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1 **The plant LINC complex at the Nuclear Envelope**

2

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4

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12

13

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15

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24 **Abbreviations and definitions:**

25

26 CDS: Cortical Division Site; The CDS is set up at the preprophase band and defines the attachment
27 site of the cell plate during cytokinesis. The CDS determines the future division plane of the cell.

28 CRWN: CRoWded Nuclei, formerly called Little Nuclei

29 ER: Endoplasmic Reticulum

30 γ -TURC: γ -Tubulin Ring Complex

31 GIP: GCP3-Interacting Protein

32 INM: Inner Nuclear Membrane

33 IPNC: International Plant Nucleus Consortium

34 KASH: Klarsicht /Anc1/Syne1 Homology

35 LAD: Lamina Associated Domain

36 LINC: LInker of Nucleoskeleton and Cytoskeleton; The LINC complex is bridging the nuclear
37 envelope and is made of KASH and SUN proteins.

38 MTOC: MicroTubule Organization Center; Plants lack centrosomes but instead develop nucleation
39 centres of microtubules at the nuclear envelope during cell division.

40 NE: Nuclear Envelope; The NE is a double membrane surrounding chromatin.

41 NMCP: Nuclear Matrix Constituent Protein

42 MT: MicroTubule

43 NEBD: Nuclear Envelope Break Down

44 NES: Nuclear Export Signal

45 NLS: Nuclear Localization Signal

46 NPC: Nuclear Pore Complex; NPC are channels involved in trafficking between nucleus and cytosol
47 and join INM and ONM.

48 ONM: Outer Nuclear Membrane.

49 PNS: Perinuclear Space at the Nuclear Envelope

50 PPB: Preprophase Band; The PPB is a dense ring of cortical microtubules that forms before the
51 prophase of mitosis.

52 RanGAP: Ran GTPase-Activating Proteins

53 rER: rough Endoplasmic Reticulum

54 SUN: Sad1/Unc84

55 TM domain: trans-membrane domain

56 WIP: tryptophan (W) – proline (P) – proline (P)-Interacting Protein

57 WIT: WPP domain–Interacting Tail-anchored

58

59 **SUMMARY**

60 Significant advances in understanding the plant nuclear envelope have been made over the past few
61 years; indeed knowledge of the protein network at the nuclear envelope is rapidly growing. One such
62 network, the Linker of Nucleoskeleton and Cytoskeleton (LINC) complex, is known in animals to
63 connect chromatin to the cytoskeleton through the nuclear envelope. The LINC complex is made of
64 Sad1/Unc84 (SUN) and Klarsicht/Anc1/Syne1 Homology (KASH) proteins which have been recently
65 characterized in plants. SUN proteins are located within the inner nuclear membrane, while the KASH
66 proteins are included into the outer nuclear membrane. SUN and KASH domains interact and bridge
67 the two nuclear membranes. In *Arabidopsis*, KASH proteins also interact with the WPP domain-
68 interacting tail-anchored protein 1 (WIT1), associated with the Nuclear Pore Complex and with
69 myosin XI-I which directly interacts with the actin cytoskeleton. Although evidence for a plant LINC
70 complex connecting the nucleus to the cytoskeleton is growing, its interaction with chromatin is still
71 unknown but knowledge gained from animal models strongly suggests its existence in plants. Possible
72 functions of the plant LINC complex in cell division, nuclear shape and chromatin organization are
73 discussed.

74

75 **An Overview of the Nuclear Envelope**

76 From the early beginning of research in genetics and cell biology, the nucleus has always been
77 a center of great interest because it includes most of the genetic material of the eukaryotic cell. While
78 its exact evolutionary origin remains uncertain, studies in *Archaea*, in which replication origins are
79 attached to the cell periphery, suggest that the genetic material, as in prokaryotes, was originally
80 attached to a membrane (Gristwood et al. 2012). To date, the origin of the nucleus cannot be resolved
81 as a specific event in the course of evolution. **Instead it** is best explained by the coevolution of up to 27
82 cell components, including pre-existing endomembranes, which have surrounded the chromatin and
83 created a specialized double membrane known as the Nuclear Envelope (NE) (Cavalier-Smith 2010).

84 At the structural level, the NE is made of a specialized Inner Nuclear Membrane (INM) and
85 Outer Nuclear Membrane (ONM) separated by a Perinuclear Space (PNS) of about 25-30nm. The NE
86 is in continuity with the Endoplasmic Reticulum (ER) and is interrupted by the nuclear pores (Figure
87 1A). Although the INM and ONM are continuous with each other and are fused together via the pore
88 membrane, they contain varying sets of proteins to fulfill different functions. The ONM is studded
89 with ribosomes similar to the rough ER (rER) and is involved in protein synthesis (Park and
90 Blackstone 2010). The ONM binds microtubules (MTs) and can act as a nucleation centre of
91 microtubules, which organize in Microtubule Organizing Centre (MTOC) at the basis of the mitotic
92 spindle during cell division (Zhang and Dawe 2011; Masoud et al. 2013). In animals, the INM
93 contains a set of proteins that interact with nuclear components including chromatin and the
94 nucleoskeleton to keep a close association between NE and nuclear content (Starr 2009; Bickmore
95 2013). The part of the nucleoskeleton associated with the INM is also referred to as lamina since in
96 animals it consists of lamin proteins. In plants, which lack lamin homologs, filamentous proteins are
97 thought to form this scaffold, which is assembled into the so-called plamina (Fiserova et al. 2009;
98 Fiserova and Goldberg 2010). Furthermore Dittmer et al. 2007 suggested that *Arabidopsis* CRoWded
99 Nuclei (CRWN, formerly Little NuClei) and their plant homologs Nuclear Matrix Constituent Proteins
100 (NMCP) may be part of the plamina based on their coiled-coil structures and their enriched
101 localization at the nuclear periphery (Masuda et al. 1997; Dittmer et al. 2007; Ciska et al. 2013).

102 While the NE provides a physical separation of the genetic material into the nucleus to
103 compartmentalize chromatin organization and function (Fransz and de Jong 2011), as well as
104 protection against external damage (Gross and Bhattacharya 2011), it constrains communication
105 between nucleus and the rest of the cell. This communication is integral to many vital processes. To
106 overcome this problem, various structural features and properties of the nuclear periphery have
107 evolved to allow exchange of molecules and signals as well as controlled access of cytoplasmic
108 components to chromatin and therefore mediate communication and connectivity between the nucleus
109 and the rest of the cell (Meier and Brkljacic 2009). Firstly, molecules such as proteins, RNA and
110 charged ions can be exchanged between cytoplasm and nucleoplasm by specialized regions traversing

111 the ONM and the INM formed by numerous Nuclear Pore Complexes (NPCs) (Tamura et al. 2010;
112 Boruc et al. 2012). This highly regulated nucleo-cytoplasmic transport across NPC can either occur by
113 passive diffusion (if the molecule is smaller than 40KDa) or involve an active transport machinery
114 (Keminer and Peters 1999). In the latter case, protein import from the cytosol into the nucleus then
115 requires a Nuclear Localization Signal (NLS) within the protein sequence while export of proteins
116 from the nucleus to the cytoplasm is mediated by nuclear export signal (NES). Additional nuclear
117 transport factors such as RanGAP convey directionality to the protein exchange (Meier and Brkljadic
118 2009). Secondly, while import of proteins is functional in interphase, cell division also requires access
119 of cytoplasmic components to chromatin. In open mitosis, this is accomplished by NE break down,
120 where the NE membranes lose their associations with nuclear components and the chromatin is
121 accessible to cytoplasmic molecules and structures such as the spindle microtubules (Evans et al.
122 2011).

123 [A third form of communication between nucleus and cytoplasm takes place by signaling](#)
124 [pathways](#). Ion channels and pumps are embedded in both INM and ONM and allow ions to be
125 imported within the nucleoplasm. To date only a few of these channels and pumps have been studied,
126 predominately those involved in Ca²⁺ signaling (Huda et al. 2013). Perinuclear calcium oscillations
127 have been found to play important roles during symbiotic interactions and are thought to trigger a
128 cascade of gene activation to help establish symbiotic interactions. While the *Arabidopsis* NE
129 proteome still needs to be probed for ion channels and pumps, examples of these have been
130 characterized in *Lotus japonicus* (Castor, Pollux), *Medicago truncatula* (Doesn't Make Infection 1,
131 DMI1) and *Solanum lycopersicum* (*Lycopersicon* Ca(2+)-ATPase 1; LCA1) (Huda et al. 2013).

132 Finally, recent evidence suggests that physical protein networks bridge the membranes of the
133 NE, similar to non-plant systems, to link nuclear components and chromatin to cytoskeletal and
134 cytoplasmic elements. Although these complexes are termed Linker of Nucleoskeleton and
135 Cytoskeleton (LINC), they also connect chromatin and other non-skeletal proteins. In animals and
136 fungi, however, their functions in nucleo-cytoskeletal linkage are better explored (Crisp et al. 2006).
137 These NE bridges consist of INM and ONM intrinsic proteins that interact with each other in the
138 periplasmic space. In plants, this area has received significant attention from research affording new
139 insights into the composition and function of *Arabidopsis* LINC complexes. This review will aim to
140 highlight the most recent advances with focus on LINC complex components and their roles in
141 forming NE protein networks, nuclei shape, cell division and their potential implication in chromatin
142 organization according to animal models.

143

144 **SUN and KASH domain proteins bridge the inner and the outer membrane of the NE**

145 LINC complexes involve specific protein components of the inner and outer nuclear
146 membrane. At the INM, the proteins that take part in this linkage are termed Sad1/UNC84 (SUN)

147 domain proteins, while the ONM proteins of the bridge are Klarsicht/Anc1/Syne1 Homology (KASH)
148 domain proteins. To complete the linkage, SUN proteins recruit nuclear components to the bridges
149 while KASH proteins interact with cytoplasmic components (Crisp et al. 2006; Starr 2011; Zhou and
150 Meier 2013).

151

152 **SUN domain proteins**

153 The SUN domain proteins were defined according to their homology to Sad1 from *Saccharomyces*
154 *pombe* and Unc-84 from *Caenorhabditis elegans*. SUN domain proteins are well conserved across all
155 eukaryotes and share at least three distinct properties. They localize to the INM, contain one or more
156 trans-membrane (TM) domains and a SUN domain (Starr 2009). [The SUN domain proteins vary in](#)
157 [size with the *C. elegans* UNC84 being one of the larger SUN proteins \(1111aa\), while yeast Sad1 and](#)
158 [the AtSUN1/AtSUN2 are respectively 514, 471 and 455 aa in size \(Haque et al., 2006; Graumann et](#)
159 [al., 2010\)](#). The mechanisms needed to target the integration of SUN domain proteins within the INM
160 are still largely unknown but according to data gained in yeast may rely on the TM domain, the NLS
161 and specific factors targeting these membrane-anchored proteins (Schuldiner et al. 2008). SUN
162 domain proteins can be divided into two sub-families according to the position of the SUN domain.
163 Cter-SUNs contain a SUN domain at the C-terminal part of the protein while the mid-SUN proteins
164 have a central (mid) SUN domain (figure 2A) (Graumann and Evans 2013a). In *Arabidopsis*, Cter-
165 SUNs are the most studied although mid-SUNs were described in other organisms from yeast to
166 human (Murphy et al. 2010; Sohaskey et al. 2010; Field et al. 2012; Friederichs et al. 2012). More
167 recently, mid-SUN domain proteins AtSUN3, AtSUN4 and AtSUN5 were also identified *in silico* in
168 *Arabidopsis* (Graumann and Evans 2013a) but their function still remains to be characterized.

169 *Arabidopsis* SUN1 and SUN2 are expressed in most tissues and organs ([Graumann et al. 2010](#)).
170 [The additional observation that double mutants severely effect reproduction \(D.E and C.T unpublished](#)
171 [data\) suggests that the two are essential genes](#). From the N- to C-termini, these two proteins include at
172 least four key features namely one NLS, a TM, a coiled-coil and a SUN domain (figure 2A). The TM
173 domain [allows](#) Cter-SUN proteins to be anchored within the INM with the N-terminus located in the
174 nucleoplasm, while the coiled-coil and SUN domain lie within the PNS (Graumann et al. 2010). Both
175 Cter-SUNs localize at the NE (figure 2B) and mutations in Cter-SUNs were associated with nuclear
176 shape modifications (figure 2C) (Zhou et al. 2012a). Their NE localization allows interactions with
177 themselves through the coiled-coil domain and with KASH proteins through the SUN domain (Zhou et
178 al. 2012a). Interaction between KASH and SUN domains implies that both domains are in close
179 proximity to the periplasmic face of the ONM (Burke 2012). The mid-SUN domain proteins were first
180 identified in maize as the plant-prevalent mid-SUN3 transmembrane (PM3) protein (Murphy et al
181 2010). In maize, ZmSUN3 and 4 mid-SUN proteins localise at the NE like Cter-SUN proteins, but
182 distinct topology models have been proposed for Cter- and mid-SUN proteins (Murphy et al 2010). In

183 contrast, in yeast, the Slp1 mid-SUN protein is located in the ER and was suggested to be involved in
184 the NE localization of the Cter-SUN protein Mps3 (Friederichs et al. 2012). Whether the *Arabidopsis*
185 mid-SUN proteins display similar ER localization to Slp1 or are true INM proteins as in maize
186 remains to be investigated.

187 It is interesting to note that both sub-families of SUN domain proteins are well conserved across
188 evolution (Murphy et al. 2010; Graumann et al. 2010; Field et al. 2012). Based on this high
189 evolutionary conservation, Cavalier Smith (2010) suggests their implication at the very beginning of
190 NE formation by linking the NE with chromatin. It is also tempting to speculate that only Cter-SUNs
191 may have the ability to interact with nucleoplasmic proteins through their N-terminal part while mid-
192 SUNs display a TM domain too close to the ends of the protein leaving only a very short tail into the
193 nucleoplasm (Figure 2A). As an example, the N-terminal domain of Sun-1 from *Dictyostelium* was
194 shown by chromatin immunoprecipitation and electrophoretic mobility shift assay to bind chromatin
195 and DNA, even though it does not contain any known DNA binding motif (Xiong et al. 2008). The
196 modes of interaction between SUN domain proteins and chromatin still remain to be investigated in
197 plants.

198

199 **KASH domain proteins**

200 The Klarsicht/Ancl/Syne1 Homology (KASH) domain proteins are C-tail anchored membrane
201 proteins found at the ONM. The KASH domain is made of a TM domain followed by 6-30 amino acid
202 residues and was first described in *Caenorhabditis elegans* (Starr and Han 2002). The KASH domain
203 is positioned in the periplasm, which places the KASH domain close to the ONM. The amino acid
204 sequence of the KASH domain is poorly conserved across kingdoms, apart from the penultimate
205 amino acid being a proline, which is essential in mediating the SUN-KASH interactions (Sosa et al.
206 2012). [In addition to the poorly conserved KASH domain, the proteins also vary tremendously in size](#)
207 [– from the “small” Nesprin 4 of approximately 40 kDa to the giant Nesprin 1 of 1000 kDa \(Razafsky](#)
208 [and Hodzic, 2009\)](#). Starr (2009) proposed four criteria to define KASH domain proteins. First, KASH
209 proteins are located at the ONM. Second, interaction between KASH and SUN requires the KASH
210 domain. Third, the ONM localization is dependent upon interaction between the KASH domain and
211 the SUN domain of SUN proteins (Crisp et al. 2006). The KASH domains are necessary and sufficient
212 for localization of the KASH proteins at the ONM. Fourth, their N-terminal domain is not conserved
213 and is located within the cytoplasm where many KASH proteins interact with components of the
214 cytoskeleton such as actin and dynein.

215 Recently, KASH proteins have been identified in *Arabidopsis*. They are called WPP
216 (tryptophan – proline – proline)-Interacting Protein (WIP) 1-3 (Zhou et al. 2012a) (figure 2A). These
217 three proteins are plant-specific and meet the KASH domain characteristics mentioned – they are
218 localized at the ONM (figure 2B), interact with the SUN domain and their ONM localization is

219 dependent on the SUN-KASH interactions. The last four amino acids of their KASH domains are
220 VVPT and thus include the cross-kingdom conserved penultimate proline. More importantly, this
221 motif has homologs in various plant species indicating that this class of plant-specific VVPT-KASH
222 proteins is conserved in plants (Zhou et al. 2012a; Zhou and Meier 2013). WIPs are able to interact
223 with the plant-specific WPP domain of WPP containing proteins including RanGAP. Interestingly,
224 deletion of Cter-SUN proteins causes loss of RanGAP association with the NE implying that in plants
225 LINC complexes are involved in nucleo-cytoplasmic transport. Another family of proteins to associate
226 with the WPP domain is the C-tail anchored WIT (WPP domain–Interacting Tail-anchored) protein
227 family. WITs interact with WIPs (Zhao et al. 2008) and are thereby associated with plant LINC
228 complexes. GFP-WIT1 localizes to the NE in a punctate (dotted) pattern indicative of an association
229 with nuclear pores (Zhao et al. 2008). However interaction of WIT1 with NPC components has not
230 been demonstrated so far. Interestingly, WIT1 also interacts with myosin XI-i connecting the SUN-
231 WIP-WIT complex with the actin cytoskeleton (Tamura et al. 2013). Finally, mutations in KASH
232 domain proteins induce nuclear shape alterations very similar to those observed for SUN domain
233 proteins (figure 2C) (Zhou et al. 2012a).

234 The function of WIP in RanGAP anchoring is specific to undifferentiated root tip cells (Xu et
235 al., 2007) and it remains unclear which RanGAP anchoring mechanisms are in place in other tissues.
236 However, tissue-specific expression of KASH proteins has also been observed in other higher
237 eukaryotes like for the human KASH proteins called Nesprins (Sosa et al. 2013). This may suggest
238 that other KASH proteins are likely to be discovered in plants in the future but this will remain
239 challenging because of the poor conservation of the KASH domain.

240

241 **Toward the existence of a Plant LINC complex**

242 The core of a LINC complex is made by interaction between the Cter-SUN and the KASH
243 domain proteins within the PNS. The structure has recently been resolved in animals using the human
244 SUN2 (hSUN2) and the human KASH proteins Nesprin 1 and 2 (Zhou et al. 2012b; Sosa et al. 2012).
245 hSUN2 organizes as trimers, a structure needed to allow hSUN2-KASH1/2 complexes to form. It is
246 then expected that a trimeric SUN2 complex anchored at the INM binds three KASH proteins
247 localized into the ONM. Homotrimers of hSUN2 form two distinct structures namely a stalk structure
248 made by an α -helix and a leaf-like structure formed by three β -sheet sandwiches (Zhou et al. 2012b;
249 Sosa et al. 2012). The stalk structure of the hSUN2 SUN domain is indeed a short coiled-coil domain
250 distinct from the classical larger coiled-coil domains found in most SUN domain proteins (see Sosa et
251 al. 2012 for more details). It is linked to the leaf-like structure, which is critical for the SUN-KASH
252 interactions (Zhou et al. 2012b; Sosa et al. 2012). In plants, both the SUN domain, which may also
253 include the short coiled-coil region (Oda and Fukuda 2011), and the classical larger coiled-coil domain
254 play a significant part in interactions among SUNs (Graumann et al. 2010). Furthermore, according to

255 sequence alignments between SUN domains, key amino acid positions such as S641 within the SUN
256 domain of hSUN2 are conserved in *Arabidopsis* SUN domain proteins and suggest LINC complexes
257 in plants with similar organization.

258 So far, all studies on LINC complexes in animals have focused on Cter-SUN proteins as the INM
259 components and only a yeast study has considered the putative role of the mid-SUN proteins. The
260 interactions between Cter-SUNs and mid-SUNs would provide evidence that mid-SUNs are secondary
261 components of the LINC complexes similar to WITs. With two Cter- and potentially three mid-SUN
262 domain proteins (SUN1-5) located at the INM and at least three ONM components (WIP1-3), plant
263 LINC complexes have the potential to be highly diverse in composition, available binding interactions
264 and thus function. Some of these protein connections, as well as functions of plant LINC complexes,
265 are presented below.

266

267 **Biological functions of plant LINC complexes**

268 The LINC complex has been proposed to play many different roles in animals such as
269 connecting the nucleoskeleton and the cytoskeleton through the NE, anchoring telomeres at the INM
270 to promote chromosome pairing, interacting with the centrosome during chromosome segregation or
271 participating in nuclear migration during development or in response to stress (Starr 2009; Starr 2011).
272 Many of these functions are still hypothetical in plants, but there is no doubt that the recent discovery
273 of SUN and KASH proteins in plants will give the opportunity to study the role of the LINC complex
274 in different aspects of nuclear function. Moreover, interactions between LINC components and
275 putative nucleoskeletal as well as DNA-associated components are currently being studied.

276

277 **The plant LINC complex and cell division**

278 One striking outcome is the central properties of these NE components during mitosis in
279 plants. Chromosome segregation during mitosis is driven by microtubules but unlike in animals,
280 microtubules are not organized by centrosomes. Instead, numerous MT nucleation sites containing the
281 conserved γ -Tubulin Ring complex (γ -TURC) are found at the cell periphery, at MT branching points
282 and the ONM (Masoud et al. 2013). The ONM is therefore instrumental in the formation of the mitotic
283 spindle (Shaw et al. 2003). In addition to the MT nucleation sites, plants have developed other cell
284 division - associated MT structures not found in animals and needed for cell division including the
285 pre-prophase band (PPB) before mitosis and the phragmoplast after mitosis (Meier and Brkljacic
286 2009; Rasmussen et al. 2013) (figure 3A).

287 The formation of the pre-prophase band is one of the earlier events [observed](#) in the process of
288 mitotic division. It marks the division plane and localizes where the new cell wall will be formed. As
289 this MT-based structure and the NE break down, the spindle poles and spindle start to form (Meier and
290 Brkljacic 2009; Rasmussen et al. 2013). Whether LINC complex components are involved in these

291 processes is currently unknown. Localization of SUN1 and SUN2 in punctate structures at the
292 beginning of mitosis might be an indicator of such involvement (figure 3). Also, it is known from
293 animal and yeast systems that SUN and KASH proteins are involved in anchorage of centromeres.
294 However, while in animal cells membranes are completely cleared from the mitotic spindle, in plants,
295 membranes traverse the spindle (Irons et al. 2003; Graumann and Evans 2011). Interestingly
296 *Arabidopsis* Cter-SUNs have been localized in these membranes (Graumann and Evans 2011) which
297 also appear to stay in close proximity to the segregating chromosomes (figure 3). In animals, SUN
298 proteins are one of the first INM proteins to re-associate with chromatin indicating they are important
299 in NE reformation. Similarly in plants, Cter-SUNs and WIPs are observed to display a dynamic
300 pattern during cell division. They first accumulate around chromatin next to the spindle pole, progress
301 from the spindle pole to the cell plate to finally surround the chromatin forming the new NE
302 (Graumann and Evans 2013b) (figure 3). A similar localization has been observed in dividing *Apium*
303 *graveolens* (celery) and *Allium cepa* (onion) cells for the nucleoskeletal NMCP, which is a homolog to
304 the *Arabidopsis* CRWN protein (Kimura et al. 2010; Ciska et al. 2013a). This kinetic of deposition
305 may suggest that plant LINC complexes are involved in establishing local connections between
306 chromatin and the reforming NE. However, NE-associated proteins that bind chromatin remain to be
307 discovered. Finally, LINC complex components and other NE proteins have also been observed at the
308 phragmoplast. This plant-specific structure consists of microtubules, microfilaments, and endoplasmic
309 reticulum elements (figure 3). The microtubules and actin filaments within the phragmoplast serve to
310 guide vesicles to build the new cell wall, which is seen at that stage between the two sister cells and
311 known as cell plate. Whether the NE proteins are functional at the phragmoplast remains questionable.
312 [The non-functional NE marker LBR-GFP targets](#) to the phragmoplast and the *Arabidopsis* Cter-SUN
313 proteins are highly mobile in this structure while they are not in the NE indicating no specific
314 interaction with other partners at the phragmoplast (Graumann et al. 2007; Graumann and Evans
315 2011).

316

317 **Plant LINC complexes and nuclear shape**

318 The nucleus has been considered by many researchers as a sphere sitting in the middle of the
319 cell. However, it is now well documented that some tissues and organs display nuclei with various
320 shapes, sizes and positions within the cell. Various plant model systems have been used to investigate
321 these variations like root hairs, hypocotyls, pollen tubes and epidermis including trichomes (Traas et
322 al. 1998; Chytilova et al. 2000). These variations in nuclear size and shape illustrate the dynamic or
323 even elastic properties of the NE. Clearly modifications in the structure and protein interactions at the
324 plant NE must occur to accommodate these changes but functions of NE components in these
325 processes remains poorly understood. To date both SUN and KASH domain proteins are among the
326 best-studied components of the plant NE. Currently, a new protein network is emerging at the NE. In

327 addition to SUN1-5, KASH (WIP1-3), WIT1-2 and myosin XI-I, at least 30 nucleoporins assembled at
328 the NPC have been identified (figure 4A).

329 To start addressing these questions, mutant analyses in *Arabidopsis* of some NE proteins
330 including LINC complex proteins has highlighted the occurrence of similar phenotypes. *sun1sun2*
331 (Cte-SUN mutant), *wip1wip2wip3* (KASH mutant) and *kaku1-1* (myosin XI-i mutant) alter nuclear
332 shape in root hairs and trichomes in which elongated nuclei become more rounded (Zhou et al. 2012b;
333 Tamura et al. 2013) (figure 4B). Conversely, over-expression of nup136, one of the plant
334 nucleoporins, induces elongated nuclei in guard cells (Tamura and Hara-Nishimura 2011). A small
335 nucleus phenotype was observed in *crwn1crwn2* (Dittmer et al. 2007). CRWN gene products are
336 proposed to be associated with the plamina, the nucleoskeletal structure underlying the INM. These
337 proteins are either core components of LINC complexes or associated with these, indicating that LINC
338 complexes are essential in maintaining nuclear shape. In addition to shape, myosin XI-i is also
339 responsible for mediating nuclear movement in root hairs as nuclei remain stationary in the mutant
340 (Tamura et al. 2013). Alterations in nuclear shape very reminiscent to the “ghost-like” phenotype
341 observed in animals for lamin mutants were also described for *gip1gip2* mutants (Janski et al. 2012).
342 GIP1 and 2 (GCP3-Interacting Protein1 and 2) are involved in microtubule assembly at the NE by
343 interacting with tubulin. This last observation may suggest that disruption of the microtubule
344 cytoskeleton network leads to modifications in plant cell morphogenesis including nuclear shape as
345 observed in the NE-associated mutants. The cytoskeleton is proposed to influence cell shape by
346 guiding the deposition of new cell wall polymers. Correct positioning of the microtubules at the NE is
347 also critical as in plants the NE is a microtubule organization center. Further investigations will be
348 needed to demonstrate that microtubule disorganization is responsible for the rounded nuclei
349 phenotype observed in NE-associated mutants.

350

351 **Future directions**

352 A new protein network including myosin XI-i, WIT, RanGAP, nucleoporins, KASH and SUN
353 proteins is now emerging (figure 4A). As a common theme, nuclear shape alterations have been
354 observed for most of the NE-associated mutants. Nuclear reshaping towards a more rounded shape
355 may suggest the release of a structural constraint such as those exerted by the cytoskeleton and this in
356 turn may alter gene expression by changing gene position within the nucleus (Versaevel et al. 2012).
357 However, this has not been formally demonstrated except for interaction between the actin
358 cytoskeleton and the myosin XI-i (Tamura et al. 2013). Other possible interactions with the
359 cytoskeleton might involve microtubules. Indeed although the *gip1gip2* double mutant displays
360 abnormal chromosome segregation with chromosome non-disjunction as expected for a component of
361 the mitotic spindle, it also induces alteration in NE shape (Janski et al. 2012). Why do spindle
362 associated proteins alter the nuclear shape? One attractive possibility would be that they are also part

363 of the NE protein network. Other partners of the mitotic spindle such as MAD2, BUB1 and BUBR3-1
364 which have been recently reviewed (Masoud et al. 2013) could also be part of the NE protein network
365 although to our knowledge no nuclear shape alterations have been recorded in mutant backgrounds for
366 those candidates. Thus, to study protein interactions of GIP, MAD2, BUB3.1 and BUBR1 (Caillaud et
367 al. 2009) with the NE-associated proteins described in this review will be of great interest. This may
368 reveal ancestral relationship between nuclear and mitotic components as hypothesized by Cavalier-
369 Smith 2010 and which may keep close together main components of the NE and chromatin during
370 nuclear break down.

371 Still, connections between the nucleoskeleton and chromatin remain largely hypothetical in
372 plants (figure 4A) while there is clear evidence in animals for interactions between the LINC complex
373 and the chromatin components through the lamins (Haque et al. 2010; Yang et al. 2013). To date
374 although there is no formal plant lamina, two lines of evidence argue in favor of its existence in plants
375 (Ciska and Moreno Díaz de la Espina 2013). First, Fiserova et al. 2009 described filament structures
376 connecting the NPC as well as 10 nm filaments within the nucleoplasm, two observations recalling the
377 lamin structure in animals. Second, *Arabidopsis* and plant homologs NMCP/CRWN were suggested to
378 be plant lamins based on their coiled-coil structures and their nuclear localization close to the NE
379 (Masuda et al. 1997; Dittmer et al. 2007; Ciska et al. 2013). Demonstration of plant analogs of the
380 lamins undoubtedly remains one of the key research issues on nuclear envelope during the next few
381 years.

382 Lamins are associated with up to 40% of the total chromatin of the human genome defining
383 the Lamina Associated Domain (LADs) (Bickmore 2013; Bickmore and van Steensel 2013). LADs
384 have been also identified in *Drosophila*, where they localize close to the NE and are relatively gene-
385 poor. Genes at the lamina are transcriptionally silent and late replicating (Pickersgill et al 2006),
386 characteristics common to heterochromatic domains. This suggests a more general role for the NE in
387 maintenance of transcriptionally silent chromatin domains such as pericentric and centric
388 heterochromatin (Vanrobays et al. 2013). These repetitive sequences can easily be visualized in
389 interphase nuclei in *Arabidopsis* as they are grouped in compact domains of chromatin called
390 chromocenters (Fransz et al. 2002). Thus it is expected that chromocenters will provide a valuable
391 chromatin marker to investigate the possible interaction between the NE and heterochromatin by
392 studying the possible effect of the NE-associated mutations described above on chromocenter features
393 such as their position within the nucleus.

394 Today's research on the NE brings together research from cell biology and chromatin
395 organization. Thanks to the International Plant Nucleus Consortium (IPNC) network formed in
396 Salzburg in 2012 at the Society for Experimental Biology Annual Main Meeting, these two research
397 communities are now actively collaborating to decipher the functions of the plant NE and its links to
398 chromatin.

399

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407

408 **FIGURE LEGENDS**

409

410 **Figure 1: The Plant Nuclear Envelope during interphase**

411 NE is made of two distinct membranes (green) called the Outer Nuclear Membrane (ONM) and the
412 Inner Nuclear Membrane (INM) forming the PeriNuclear Space (PNS). The ONM interacts with
413 microtubules (MT) in random organization except during cell division where MTs grouped together as
414 MicroTubule Organization Centers (MTOCs) to allow chromosome segregation (see also figure 3A).
415 The NE is interrupted by numerous Nuclear Pore Complexes (NPCs; orange) and is connected with
416 the rough Endoplasmic Reticulum (rER). The plamina (black) is the putative plant lamina. According
417 to the animal models, NE, NPCs and plamina are expected to interact with chromatin (purple) within
418 the nucleoplasm.

419

420 **Figure 2: SUN and KASH domain proteins**

421 **A) Schematic representation of protein structures.** Trans-membrane (TM), coiled-coil, SUN, WPP and
422 KASH domains are shown. The KASH domain includes both the TM and the plant-specific VVPT
423 motif (read arrow). **B) Nuclear Envelope localization of GFP-AtSUN1 and CFP-AtWIP1 in leaves.**
424 Scale bar=10 μ m. **C) Nuclear shape in SUN and KASH mutant backgrounds in leaf, trichome and**
425 **vascular tissues.** More rounded nuclei were observed in both mutant backgrounds and in all three
426 tissues. Tissues were stained with ethidium bromide. Scale bar=10 μ m.

427

428 **Figure 3: NE dynamics through the cell division**

429 **A) Keys features during plant cell division.** Only chromatin (purple), NE and ER (green),
430 microtubules (MT) (blue) and cell wall (brown) are indicated in this scheme. At the initiation of
431 mitosis, chromatin compaction starts and MT are reorganized in an annular band called the
432 PreProphase Band (PPB) just below the plasma membrane. The PPB disappears early during mitosis
433 but leaves the Cortical Division Site (CDS) defining the future division plane of the cell. At the NE,
434 MTs are also reorganized to the two opposite sides of the nucleus and formed MT Organization
435 Centers (MTOCs). During the Nuclear Envelope Break Down (NEBD), spindles are connecting the
436 chromosomes to ensure their segregation. During that stage, Cter-SUNs are observed in close
437 proximity to the chromosome (green spheres). NE is reforming around chromatin first facing the
438 spindle pole and finally proximal to the cell plate (green arrows). Finally, the cell plate (the newly
439 formed cell wall) is formed along the phragmoplast (blue) before fusion between the new and parental
440 cell wall. The cell plate is a disk-like structure bound at the CDS at cytokinesis and located at the
441 center of the phragmoplast which is a cytoskeletal structure including microtubules and actin.

442 **B) SUN protein during cell division.** BY2 cell expressing the SUN1–YFP (green) and the chromatin
443 marker histone H2B–CFP (magenta) through the cell cycle (redrawn from Graumann and Evans
444 2011). During the cell cycle SUN proteins remain always very close to chromatin. They accumulate in
445 the reforming NE at phragmoplast and cell plate. Scale bar=10 μm .

446

447 **Figure 4: Protein network at the Plant Nuclear Envelope**

448 **A) Protein interactions at the plant NE.** Known interactions (green circles) involving SUN, KASH,
449 WIT, RanGAP, Myosin and Actin cytoskeleton as described in the text. Hypothesized interactions
450 (yellow circles) include WIT and other NPC components (nups), nups and SUN with the plamina as
451 well as nups, plamina and SUN with chromatin. **B) Nuclear shape alterations in NE-associated**
452 **mutations.** Pictures were reproduced with permission from Tamura et al. 2013 (*kaku1-1*), Zhou et al.
453 2012 (*wip1wip2wip3* and *sun1sun2*), Tamura and Hara-Nishimura 2011 (*OEX-nup136*) and Sakamoto
454 and Takagi 2013 (*crwn1crwn2* also previously referred to as *linc1linc2* in Dittmer et al 2007).

455

456 **REFERENCES**

- 457 Bickmore WA (2013) The Spatial Organization of the Human Genome. *Annu Rev Genomics Hum*
458 *Genet* 14:67–84.
- 459 Bickmore WA, van Steensel B (2013) Genome Architecture: Domain Organization of Interphase
460 Chromosomes. *Cell* 152:1270–1284.
- 461 Boruc J, Zhou X, Meier I (2012) Dynamics of the Plant Nuclear Envelope and Nuclear Pore. *Plant*
462 *Physiol* 158:78–86.
- 463 Burke B (2012) It Takes KASH to Hitch to the SUN. *Cell* 149:961–963.
- 464 Caillaud M-C, Paganelli L, Lecomte P, Deslandes L, Quentin M, Pecrix Y, Le Bris M, Marfaing N,
465 Abad P and Favery B (2009) Spindle Assembly Checkpoint Protein Dynamics Reveal Conserved and
466 Unsuspected Roles in Plant Cell Division. *PLoS ONE* 4:e6757.
- 467 Cavalier-Smith T (2010) Origin of the cell nucleus, mitosis and sex: roles of intracellular coevolution.
468 *Biol Direct* 5:7–7.
- 469 Chytilova E, Macas J, Sliwinska E, Rafelski SM, Lambert GM and Galbraith DW (2000) Nuclear
470 Dynamics in *Arabidopsis thaliana*. *Mol Biol Cell* 11:2733–2741.
- 471 Ciska M, Masuda K and Moreno Díaz de la Espina S (2013) Lamin-like analogues in plants: the
472 characterization of NMCP1 in *Allium cepa*. *J Exp Bot* 64:1553–1564.
- 473 Ciska M and Moreno Díaz de la Espina S (2013) NMCP/LINC proteins: Putative lamin analogs in
474 plants? *Plant Signal. Behav.* 8:e26669.
- 475 Crisp M, Liu Q, Roux K, Rattner JB, Shanahan C, Burke B, Stahl PD and Hodzic D (2006) Coupling
476 of the nucleus and cytoplasm role of the LINC complex. *J Cell Biol* 172:41–53.
- 477 Dittmer TA, Stacey NJ, Sugimoto-Shirasu K, Richards EJ (2007) LITTLE NUCLEI genes affecting
478 nuclear morphology in *Arabidopsis thaliana*. *Plant Cell* 19:2793–2803.
- 479 Evans DE, Shvedunova M, Graumann K (2011) The nuclear envelope in the plant cell cycle: structure,
480 function and regulation. *Ann Bot* 107:1111–1118.
- 481 Field M, Horn D, Alford S, Koreny L and Rout MP (2012) Telomeres, tethers and trypanosomes.
482 *Nucleus* 3:0–8.
- 483 Fiserova J, Kiseleva E, Goldberg MW (2009) Nuclear envelope and nuclear pore complex structure
484 and organization in tobacco BY-2 cells. *Plant J* 59:243–255.
- 485 Fiserova J, Goldberg MW (2010) Relationships at the nuclear envelope: lamins and nuclear pore
486 complexes in animals and plants. *Biochem Soc Trans* 38:829.
- 487 Fransz P, de Jong H (2011) From nucleosome to chromosome: a dynamic organization of genetic
488 information. *Plant J* 66:4–17.

489 Franz P, De Jong JH, Lysak M, Castiglione MR and Schubert I (2002) Interphase chromosomes in
490 *Arabidopsis* are organized as well defined chromocenters from which euchromatin loops emanate.
491 Proc Natl Acad Sci U S A 99:14584–14589.

492 Friederichs JM, Gardner JM, Smoyer CJ, Whetstine CR, Gogol M, Slaughter BD and Jaspersen SL
493 (2012) Genetic Analysis of Mps3 SUN Domain Mutants in *Saccharomyces cerevisiae* Reveals an
494 Interaction with the SUN-Like Protein Slp1. *G3 Genes Genomes Genetics* 2:1703–1718.

495 Graumann K, Irons SL, Runions J, Evans DE (2007) Retention and mobility of the mammalian lamin
496 B receptor in the plant nuclear envelope. *Biol Cell Auspices Eur Cell Biol Organ* 99:553–562.

497 Graumann K, Runions J, Evans DE (2010) Characterization of SUN-domain proteins at the higher
498 plant nuclear envelope. *Plant J* 61:134–144.

499 Graumann K, Evans DE (2011) Nuclear envelope dynamics during plant cell division suggest
500 common mechanisms between kingdoms. *Biochem J* 435:661–667.

501 Graumann K, Evans DE (2013a) The nuclear envelope - structure and protein interactions. *Plant Nucl.*
502 *Struct. Genome Archit. Gene Regul.* WILEY-BLACKWELL, pp 19–55

503 Graumann K, Evans DE (2013b) The nuclear envelope - Structure and protein interactions. *Annu Plant*
504 *Rev* 46:19–56.

505 Gristwood T, Duggin IG, Wagner M, Albers SV and Bell SD (2012) The sub-cellular localization of
506 *Sulfolobus* DNA replication. *Nucleic Acids Res* 40:5487–5496.

507 Gross J, Bhattacharya D (2011) Endosymbiont or host: who drove mitochondrial and plastid
508 evolution? *Biol Direct* 6:12.

509 Haque F, Mazzeo D, Patel JT, Smallwood DT, Ellis JA, Shanahan CM and Shackleton S (2010)
510 Mammalian SUN Protein Interaction Networks at the Inner Nuclear Membrane and Their Role in
511 Laminopathy Disease Processes. *J Biol Chem* 285:3487–3498.

512 [Haque F, Lloyd DJ, Smallwood DT, Dent CL, Shanahan CM, Fry AM, Trembath RC and Shackleton
513 S \(2006\) SUN1 Interacts with Nuclear Lamin A and Cytoplasmic Nesprins To Provide a Physical
514 Connection between the Nuclear Lamina and the Cytoskeleton. *Molecular and Cellular Biology* 26:
515 3738–3751.](#)

516 Huda KMK, Banu MSA, Tuteja R, Tuteja N (2013) Global calcium transducer P-type Ca²⁺-ATPases
517 open new avenues for agriculture by regulating stress signalling. *J Exp Bot* 64:3099–3109.

518 [Irons SL, Evans DE, and Brandizzi F \(2003\) The first 238 amino acids of the human lamin B receptor
519 are targeted to the nuclear envelope in plants. *J. Exp. Bot.* 54: 943–950.](#)

520 Janski N, Masoud K, Batzenschlager M, Herzog E, Evrard J-L, Houlné G, Bourge M, Chabouté M-E
521 and Schmit A-C (2012) The GCP3-Interacting Proteins GIP1 and GIP2 Are Required for γ -Tubulin
522 Complex Protein Localization, Spindle Integrity, and Chromosomal Stability. *Plant Cell* 24:1171–
523 1187.

524 Keminer O, Peters R (1999) Permeability of Single Nuclear Pores. *Biophys J* 77:217–228.

525 Kimura Y, Kuroda C, Masuda K (2010) Differential nuclear envelope assembly at the end of mitosis
526 in suspension-cultured *Apium graveolens* cells. *Chromosoma* 119:195–204.

527 Masoud K, Herzog E, Chabouté M-E, Schmit A-C (2013) Microtubule nucleation and establishment
528 of the mitotic spindle in vascular plant cells. *Plant J* 75:245–257.

529 Masuda K, Xu ZJ, Takahashi S, Ito A, Ono M, Nomura K and Inoue M (1997) Peripheral framework
530 of carrot cell nucleus contains a novel protein predicted to exhibit a long alpha-helical domain. *Exp*
531 *Cell Res* 232:173–181.

532 Meier I, Brkljadic J (2009) Adding pieces to the puzzling plant nuclear envelope. *Curr Opin Plant Biol*
533 12:752–759.

534 Murphy SP, Simmons CR, Bass HW (2010) Structure and expression of the maize (*Zea mays* L.)
535 SUN-domain protein gene family: evidence for the existence of two divergent classes of SUN proteins
536 in plants. *BMC Plant Biol* 10:269–269.

537 Oda Y, Fukuda H (2011) Dynamics of *Arabidopsis* SUN proteins during mitosis and their
538 involvement in nuclear shaping. *Plant J* 66:629–641.

539 Park SH, Blackstone C (2010) Further assembly required: construction and dynamics of the
540 endoplasmic reticulum network. *EMBO Rep* 11:515–521.

541 [Pickersgill H, Kalverda B, de Wit E, Talhout W, Fornerod M, and van Steensel B \(2006\)](#)
542 [Characterization of the *Drosophila melanogaster* genome at the nuclear lamina. *Nat. Genet.* 38: 1005–](#)
543 [1014.](#)

544 Rasmussen CG, Wright AJ, Müller S (2013) The role of the cytoskeleton and associated proteins in
545 determination of the plant cell division plane. *Plant J* 75:258–269.

546 [Razafsky D, and Hodzic D \(2009\) Bringing KASH under the SUN: the many faces of nucleo-](#)
547 [cytoskeletal connections. *J Cell Biol* 186: 461–472.](#)

548 Schuldiner M, Metz J, Schmid V, Denic V, Rakwalska M, Schmitt HD, Schwappach B and Weissman
549 JS (2008) The GET Complex Mediates Insertion of Tail-Anchored Proteins into the ER Membrane.
550 *Cell* 134:634–645.

551 Shaw SL, Kamyar R, Ehrhardt DW (2003) Sustained Microtubule Treadmilling in *Arabidopsis*
552 Cortical Arrays. *Science* 300:1715–1718.

553 Sohaskey ML, Jiang Y, Zhao JJ, Mohr A, Roemer F and Harland RM (2010) Osteopotential regulates
554 osteoblast maturation, bone formation, and skeletal integrity in mice. *J Cell Biol* 189:511–525.

555 Sosa BA, Kutay U, Schwartz TU (2013) Structural insights into LINC complexes. *Curr Opin Struct*
556 *Biol* 23:285–291.

557 Sosa BA, Rothballer A, Kutay U, Schwartz TU (2012) LINC Complexes Form by Binding of Three
558 KASH Peptides to Domain Interfaces of Trimeric SUN Proteins. *Cell* 149:1035–1047.

559 Starr DA (2009) A nuclear-envelope bridge positions nuclei and moves chromosomes. *J Cell Sci*
560 122:577–586.

561 Starr DA (2011) KASH and SUN proteins. *Curr Biol* 21:R414–R415. doi: 10.1016/j.cub.2011.04.022

562 Starr DA, Han M (2002) Role of ANC-1 in Tethering Nuclei to the Actin Cytoskeleton. *Science*
563 298:406–409.

564 Tamura K, Fukao Y, Iwamoto M, Haraguchi T and Hara-Nishimura I (2010) Identification and
565 Characterization of Nuclear Pore Complex Components in *Arabidopsis thaliana*. *Plant Cell Online*
566 22:4084–4097.

567 Tamura K, Hara-Nishimura I (2011) Involvement of the nuclear pore complex in morphology of the
568 plant nucleus. *Nucleus* 2:168–172.

569 Tamura K, Iwabuchi K, Fukao Y, Kondo M, Okamoto K, Ueda H, Nishimura M and Hara-Nishimura
570 I (2013) Myosin XI-i Links the Nuclear Membrane to the Cytoskeleton to Control Nuclear Movement
571 and Shape in *Arabidopsis*. *Curr Biol* 23: 1776-1781.

572 Traas J, Hülskamp M, Gendreau E, Höfte H (1998) Endoreduplication and development: rule without
573 dividing? *Curr Opin Plant Biol* 1:498–503.

574 Vanrobays E, Thomas M, Tatout C (2013) Heterochromatin positioning and Nuclear Architecture.
575 *Plant Nucl. Struct. Genome Archit. Gene Regul.* WILEY-BLACKWELL, pp 157–190

576 Versaevel M, Grevesse T, Gabriele S (2012) Spatial coordination between cell and nuclear shape
577 within micropatterned endothelial cells. *Nat Commun* 3:671.

578 Xiong H, Rivero F, Euteneuer U, Mondal S, Mana-Capelli S, Laroche D, Vogel A, Gassen B and
579 Noegel AA (2008) Dictyostelium Sun-1 Connects the Centrosome to Chromatin and Ensures Genome
580 Stability. *Traffic* 9:708–724.

581 [Xu XM, Meulia T and Meier I \(2007\) Anchorage of Plant RanGAP to the Nuclear Envelope Involves
582 Novel Nuclear-Pore-Associated Proteins. *Current Biology* 17: 1157–1163.](#)

583 Yang L, Munck M, Swaminathan K, Kapinos LE, Noegel AA and Neumann S (2013) Mutations in
584 LMNA Modulate the Lamin A - Nesprin-2 Interaction and Cause LINC Complex Alterations. *PLoS*
585 *ONE* 8:e71850.

586 Zhang H, Dawe RK (2011) Mechanisms of plant spindle formation. *Chromosome Res* 19:335–344.

587 Zhao Q, Brkljacic J, Meier I (2008) Two Distinct Interacting Classes of Nuclear Envelope–Associated
588 Coiled-Coil Proteins Are Required for the Tissue-Specific Nuclear Envelope Targeting of *Arabidopsis*
589 RanGAP. *Plant Cell Online* 20:1639–1651.

590 Zhou X, Graumann K, Evans DE, Meier I (2012a) Novel plant SUN–KASH bridges are involved in
591 RanGAP anchoring and nuclear shape determination. *J Cell Biol* 196:203–211.

592 Zhou Z, Du X, Cai Z, Song X, Zhang H, Mizuno T, Suzuki E, Yee MR, Berezov A, Murali R, Wu SL,
593 Karger BL, Greene MI and Wang Q (2012b) Structure of Sad1-UNC84 Homology (SUN) Domain
594 Defines Features of Molecular Bridge in Nuclear Envelope. *J Biol Chem* 287:5317–5326.

595 Zhou X, Meier I (2013) How plants LINC the SUN to KASH. *Nucl Austin Tex* 4:206–215.

596

Figure 1

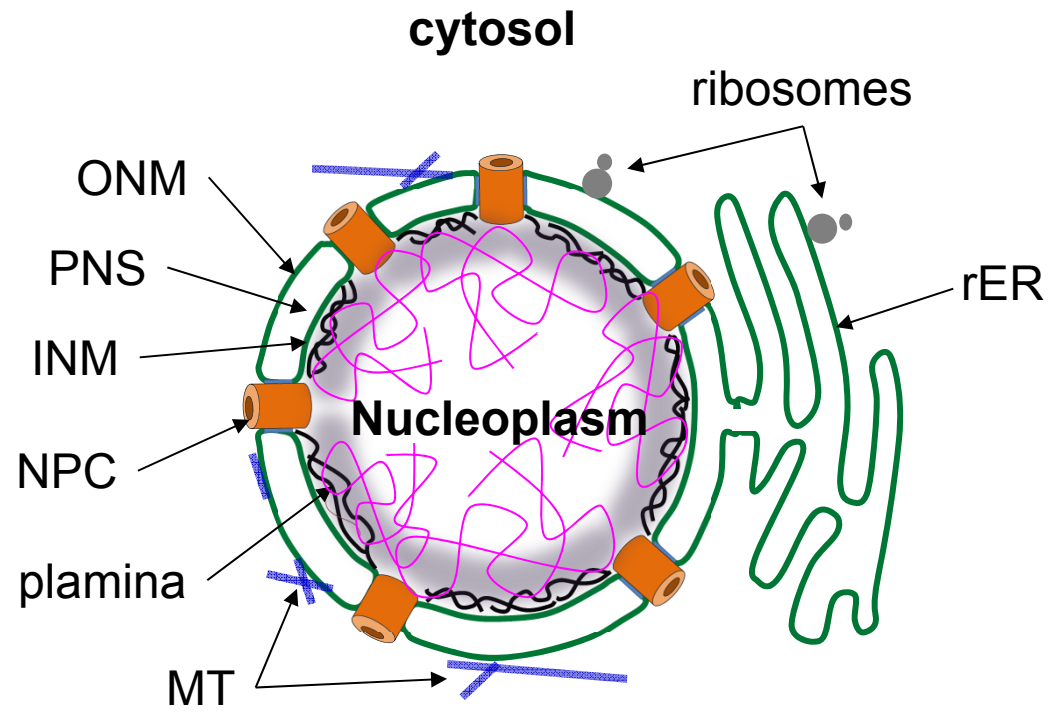
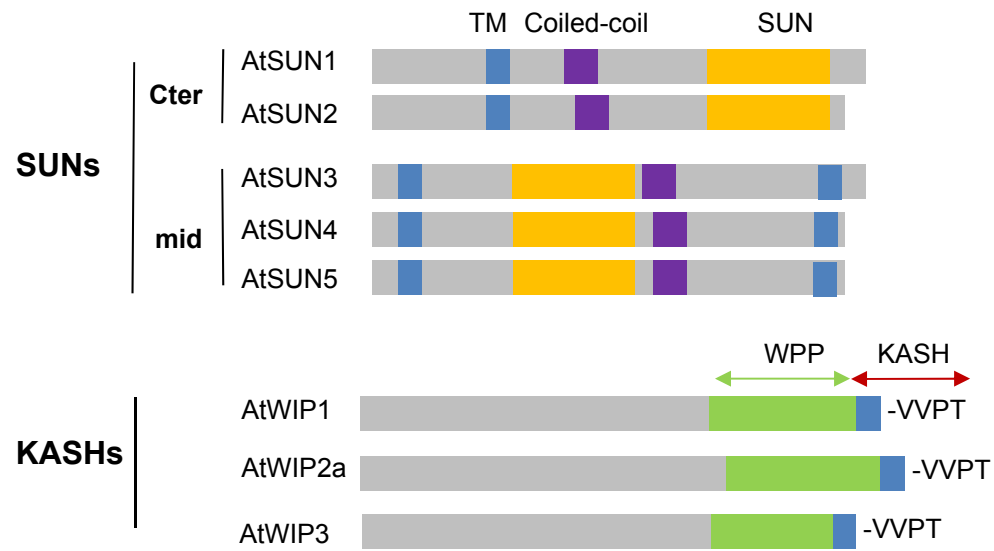
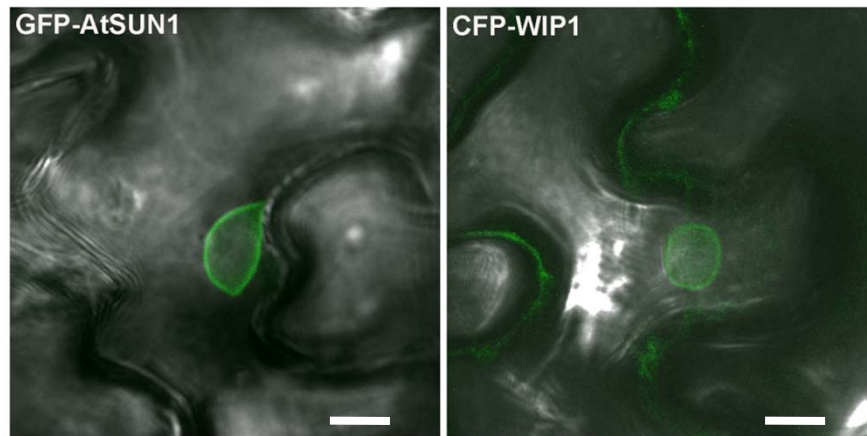


Figure 2

A



B



C

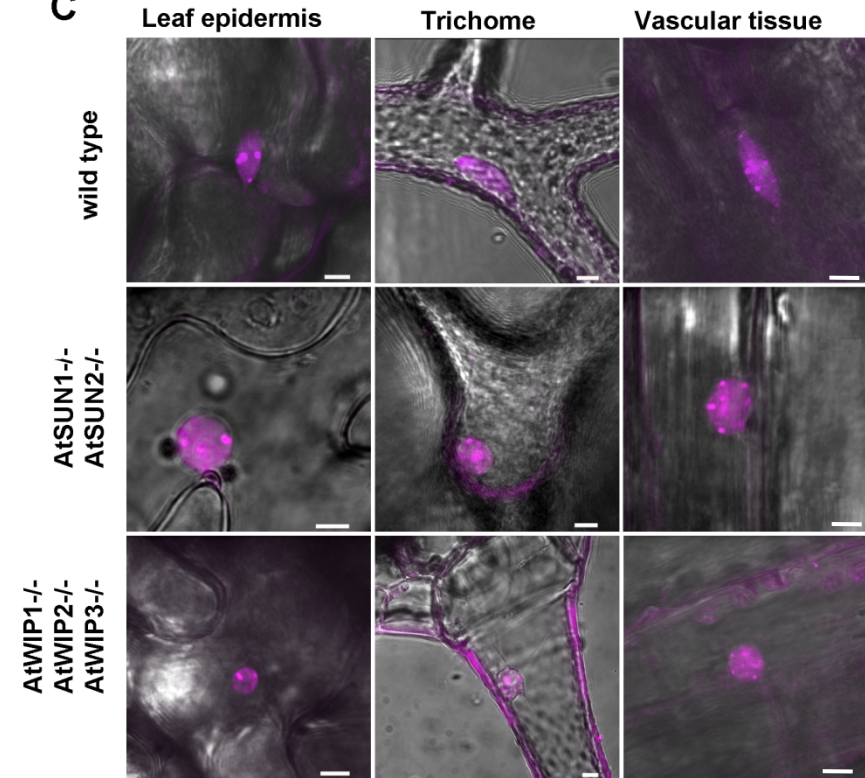
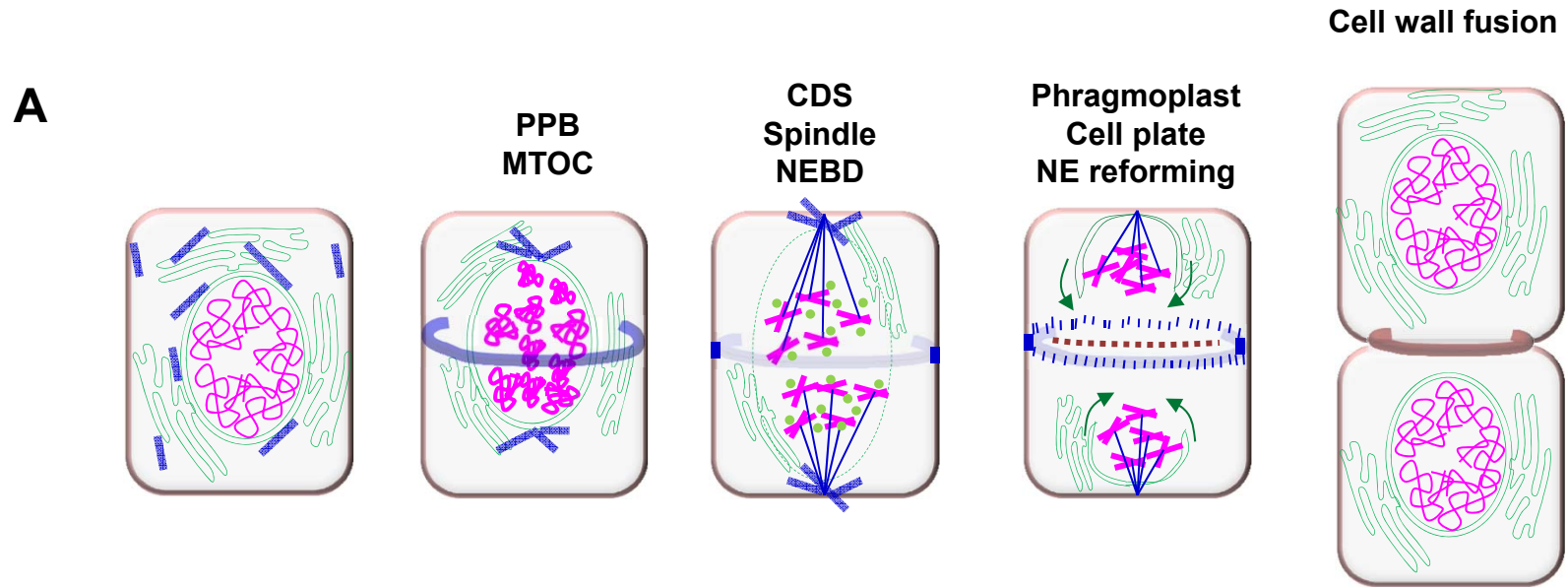


Figure 3



B Interphase Prophase Prometaphase telophase Cytokinesis

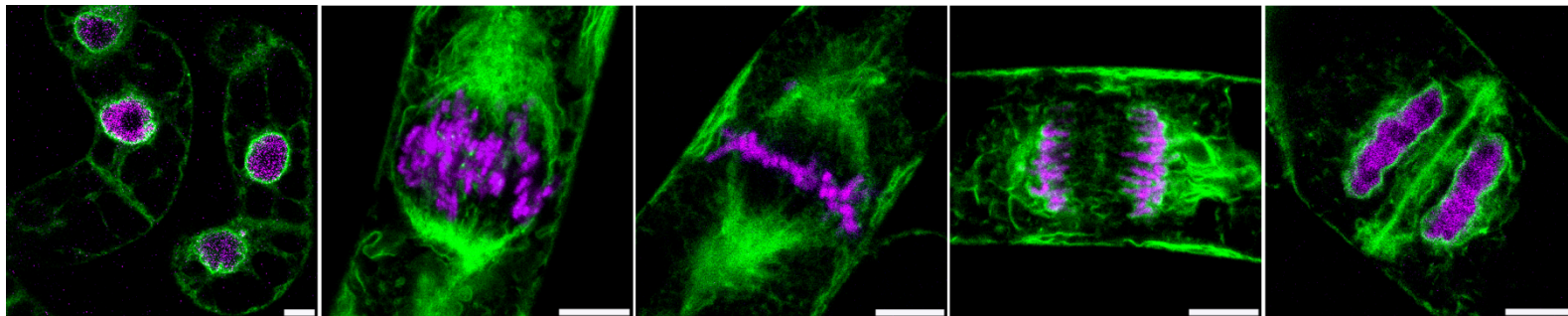


Figure 4

