Doye, 1997; Maeshima et al., 2006).

Several proteins with significant similarity to animal and yeast Nups have been identified in forward genetic screens for diverse pathways. In addition, reverse genetic approaches with Nup homologs have been performed (Zhang and Li, 2005; Dong et al., 2006; Kanamori et al., 2006; Jacob et al., 2007; Saito et al., 2007; Wiermer et al., 2007; Xu et al., 2007b; Zhao and Meier, 2011). In general, however, it has proven difficult to assign plant Nup identity solely based on sequence similarity.

A comprehensive proteomic study of the Arabidopsis nuclear pore has now added several additional plant Nups (Tamura et al., 2010). Using nuclear pore-associated GFP-Rae1 as their starting point, the authors performed a series of immunoprecipitations coupled with mass spectrometry, added more thorough sequence similarity searches, and identified together eight known and 22 novel Nups (Fig. 1A). Only the homologs for human Nup358, Nup188, Nup153, Nup45, Nup37, NUCLEAR DIVISION CYCLE1 (NDC1), and Pore membrane protein121 (Pom121) were absent in both the immunoprecipitations and the genome data.

A candidate for Arabidopsis NDC1, however, had been proposed by Stavru et al. (2006). AtNDC1 (At1g73240) has sequence similarity to yeast Ndc1p and is predicted to contain six transmembrane domains shared by all NDC1 proteins (Stavru et al., 2006). When fused N terminally to GFP, AtNDC1 is localized at the NE in Arabidopsis root tip cells (Fig. 1B), thus adding AtNDC1 to the list of likely Arabidopsis Nups (Fig. 1A).

An FG-Nup identified both as Nup136 (Tamura et al., 2010) and as Nup1 (Lu et al., 2010) appears to be unique to plants. Its cell cycle dynamics include dispersal at metaphase, accumulation around the chromosomes in late anaphase/early telophase, and reestablishment at the NE in late telophase. Nup136 mutants have complex developmental phenotypes reminiscent of other Nup mutants (Zhang and Li, 2005; Parry et al., 2006; Xu et al., 2007b; Zhao and Meier, 2011). Together, Tamura et al. (2010) provide a copious amount of new and confirmatory data about the plant NPC that have the potential to spark a much-needed systematic, multiprong functional investigation of the plant nuclear pore.

DYNAMIC INTERACTION OF CHROMATIN WITH THE NE AND NPC

Electron micrographs have long shown that heterochromatin accumulates under the NE, with gaps at the NPCs, while euchromatin is more centrally localized. This is true for most higher eukaryotes, including plants (Solovei et al., 2009). Large areas of gene-poor chromatin in humans are associated with the nuclear lamina (lamina-associated domains [LADs]). Thousands of genes are present in LADs in a low-density arrangement, and most genes within LADs have very low expression levels (Guelen et al., 2008). The mammalian histone deacetylase HDAC3 accumulates at the nuclear periphery, binds to lamina-associated proteins, and induces histone deacetylation (Somech et al., 2005). Histone methylation marks involved in silencing are enriched at the NE (Yokochi et al., 2009). Depletion of lamins causes the large-scale misregulation of gene expression (Malhas et al., 2007). Several transcription factors directly interact with proteins of the nuclear lamina. The transcription factor Oct1, for example, binds Lamin B1 and is enriched at the NE, dependent on Lamin B1. In a Lamin B1 mutant, the expression of Oct1-dependent genes is deregulated, suggesting that the physical association of Oct1 with lamins is involved in gene regulation (Malhas et al., 2009; Malhas and Vaux, 2009). Interestingly, artificial tethering of genes to the NE has resulted in the repression of some, but not all, tested genes, suggesting that while the NE environment can be sufficient to repress genes, active transcription also can occur at the NE (Finlan et al., 2008; Kumaran and Spector, 2008; Reddy et al., 2008).

In contrast to the NE, the NPC has been recognized as a site of transcriptional activation (Gerber et al.,

2004; Akhtar and Gasser, 2007). In yeast, a connection between the chromatin-bound Spt-Ada-Gcn5 acetyltransferase (SAGA) transcriptional coactivator complex, the nuclear pore protein Mlp1, and the RNA export complex TREX-2 (also known as the Thp1-Sac3-Cdc31-Sus1 complex) is implied in this activation. The SAGA histone acetyl transferase component Gcn5, the plant Mlp1 homolog NUA, and subunits of TREX-2 have all been identified in Arabidopsis, making it worthwhile to test if a similar connection might be involved in regulating plant gene expression (Stockinger et al., 2001; Xu et al., 2007b; Lu et al., 2010; Yelina et al., 2010). Nucleoporins are bound to hundreds of genomic sites, as identified by chromatin immunoprecipitation experiments and fusion of Nups to micrococcal nuclease (Schmid et al., 2006; Capelson et al., 2010; Vaquerizas et al., 2010; Wälde and Kehlenbach, 2010). Genes associated with Nups are typically highly to moderately expressed, in contrast to the LAD-located genes. Nups also contact chromatin away from the NPC, and interactions with the most highly active genes actually occur in the nucleoplasm (Kalverda and Fornerod, 2010; Kalverda et al., 2010).

The rich and growing evidence on the regulation of gene expression by both NE and NPC components should encourage the plant community to also investigate this so far untouched question in plant model systems. Specifically, addressing whether the putative lamin-like plant proteins affect gene expression, investigating the spatial distribution of histone marks and of gene-rich and gene-poor areas of the genome, and testing Nup-chromatin interactions could open up a new area of investigation into the spatial organization of gene expression in plants.

DUAL ROLES OF NE COMPONENTS DURING MITOSIS

Plants, like all higher eukaryotes, undergo open mitosis when the NE breaks down and the separation of the nucleoplasm from the cytosol vanishes, until the NE reforms after a cell completes division. A cell needs to accurately segregate not only the genetic material and all the organelles but also the NE membranes with its specific protein components. According to the ER-retention model (Collas and Courvalin, 2000), some NE components are retained in the mitotic ER network during cell division, but numerous other ones localize to diverse mitotic structures and play crucial roles in consecutive stages of the division process (Rabut and Ellenberg, 2001; Griffis et al., 2004; Xu et al., 2008; Lee et al., 2009). Both the localization patterns and a variety of developmental phenotypes point to these functions.

Preprophase/Prophase

One of the canonical mitotic functions of the plant NE is to act as a microtubule (MT) organizing center (MTOC; Stoppin et al., 1994; Canaday et al., 2000). Plant cells undergo drastic MT array rearrangements during cell division, forming cortical and radial MTs, the preprophase band (PPB), the spindle, and phragmoplast structures. At the onset of mitosis, the cortical MTs depolymerize and rearrange into the PPB surrounding the nucleus. This initial cytoskeletal change is crucial for the fate of a dividing cell, since this transient MT array demarcates the future cortical division site, where a cell will separate into two daughter cells (Van Damme and Geelen, 2008; Müller et al., 2009). RanGAP1 is a NE-associated protein that is delivered to the PPB in an MT-dependent manner, and it remains associated with the cortical division site during mitosis and cytokinesis, constituting a continuous positive marker of the plant division plane (Xu et al., 2008). RanGAP1 is thus a molecular landmark left behind by the PPB, which later guides the phragmoplast and the forming cell plate, since the silencing of RanGAP1 in Arabidopsis roots leads to mispositioned cell walls similar to other mutants with division plane defects (Smith et al., 2001; Xu et al., 2008). At this stage, another NE-associated protein, Rae1, is targeted to the PPB (Lee et al., 2009; Fig. 2). This localization of Rae1 reflects its association with mitotic MTs throughout mitosis as well as at least partial involvement of the PPB in spindle assembly, since the RNA interference inhibition of *Nicotiana benthamiana* Rae1 (NbRae1) in BY-2 cells led to the formation of disorganized or multipolar spindles and defects in chromosome segregation (Lee et al., 2009). Indeed, in plants, the PPB marks the plane perpendicular to the axis of symmetry, the spindle (Lloyd and Chan, 2006). The PPB is linked to and cross-communicates with the nucleus through bridging MTs, which partly mediates the establishment of the bipolarity of a cell and the central positioning of the nucleus (Granger and Cyr, 2001; Ambrose and Wasteneys, 2008). This arrangement facilitates the formation of the prophase spindle perpendicular to the PPB.

At this stage, the NE, acting as an MTOC, promotes the nucleation of MTs on its surface (Stoppin et al., 1994, 1996; Canaday et al., 2000). An essential factor of the MT-nucleating complex is the γ-tubulin ring complex, which is conserved among the kingdoms (Schmit, 2002). In mammals, the minimal complex functioning as an MTOC is composed of γ-tubulin, γ-TUBULIN COMPLEX PROTEIN2 (GCP2), and GCP3, which all have orthologs in the Arabidopsis genome (Canaday et al., 2004). Besides their sequence similarity, γ-tubulin, AtGCP2, and AtGCP3 were detected in the same complex in vivo, localized at the NE and the cell cortex, and were required for MT nucleation in Arabidopsis, corroborating the conserved function of the plant γ-tubulin ring complex (Erhardt et al., 2002; Seltzer et al., 2007). Interestingly, a nuclear rim-associated fraction of histone H1 was shown to have MT-organizing activity in BY-2 cells and to promote MT nucleation through the formation of complexes with tubulin and the elongation of radial MTs (Hotta et al., 2007; Nakayama et al., 2008; Fig. 2). Recently, a biophysical interaction between Ran and histone H1 and their colocalization at the nuclear

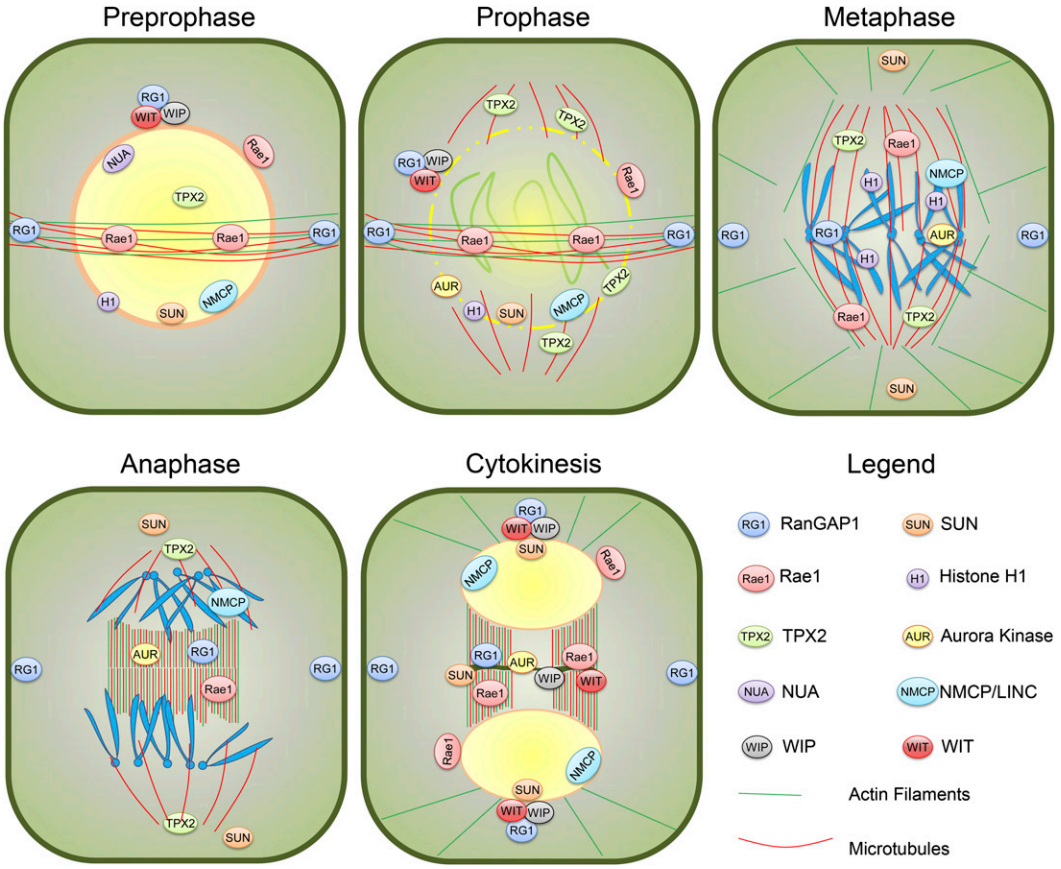

Figure 2. Mitotic locations of NE-associated proteins. See text for details.

rim have indicated a possible role for histone H1 in the organization of MTs adjacent to the NE in *Leishmania donovani* (Smirlis et al., 2009).

Prior to the disappearance of the PPB in plant prophase, a rapid NE breakdown occurs (Dixit and Cyr, 2002). Both processes seem to require phosphorylation events carried out by a cyclin-dependent kinase (CDK) and its regulatory protein, cyclin B (CYCB). The CDK/CYCB complex promotes PPB disassembly in plants (Hush et al., 1996), the depolymerization of nuclear lamins in vertebrates, *Caenorhabditis elegans*, and yeast (Nigg, 1992; Daigle et al., 2001; Galy et al., 2008), and the disassembly of nucleoporins in animal cells (Macaulay et al., 1995; Favreau et al., 1996). This mitotic phosphorylation releases lamins and some nuclear membrane and nuclear pore proteins, enabling progression through the NE breakdown. Among plant nuclear pore proteins with dynamic mitotic relocalization, there is, for instance, NUA (the Arabidopsis homolog of Tpr/Mlp1/Mlp2/Megator; Jacob et al., 2007; Xu et al., 2007b) and Rae1 (Lee et al., 2009; Fig. 2).

Metaphase

The Ran gradient controls the spindle assembly in animal cells. High concentrations of RanGTP around chromosomes (and high RanGDP concentration at the cell periphery) attract importins and release nuclear localization signal-containing cargo proteins (Dasso, 2001; Weis, 2003). These cargos are, for instance, spindle assembly factors, such as targeting protein for Xklp2 (TPX2), Rae1, and NuMA (for Nucleus and Mitotic Apparatus; Carazo-Salas et al., 1999; Kaláb et al., 1999, 2006; Ohba et al., 1999; Wilde and Zheng, 1999; Wiese et al., 2001; Caudron et al., 2005). Arabidopsis TPX2 is nuclear in interphase, but it is actively exported in prophase, enriched around the NE, and then accumulates in the vicinity of the prospindle (Vos et al., 2008; Fig. 2). After its release from importin-dependent inhibition, TPX2 promotes spindle formation around chromosomes through MT nucleation (Gruss and Vernos, 2004; Vos et al., 2008). Simultaneously, human TPX2 targets Aurora A to the spindle and activates it (Bayliss et al., 2003; Gruss and Vernos, 2004; Kawabe et al., 2005; Vos et al., 2008). In plant and animal cells, the coordination of chromosomal and cytoskeletal events in mitosis is partly mediated by the chromosomal passenger complex. Aurora kinases (in Arabidopsis, Aurora1 and -2) are thought to play this role through mediating the positioning information of the PPB to the formation of the bipolar prophase spindle (Carmena and Earnshaw, 2003; Vagnarelli and Earnshaw, 2004; Demidov et al., 2005). At the onset of

prophase, AtAurora1 and AtAurora2 are associated with the ONM and then gradually migrate to the poles of the prospindle as mitosis progresses (Demidov et al., 2005; Fig. 2).

Tobacco NbRae1, a homolog of Rae1/mrnp41 in metazoans, Gle2p (for GLFG lethal 2p) in *Saccharomyces cerevisiae*, and Rae1 in *Schizosaccharomyces pombe*, exhibits a mitotic function besides its role as an mRNA export factor associated with the NPC (Whalen et al., 1997; Pritchard et al., 1999; Griffis et al., 2004; Lee et al., 2009). Mammalian Rae1 is a mitotic spindle checkpoint component in conjunction with Bub3 and forms a complex with Nup98 and the Cdh1-activated anaphase-promoting complex, preventing the degradation of Securin before anaphase (Whalen et al., 1997; Babu et al., 2003; Jeganathan et al., 2005). NbRae1 associates with the spindle and was shown to function in the proper spindle organization and chromosome segregation (Lee et al., 2009; Fig. 2). NbRae1 silencing resulted in delayed progression of mitosis, which led to plant growth arrest, reduced cell division activities in the shoot apex and the vascular cambium, and increased ploidy levels in mature leaves. Together, these results suggest a conserved function of the Rae1 proteins in spindle organization among eukaryotes, which is distinct from their roles at the interphase NE.

In metaphase, while histone H1 relocalizes along the condensed chromosomes (Nakayama et al., 2008), Aurora3 and -1 are associated with centromeric regions of chromosomes (Demidov et al., 2005; Kawabe et al., 2005) and RanGAP1 localizes to kinetochores and the spindle (Joseph et al., 2002; Xu et al., 2008). Mammalian RanGAP1 is targeted to kinetochores in a SUMO-dependent manner (Joseph et al., 2002, 2004). Thus, it remains enigmatic how Arabidopsis RanGAP1, which lacks the SUMOylation domain, is targeted to kinetochores. In view of human RanGAP1, found only on the attached sister chromatids (Joseph et al., 2004), the exact timing of kinetochore association and the function of plant RanGAP1 at this cellular location remains to be verified.

Recently, the cell cycle dynamics of *Apium graveolens* NMCP1 and NMCP2 (AgNMCP1 and AgNMCP2) were investigated (Kimura et al., 2010). Both proteins associate with the NE in interphase, disassemble simultaneously during prometaphase, and reaccumulate around the reforming nuclei (Fig. 2). However, while AgNMCP1 was mainly localized to the spindle and accumulated on segregating chromosomes, AgNMCP2 dispersed in the mitotic cytoplasm in vesicular structures that could be distinguished from the bulk endomembrane system. This vesicular signal might represent the NE membranes absorbed into the ER network upon NE breakdown.

Two Arabidopsis homologs of the spindle pole body protein Sad1 were initially discovered in a survey for cytokinesis-related genes (Hagan and Yanagida, 1995; Van Damme et al., 2004). These Arabidopsis SUN domain proteins are NE markers in plants (Graumann et al., 2010). Oda and Fukuda (2011) and Graumann and Evans (2011) carefully followed the localization dynamics of both proteins through the cell cycle using transgenic Arabidopsis plants and stably transformed BY-2 cells, respectively. Both groups reported the localization of SUNs in mitotic ER membranes and an asymmetric reassociation with the decondensing telophase chromatin, with an envelope-like structure first appearing at the surface next to the spindle poles and a delayed reappearance of the envelope at the surface close to the phragmoplast (Fig. 2). This might indicate that NE assembly lags behind at the phragmoplast-proximal surface of the daughter nuclei, and potentially this area remains open longer to nonrestricted exchange between nucleus and cytoplasm. Alternatively, because SUN1/2 are nuclear proteins, it might indicate that nuclear pores at the phragmoplast-proximal surface lag behind in regaining full import capacity. These scenarios can be distinguished by also following ONM and NPC proteins as well as generic markers for active nuclear import.

Anaphase/Telophase

As chromosomes migrate to opposing spindle poles, a plant-specific MT structure, the phragmoplast, is formed to allow the completion of cell division through the assembly of a new cell wall between the separating sister nuclei (Verma, 2001; Jürgens, 2005). Besides the proteins involved in vesicular trafficking and fusion (for review, see Van Damme and Geelen, 2008), some NE-associated proteins have been found to mark the phragmoplast and/or the cell plate as well. The localization of Rae1 and SUN1/2 at the cell plate (and the phragmoplast for Rae1; Fig. 2) suggests a tight linkage between the NE components and the cytoskeleton during mitosis. Thus, it would be of utmost interest to identify plant interactors of SUN proteins both at the NE and at the cell plate. Such data would shed more light on molecular bridges across the perinuclear space, linking the nucleoskeleton to the cytoskeleton, as well as on functions of NE proteins in cell division.

Apart from Rae1, other nuclear rim-associated proteins colocalize with SUNs at the cell plate as well. For instance, Arabidopsis ONM proteins, WIP1, WIP2, WIT1, and WIT2, are redistributed to the cell plate during cytokinesis (Patel et al., 2004; Xu et al., 2007a; Zhao et al., 2008; Fig. 2). Both WITs and WIPs are required for RanGAP1 anchoring to the NE in the root meristem, but only one of the protein families, either WIPs or WITs, is sufficient to target RanGAP1 to the NE in differentiated cells (Zhao et al., 2008). The cell plate localization of RanGAP1 (as well as its PPB and cortical division site association), on the other hand, is independent on both WIPs and WITs, suggesting that interphase and mitotic targeting of RanGAP1 require different mechanisms. Therefore, identification of the molecular players involved in RanGAP1 localization and function(s) during plant cell division would be of great importance.

OUTLOOK

Over the past years, much progress has been made in unraveling the molecular players residing at the nuclear periphery in animal, yeast, and plant cells. Numerous INM, ONM, as well as nuclear lamina and nuclear pore proteins have been brought to the stage via homology-based reverse genetics, forward genetics, or proteomics approaches. The NE components have been shown not only to separate the nucleoplasm from the cytosol and to constitute a selective barrier for nucleocytoplasmic transport but are also involved in nuclear mobility, signal transduction, chromatin attachment, and transcriptional activation and repression. Subcellular localization as well as thorough phenotypic analyses have delivered additional spatiotemporal information regarding NE-associated proteins. Namely, in plants, these molecular players have been implicated in such mitotic events as spindle assembly, chromosome segregation, MTOC-like function, cortical division site demarcation, and NE reformation upon cytokinesis. The concept of NE components having additional roles throughout cell division is fascinating but very challenging to dissect experimentally. Therefore, certain biological questions remain to be addressed. In vivo "fishing expeditions" using NE molecules as baits would possibly elucidate the protein interactors involved in particular processes of cell division as well as targeting mechanisms of these molecules to diverse cellular addresses. Furthermore, the precise dynamic localization of a given protein, and the order of disassembly/reassembly of plant NE/NPC components, could be tackled with high-resolution imaging techniques, such as multicolor confocal laser scanning microscopy, in-lens field emission scanning electron microscopy, and three-dimensional structured illumination microscopy.

ACKNOWLEDGMENTS

We thank Thushani Rodrigo-Peiris for help in generating the GFP-NDC1-expressing Arabidopsis line.

Received August 11, 2011; accepted September 23, 2011; published September 26, 2011.

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