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Nuclear Entanglement: New Insights Into the Role of Cytoskeleton and Nucleoskeleton in Plant Nuclear Function

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ABSTRACT

Of the three types of cytoskeleton known in animals—actin, microtubules, and intermediate filaments—only actin and microtubules exist in plants. Both play important roles in cellular shaping, organelle movement, organization of the endomembrane system, and cell signaling. An emerging, but often overlooked role of the plant cytoskeleton is its dynamic and mutually influential interaction with the nucleus. Here, we summarize recent advances in understanding the role of the cytoskeleton in plant nuclear movement in different biological contexts, a role for nuclear envelope-associated proteins in reorganizing the actin and microtubule cytoskeleton, and the molecular nature of the nucleus-cytoskeleton interface and specific proteins contributing to it. In animals, the nucleoskeleton consists of the nuclear lamina, an intermediate-filament meshwork underlying the nuclear envelope. Plants have evolved an equivalent of this structure, built by different types of proteins. Here, we highlight recent advances in understanding its filamentous organization, newly discovered protein interactions connecting it to nuclear pores, and exciting new evidence that—just like the animal lamina—the plant lamina is involved in chromatin reorganization and epigenetic changes. Together, these new developments create new opportunities toward a deeper understanding of this important regulatory connection between the cytoskeleton and the cell's largest organelle.

1 | Introduction

In most eukaryotic cells, the nucleus is the single largest organelle. It is surrounded by a double membrane (the nuclear envelope, NE) which is perforated by large proteinaceous complexes termed nuclear pore complexes (NPCs). The NE consists of two membranes separated by the NE lumen or perinuclear space. The outer nuclear membrane (ONM) is contiguous with the ER while the inner nuclear membrane (INM), which faces the nucleoplasm, contains a distinct protein complement. The NPCs are large protein complexes that are embedded into the NE, at sites where the INM and ONM are fused, and form a channel to allow selective transport of macromolecules between the cytoplasm and the nucleoplasm (D'Angelo and Hetzer 2008). Thus, the NE simultaneously connects and separates the cellular command center of the chromatin from the factory floor of the cytoplasm.

In addition to the NPC, LINC (linker of nucleoskeleton and cytoskeleton) complexes provide a direct link between cytoplasm and nucleoplasm. LINC complexes consist of two types of transmembrane proteins, KASH (Klarsicht, ANC-1, Syne homology) domain-containing proteins at the ONM and SUN (Sad1 and UNC-84) domain-containing proteins at the INM. The KASH domain interacts with the SUN domain in the perinuclear space. In metazoans, the cytoplasmic domains of KASH proteins often interact with filaments or motors of the cytoskeleton. The nucleoplasmic domain of SUN proteins can contact the lamina, an intermediate-filament meshwork at

the nuclear surface of the NE consisting of nuclear lamins and lamin-associated proteins (Dultz and Ellenberg 2007; Starr and Fridolfsson 2010).

While most textbook figures depict the nucleus as a sphere placed in the center of the cell, nuclei come in a variety of shapes and can undergo regulated subcellular position changes. In animals, nuclear morphology changes have been linked to diseases like cancer (Chow et al. 2012) and laminopathies, including Hutchinson–Gilford Progeria Syndrome and Emery–Dreifuss muscular dystrophy (Burke and Stewart 2014; Janin et al. 2017). In several cases, these are linked to mutations either in lamins and lamin-associated proteins or to mutations in LINC complexes. Nuclear positioning and movement are essential prerequisites for several developmental pathways. Examples from vertebrates include fertilization, wound healing, developing myotubes, the developing central nervous system, and nuclear migration in cells that migrate through constricted spaces (Starr and Fridolfsson 2010; Bone and Starr 2016; Lee and Burke 2018).

The cytoskeleton is an important player in regulating the shape and positioning of the cell nucleus, by either transducing forces generated by motor proteins or pushing the nuclear membrane directly via filament reorganization. LINC complexes play a major role in acting as adaptors for actin and microtubules at the cytoplasmic surface of the nuclear envelope. Two prominent, well-understood examples of F-actin moving nuclei by connecting to LINC complexes are the TAN lines and perinuclear actin caps that move the nucleus during cellular polarization and migration of fibroblasts (Davidson and Cadot 2021).

While less is known about the connections between the nucleus, cytoskeleton, and the nucleoskeleton in plants, recent research has already highlighted both similarities with and differences from the metazoan situation (Meier et al. 2017). While plant nuclear ultrastructure reveals an inner nuclear membrane-associated meshwork similar to the animal lamina (Ciska et al. 2013), plant genomes do not encode obvious lamin homologs. Instead, plant-specific long coiled-coil proteins with structural similarity to animal lamins appear to replace this meshwork (Dittmer et al. 2007; Ciska et al. 2013; Kimura et al. 2014).

Plant SUN proteins can be easily recognized as the plant homologs of animal SUN proteins (Graumann et al. 2010; Oda and Fukuda 2011; Evans et al. 2014). They share with non-plant SUN proteins an N-terminal domain with a nuclear localization signal, a transmembrane domain, a coiled-coil domain, and the SUN domain. They are found throughout the land plants, suggesting that they are broadly conserved and evolutionarily ancient (Zhou and Meier 2013).

Unlike SUN proteins, plants do not have sequence homologs of known animal KASH proteins (Zhou and Meier 2013). Based on binding and localization characteristics, Arabidopsis WIP1, WIP2, and WIP3 were identified as plant analogs of KASH proteins (Zhou et al. 2012). WIPs are outer nuclear membrane–associated, plant-specific proteins that anchor the Arabidopsis Ran GTPase activating protein (AtRanGAP) to the NE (Xu et al. 2007; Boruc et al. 2015). They have a cytoplasmic coiled-coil domain, a transmembrane domain, and a short tail domain that ends in the highly conserved tripeptide VPT (Zhou et al. 2012). Two coiled-coil, NE-associated proteins, WIT1 and WIT2, bind to WIP1, WIP2, and WIP3 (Zhao et al. 2008). In the current model, a complex consisting of SUN, WIP, and WIT is associated with the NE in plants. Additional plant KASH proteins include SUN-interacting nuclear envelope proteins 1–5 (SINE1–5), which share the VPT motif with WIPs (Zhou et al. 2014). The paralogous Arabidopsis KASH proteins SINE1 and SINE2 function during stomatal dynamics induced by light–dark transitions and abscisic acid (ABA). They have an N-terminal domain with similarity to armadillo repeat domains, and SINE1, but not SINE2, colocalizes with actin (Zhou et al. 2014; Biel et al. 2020a).

Plant nuclei can undergo a variety of shape changes and are highly mobile in certain cell types (Griffis et al. 2014). The most prominent migration of a plant nucleus is likely that of the pollen vegetative nucleus along the entire pollen tube prior to fertilization (Zhou and Meier 2014). Nuclei move in leaf epidermal cells based on light signals and can be both attracted and repelled by plant-microbe interactions. Nuclei undergo specific movement patterns in trichomes (leaf hairs) and root hairs and can move in response to mechanical stimuli (Griffis et al. 2014). Many of these movements have been shown to depend on the actin cytoskeleton. A specific aspect of nuclear movement is the re-positioning of the nucleus prior to cell division, as it occurs as part of the cell cycle and is often determined by the pre-prophase band. However, other, more complex regulators overlay this concept in the case of asymmetric cell division.

In this review, we attempt to give an overview of recent advances in understanding the multifaceted connections between the plant nucleus and the cytoskeleton as it relates to nuclear shape and movement and to asymmetric cell division on one hand, and the progress made in better structurally and functionally characterizing the plant equivalent of the nuclear lamina on the other hand. While many open questions remain, the field is clearly advancing toward a broader survey of phenomena and a more detailed understanding of gene and protein functions. Importantly, this includes investigations of many more plant species, allowing for potentially insightful comparison between dicots and monocots or basal and advanced land plants.

2 | The Role of the Cytoskeleton in Nuclear Movement

2.1 | Cytoskeletal Dynamics During Fertilization and Post-Fertilization Nuclear Movement

Plants have evolved a unique double fertilization process in which two female gametophytic cells, known as the egg and central cell, are each fertilized by a sperm cell, which then develop into the embryo and endosperm, respectively (Kawashima and Berger 2015). The male germ unit (MGU) is comprised of two sperm cells and the vegetative nucleus (VN) of the pollen grain, which are connected by a cytoplasmic projection from the sperm cells that wraps around the nucleus (Lalanne and Twell 2002; Borg et al. 2009; McCue et al. 2011). In most flowering plants, the MGU travels as a unit through the growing pollen tube, with the VN leading the sperm cells (Figure 1C, panel 6) (McCue et al. 2011). Several lines of evidence show that the sperm cells

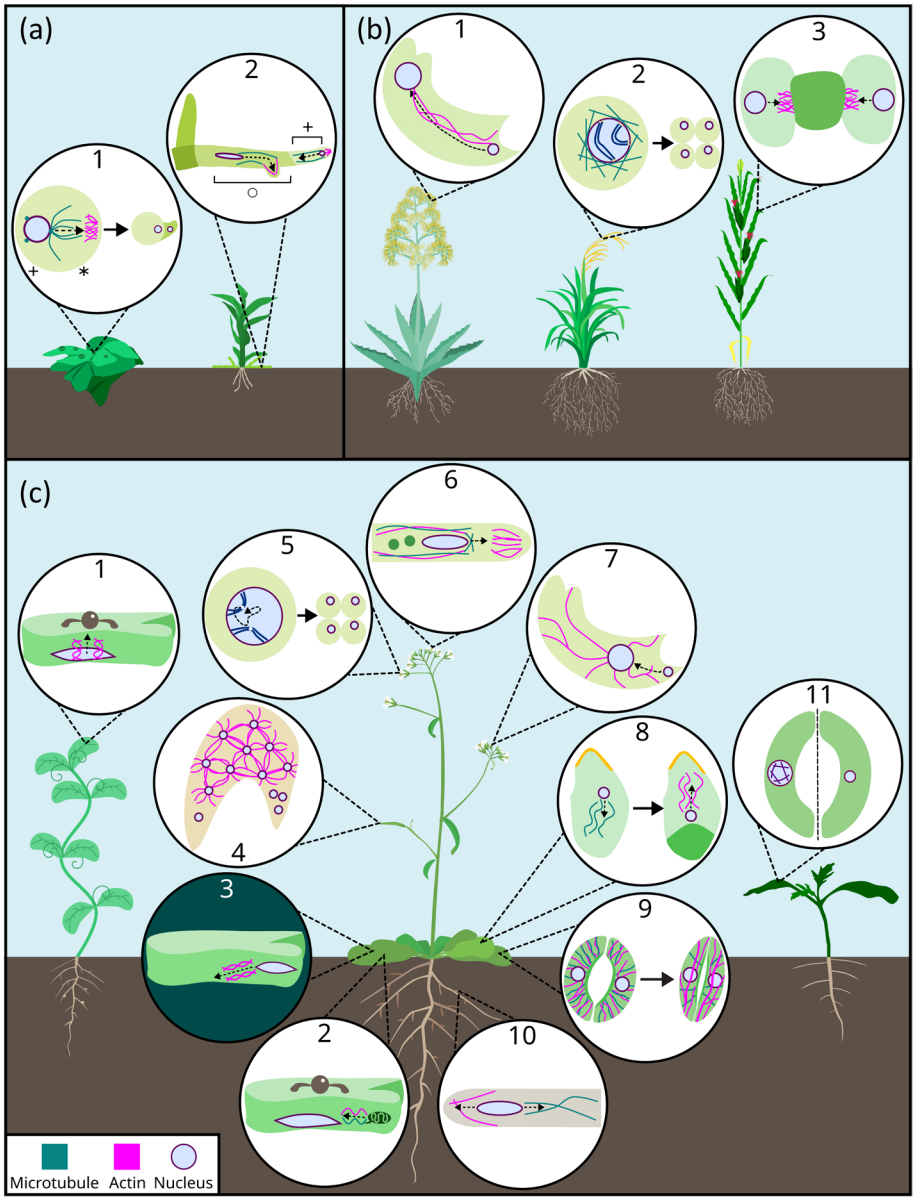

FIGURE 1 | The nucleo-cytoskeletal interface is important in cellular processes across species and tissue types. (A) Nuclear migration in the basal land plants *Marchantia polymorpha* (left), and *Physcomitrium patens* (right). In *Marchantia*, the nucleus migrates from the apical side (+) to the basal side (*) along actin and microtubules during the first spore cell division (1). In *Physcomitrium patens*, nuclear migration occurs in subapical (○) and apical (+) protonema cells (2) along microtubules. (B) The nuclear envelope interface in monocots. In *Agave inaequidens* (left), an F-actin mega-cable contributes to sperm cell nuclear migration through the central cell (1). In *Oryza sativa* (middle) meiosis, the nuclear envelope-cytoskeletal interface is required for spindle assembly (2). During *Zea mays* (right) subsidiary cell division, the nucleus migrates toward an actin patch (3). (C) Dicot nucleo-cytoskeletal interfaces. In *Pisum sativum* (left, 1) actin directs nuclear migrations during fungal responses A wide variety of cellular processes in *Arabidopsis thaliana* involve the nucleo-cytoskeletal interface (middle). (2) Chloroplasts (black) are transported along actin to the nucleus during pathogen defense. (3) Dark-induced nuclear migration in leaves requires the actin cytoskeleton. (4) Nuclei are positioned in the endosperm coencytium by actin filaments. (5) Rapid centromeric movements during meiosis require INM SUN proteins. (6) Pollen tube MGU movement has contributions from both microtubules and actin. (7) Sperm cell nuclear migration through the central cell is coordinated through an actin reorganization. (8) Nuclei migrate to and away from an asymmetric division site in meristemoid mother cells. (9) Actin and microtubule reorganization is regulated by ONM KASH proteins during stomatal closure. (10) Actin and microtubules act in opposing directions during root hair cell growth. *Solanum lycopersicum* guard cell nuclear shape (right, 11) is regulated by SlNMCP proteins. Images not to scale.

can also be transported independently of the VN (Ge et al. 2011; Zhou and Meier 2014), but the VN is required for pollen tubes to burst (Zhou and Meier 2014; Moser et al. 2020). VN transport requires WIP KASH proteins, suggesting that the VN may be actively linked to the cytoskeleton during its transit (Zhou and Meier 2014). The sperm cells move in a saltatory backward and forward motion controlled by constant inward movement of actin filaments during migration through the pollen tube (Kliwer and Dresselhaus 2010; Schattner et al. 2021). The sperm cells of flowering plants are not self-propelling, but they must track close to the tip of the pollen tube to be delivered to the egg (Li et al. 2018; Johnson et al. 2019).

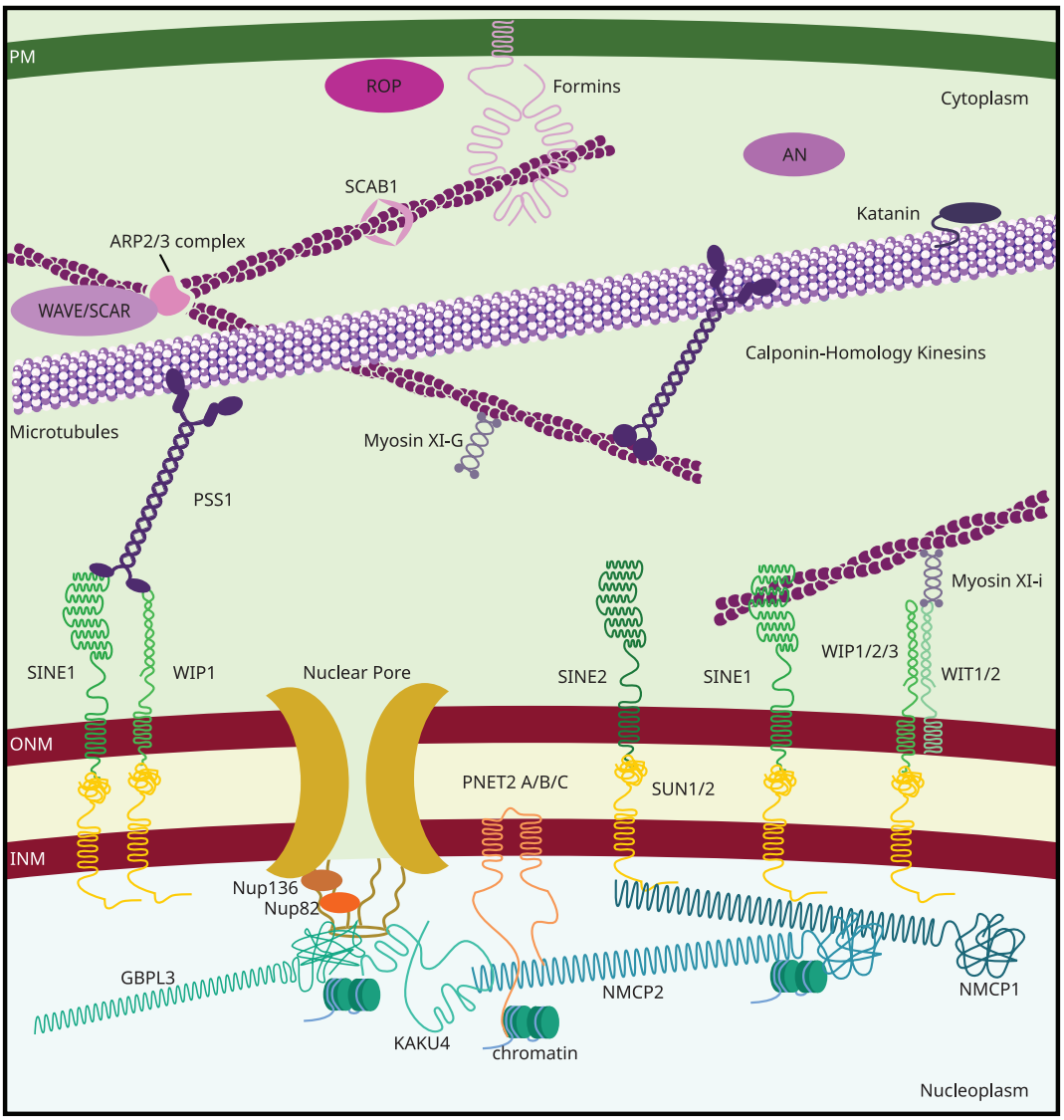

FIGURE 2 | Proteins involved in the nucleo-cytoskeletal interface. Actin-nucleating proteins include formins, which can be at the plasma membrane (PM). The ARP2/3 complex, which is regulated by the WAVE/SCAR complex, is responsible for actin branching, and SCAB1 is an actin bundling protein. ANGUSTIFOLIA (AN), ROPs, and Myosin XI-G regulate the organization of the actin cytoskeleton, and Katanin is a microtubule-severing protein. Myosin XI-i is involved in nuclear migrations, along with a variety of Calponin-Homology Kinesins. PSS1 interacts with microtubules during meiosis. The cytoskeleton is linked to the nuclear envelope KASH proteins on the outer nuclear membrane (ONM), which form LINC complexes by interacting with SUN proteins on the inner nuclear membrane (INM). SUN proteins, along with the INM protein PNET2, can interface with the nuclear lamina, which consists of NMCP1- and NMCP2-type proteins as well as KAKU4 and GBPL3, which connect the lamina to the nuclear pore via Nup82 and Nup136. NMCP1 and 2, as well as PNET2, KAKU4, and GBPL3, provide a scaffold for chromatin.

Recent work has begun to dissect the mechanism of MGU movement. Schattner et al. (2021) examined the characteristics and mechanics of sperm cell transport and observed bidirectional motion in the absence of the VN, adding to the evidence that sperm cells are actively, rather than passively, transported (Zhou and Meier 2014; Schattner et al. 2021). Sperm cells are enclosed in a microtubule cage structure within the pollen tube (Laitiainen et al. 2002; Poulter et al. 2008) which Schattner et al. (2021) found moves with the sperm cells and changes orientation as the sperm cells change order (Schattner et al. 2021). They additionally used *Oryza sativa* Calponin-Homology Kinesin (KCH) to model the mechanics of sperm cell transport (Figure 2, Table 1). Kinesins with calponin homology domains (KCHs) are a subgroup of the kinesin-14 family, microtubule minus-end directed motors, which bind actin and move along microtubules with two different velocities (Walter et al. 2015). Schattner et al. (2021) found that the movement of sperm cells in pollen tubes could be recreated using a tug-of-war model, with cortical KCHs acting in multiple directions, and the randomly arrayed microtubules encompassing the sperm cells (Müller et al. 2008; Schattner et al. 2021).

Further work dissecting MGU, and specifically VN, movement has begun to characterize the dynamics of microtubules, actin filaments, and KCHs during transport of the MGU. Wang et al. (2024) establish that depolymerization of microtubules and inhibition of kinesins result in an increased velocity and amplitude of both forward and backward movements of the

TABLE 1 | Proteins described in this paper.

Protein name	Species	UniProt #	Protein interactors	Cellular role	Subcellular localization	References
Cytoskeletal Proteins						
ARP2/3 complex				Actin branching	Cytoplasm	Qin et al. (2021), Moser et al. (2024)
AtANGUSTIFOLIA	*A. thaliana*	O23702		Dark nuclear positioning	Cytoplasm	Iwabuchi et al. (2019)
AtKIN14G	*A. thaliana*	O81635		Positional and forward movement of the VN	Cytoplasm	Wang et al. (2024)
AtKIN14H	*A. thaliana*	F4HZF0		Positional and forward movement of the VN	Cytoplasm	Wang et al. (2024)
AtKIS1	*A. thaliana*	F4JX00		Induces stomule formation	Cytoplasm	Meier et al. (2023)
AtMyosin XI-g	*A. thaliana*	F4IUG9		Sperm nuclear migration	Cytoplasm	Ali et al. (2020)
AtMyosin XI-i	*A. thaliana*	Q0WPU1	AtWIT1/2	Root hair nuclear movement, dark induced leaf nuclear positioning, pre-ACD nuclear movement	Cytoplasm	Tamura et al. 2013, Iwabuchi et al. (2016), Muroyama et al. (2020)
AtPSS1	*A. thaliana*	F4HXY7	AtWIP1	Meiotic synapsis, crossovers, and telomere dynamics	Cytoplasm	Duroc et al. (2014)
AtSCAB1	*A. thaliana*	O48791		Actin bundling	Cytoplasm	Moser et al. (2024)
AtSCAR2	*A. thaliana*	Q5XPJ9		Sperm nuclear migration	Cytoplasm	Ali et al. (2020)
Formins	*A. thaliana*			Actin organization, root hair nuclear movement, movement of F-Actin in central cell	Cytoplasm, Plasma membrane	Zhang et al. (2019), Ali and Kawashima (2021)
MpKatanin	*M. polymorpha*	A0AAF6BBW9, A0A2 R6WB11		Microtubule severing, polar organizer regulation	Cytoplasm	Attrill and Dolan (2024)
OsKCH1	*O. sativa*	Q0IMS9		Sperm cell transport	Cytoplasm	Schattner et al. (2021)
OsPSS1	*O. sativa*	F9W301	OsSINE1, OsWIP1	Meiotic spindle assembly, microtubule bundling, synapsis, crossovers	Cytoplasm	Zhou et al. (2024), Zhang et al. (2020)
PpKCHa	*P. patens*	A0A2K1JII6		Nuclear movement and tip growth	Cytoplasm	Yamada and Goshima (2018)
PpKCHb	*P. patens*	A0A2K1L0S0		Nuclear movement and tip growth	Cytoplasm	Yamada and Goshima (2018)
PpKCHc	*P. patens*	A0A2K1J503		Nuclear movement and tip growth	Cytoplasm	Yamada and Goshima (2018)

(Continues)

TABLE 1 | (Continued)

Protein name	Species	UniProt #	Protein interactors	Cellular role	Subcellular localization	References
PpKCHd	*P. patens*	A0A2K1IHC6		Nuclear movement and tip growth	Cytoplasm	Yamada and Goshima (2018)
PpROP1	*P. patens*	Q9M5B8		Actin organization, formation of membrane bulge, direction of nuclear migration	Cytoplasm, Plasma membrane, Subapical bulge, Cell plate	Yi and Goshima (2020)
PpROP2	*P. patens*	Q9XER7		Actin organization, formation of membrane bulge, direction of nuclear migration	Cytoplasm, Plasma membrane, Subapical bulge, Cell plate	Yi and Goshima (2020)
PpROP3	*P. patens*	Q9S821		Actin organization, formation of membrane bulge, direction of nuclear migration	Cytoplasm, Plasma membrane, Subapical bulge, Cell plate	Yi and Goshima (2020)
PpROP4	*P. patens*	Q9M5B7		Actin organization, formation of membrane bulge, direction of nuclear migration	Cytoplasm, Plasma membrane, Subapical bulge, Cell plate	Yi and Goshima (2020)
WAVE/SCAR Complex	*A. thaliana*			Sperm nuclear migration	Cytoplasm	Ali et al. (2020)
ONM Proteins						
AtSINE1	*A. thaliana*	Q5XVI1	AtSUN1/2	Actin and microtubule organization	Outer Nuclear Membrane	Zhou et al. (2014), Biel et al. (2020a, 2020b), Biel et al. (2022)
AtSINE2	*A. thaliana*	Q9SQR5	AtSUN1/2	Actin and microtubule organization	Outer Nuclear Membrane	Zhou et al. (2014), Biel et al. (2020a, 2020b), Biel et al. (2022)
AtWIP1	*A. thaliana*	Q8GXA4	AtWIT1/2, AtPSS1	Nuclear migration in pollen and root hairs	Outer Nuclear Membrane	Zhou et al. (2012), Zhou and Meier (2014), Moser et al. (2020)
AtWIP2	*A. thaliana*	Q9FH18	AtWIT1/2, AtPSS1	Nuclear migration in pollen and root hairs	Outer Nuclear Membrane	Zhou et al. (2012), Zhou and Meier (2014), Moser et al. (2020)
AtWIP3	*A. thaliana*	Q94AV5	AtWIT1, AtWIT2	Nuclear migration in pollen and root hairs	Outer Nuclear Membrane	Zhou et al. (2012), Zhou and Meier (2014), Moser et al. (2020)
AtWIT1	*A. thaliana*	Q8L7E5	AtWIP1/2/3, AtMyosin XI-i	Nuclear migration in pollen and root hairs	Outer Nuclear Membrane	Zhou et al. (2012), Tamura et al. (2013), Zhou and Meier (2014), Moser et al. (2020)

(Continues)

TABLE 1 | (Continued)

Protein name	Species	UniProt #	Protein interactors	Cellular role	Subcellular localization	References
AtWIT2	*A. thaliana*	A8MQR0	AtWIP1/2/3, AtMyosin XI-i	Nuclear migration in pollen and root hairs	Outer Nuclear Membrane	Zhou et al. (2012), Tamura et al. 2013, Zhou and Meier (2014), Moser et al. (2020)
OsSINE1	*O. sativa*	Q0IS00	OsPSS1, OsSUN1, OsSUN2		Outer Nuclear Membrane	Zhang et al. (2020)
OsWIP1	*O. sativa*	A0A0P0WBS6, Q7XQM6	OsPSS1, OsSUN1, OsSUN2		Outer Nuclear Membrane	Zhang et al. (2020)
ZmMLKS2	*Z. mays*	A0A1D6KGN6		Nuclear migration during subsidiary cell development	Outer Nuclear Membrane	Gumber et al. (2019), Ashraf et al. (2023)
INM Proteins						
AtPNET2_A	*A. thaliana*	Q9SHQ6	AtCRWN1		Inner Nuclear Membrane	Tang et al. (2022a)
AtPNET2_B	*A. thaliana*	Q9FJW2	AtCRWN1		Inner Nuclear Membrane	Tang et al. (2022a)
AtPNET2_C	*A. thaliana*	Q0WVK0			Inner Nuclear Membrane	Tang et al. (2022a)
AtSUN1	*A. thaliana*	Q9FF75	AtCRWN1, AtSINE1, AtSINE2, AtWIP1, AtWIP2, AtWIP3, AtSUN2	Rapid centromeric meiotic movements; Nuclear shape determination	Inner Nuclear Membrane	Graumann et al. (2010), Graumann (2014), Zhou et al. (2012), Zhou et al. (2014), Zhou et al. (2015)
AtSUN2	*A. thaliana*	Q9SG79	AtSUN1	Rapid centromeric meiotic movements; Nuclear shape determination	Inner Nuclear Membrane	Graumann et al. (2010), Zhou et al. (2015)
OsSUN1	*O. sativa*	Q53WN9	OsSUN1, OsSUN2, OsSUN1, OsWIP1	Meiotic crossover events	Inner Nuclear Membrane	Zhang et al. (2020)
OsSUN2	*O. sativa*	Q0JNS8, A2ZRL2	OsSUN1, OsSUN2, OsSUN1, OsWIP1	Meiotic crossover events	Inner Nuclear Membrane	Zhang et al. (2020)
PpSUN2	*P. patens*	A0A2K1JVS6		Nuclear migration, microtubule association with the nucleus	Inner Nuclear Membrane	Yoshida et al. (2023)
Nucleoskeleton & Associated Proteins						
AtCRWN1	*A. thaliana*	F4HRT5	AtCRWN2, AtCRWN3, AtCRWN4, AtKAKU4, AtSUN1/2, AtPNET2_A, AtPNET2_B, AtGBPL3	Nuclear Shape and Size Determination	Nuclear Periphery	Dittmer et al. (2007), Wang et al. (2013), Sakamoto and Takagi (2013), Sakamoto et al. (2020)

(Continues)

TABLE 1 | (Continued)

Protein name	Species	UniProt #	Protein interactors	Cellular role	Subcellular localization	References
AtCRWN2	*A. thaliana*	Q9SAF6	AtCRWN1, AtCRWN3	Nuclear Shape and Size Determination	Nucleoplasm/Nuc. Periph.	Dittmer et al. (2007), Wang et al. (2013), Sakamoto and Takagi (2013), Sakamoto et al. (2020)
AtCRWN3	*A. thaliana*	Q9CA42	AtCRWN1, AtCRWN3, AtKAKU4, AtGBPL3	Nuclear Shape and Size Determination	Nucleoplasm/Nuc. Periph.	Dittmer et al. (2007), Wang et al. (2013), Sakamoto and Takagi (2013), Sakamoto et al. (2020)
AtCRWN4	*A. thaliana*	Q9FLH0		Nuclear Shape and Size Determination	Nuclear Periphery	Dittmer et al. (2007), Wang et al. (2013), Sakamoto and Takagi (2013), Sakamoto et al. (2020)
AtGBPL3	*A. thaliana*	F4KG14	AtCRWN1, AtCRWN2, AtCRWN3, AtNup88, AtNup136		Nuclear Pore Complex	Tang et al. (2022b)
AtKAKU4	*A. thaliana*	Q949W6	AtCRWN1, AtCRWN2, AtCRWN3, AtNup88, AtNup136	Nuclear Shape and Size Determination	Nuclear Periphery	Goto et al. (2014), Tang et al. (2022b), Mermet et al. (2023)
MpNMCP1	*M. polymorpha*	A0A2R6W3X2			Nuclear Periphery	Wang et al. (2023)
SlNMCP1A	*S. lycopersicum*	A0A3Q7F9Q1		Nuclear Shape and Size Determination		Blunt et al. (2023)
SlNMCP1B	*S. lycopersicum*	A0A3Q7FJQ3		Nuclear Shape and Size Determination		Blunt et al. (2023)
SlNMCP2	*S. lycopersicum*	A0A3Q7FYW9				Blunt et al. (2023)
ZmKAKU41	*Z. mays*	A0A1D6JGB5		Nuclear Shape and Size Determination	Nuclear Periphery	Gumber et al. (2019), McKenna et al. (2021)
ZmKAKU42	*Z. mays*	A0A1D6DVM2			Nuclear Periphery	Gumber et al. (2019), McKenna et al. (2021)
ZmNCH1	*Z. mays*	K7U7Q6			Nuclear Periphery	Gumber et al. (2019), McKenna et al. (2021)
ZmNCH2	*Z. mays*	A0A1D6NAM9			Nuclear Periphery	Gumber et al. (2019), McKenna et al. (2021)

vegetative nucleus (Wang et al. 2024). Microtubules are required for fine positioning of the vegetative nucleus and keeping pace with the tip of the growing pollen tube, while actomyosin-based cytoplasmic streaming determines the overall velocity and direction of vegetative nuclear movement (Figure 1C, panel 6) (Wang et al. 2024). They further identify two KCH kinesins, AtKIN14G and AtKIN14H, which play roles along with microtubules in directional positioning and forward movement of the VN (Figure 2, Table 1). This characterization of the specific roles of microtubules, kinesins, and actomyosin gives new insight into this collaborative network that fine-tunes the velocity, directionality, and positioning of the vegetative nucleus during pollen tube growth. Further work to characterize the nature of this nucleo-cytoskeletal interface, including new kinesins and players such as KASH proteins at the nuclear envelope, will increase our understanding of MGU movement.

During double fertilization in flowering plants, one sperm cell fuses with the egg cell, while the second sperm cell fuses with the central cell, which is typically, except for some basal angiosperms, a homodiploid cell derived from the fusion of two cells of the female gametophyte (Li and Yang 2020). The triploid offspring of this event develops into the endosperm, the nourishing tissue of the seed. In both cellular fusions, migration of the sperm nucleus through the cell is required prior to karyogamy. While it is understood that this process is actin-dependent, the molecular and cellular mechanisms of F-actin regulation during these double-fertilization events are largely unknown (Kawashima et al. 2014).

Ali et al. (2020) have shown that after plasmogamy of the sperm cell and central cell, inhibition of the WAVE/SCAR complex causes impairment of the central cell F-actin meshwork (Figure 1C, panel 7, Figure 2, Table 1), which impacts sperm nuclear migration (Ali et al. 2020). SCAR2, a member of the WAVE/SCAR complex which typically activates the ARP2/3 complex, controls the central cell F-actin meshwork movement and therefore nuclear movement (Ali et al. 2020). In contrast, inhibition of the ARP2/3 complex had no effect on the F-actin meshwork movement of the central cell, suggesting that an ARP2/3-independent WAVE/SCAR-signaling pathway regulates these F-actin dynamics (Ali et al. 2020). In addition, an AtMyosin XI-g knockout mutant had a slowed F-actin meshwork movement and delayed sperm nuclear migration in the central cell (Ali et al. 2020). Since sperm nuclear movement via F-actin is ARP2/3 independent, other actin nucleators, such as formin, could potentially be involved. Indeed, inhibition of formins reduced the dynamic inward movement of F-actin in the central cell (Figure 2, Table 1) (Ali and Kawashima 2021). Thus, WAVE/SCAR and class XI myosins, but not the ARP2/3 complex, play important roles in sperm nuclear migration (Ali et al. 2020). Whether formins are also involved in migration of the sperm nucleus in the central cell remains to be addressed.

Unlike in Arabidopsis, where the central cell nucleus is polarized toward the micropyle, the reception point for the pollen tube (Sprunck and Groß-Hardt 2011), in the Asparagaceae family it is polarized away from the micropyle (Davis 1967). Thus, after plasmogamy of the sperm cell and central cell, the sperm nucleus must migrate an unusually long distance through the central cell before karyogamy can occur. In Arabidopsis, the sperm nucleus travels approximately 1 μm (Kawashima and Berger 2015), while in the Asparagaceae species *Agave tequilana*, the distance is 200 times longer (Figure 1B, panel 1) (González-Gutiérrez et al. 2014). The cellular and cytoskeletal layout of mature embryo sacs of previously uncharacterized *Agave inaequidens* was characterized throughout fertilization (González-Gutiérrez et al. 2021). A thick F-actin mega-cable connected the central cell nucleus with the micropylar pole near the egg cell (Figure 1B, panel 1) (González-Gutiérrez et al. 2021). The sperm nucleus traveled through this F-actin mega-cable to fuse with the central cell nucleus (González-Gutiérrez et al. 2021). As the endosperm began to develop, disassembly of the mega-cable and formation of new F-actin structures occurred (Tseng et al. 2018; González-Gutiérrez et al. 2021). The observed F-actin mega-cable might be a solution that has evolved in plants which require long-distance transport of the sperm nucleus inside the central cell, such as in the Asparagaceae family (González-Gutiérrez et al. 2021). Together with Arabidopsis, this suggests that actin dynamics are a critical nuclear transport mechanism. Further investigation of evolutionary differences in actin dynamics, as well as actin-nuclear connections, will provide a clearer understanding of these dynamics.

The endosperm functions as a nourishing tissue for the growing embryo during seed development in flowering plants. There are four phases of endosperm development in Arabidopsis: coenocyte, cellularization, differentiation, and cell death (Orozco-Arroyo et al. 2015). The nuclear and cytoskeletal dynamics in early endosperm development have been newly characterized (Ali et al. 2023). As the multinucleate coenocytic endosperm develops, microtubules organize around each nucleus into aster-shaped structures that connect to the plasma membrane and provide a platform for the formation of actin asters around the nucleus (Figure 1C, panel 4) (Ali et al. 2023). During the coenocytic phase, actin restricts nuclear movement to equally space the nuclei and controls the size of the endosperm and seed (Ali et al. 2023).

Taken together, these important advances in characterizing the cytoskeleton during fertilization and post-fertilization show how critical cytoskeletal components and factors work together to accomplish the many nuclear positioning and rearrangements required for embryo and endosperm development.

2.2 | Nuclear Movement in Somatic Tip-Growing Cells

Similar to pollen tubes, root hairs are tip-growing cells which are formed by protrusions of elongated root epidermal cells. In Arabidopsis, root hairs are approximately 10 μm in diameter and can grow to be 1 mm or more in length. Root hairs go through four stages of development; namely differentiation, initiation, polar growth, and maturation (Grierson et al. 2014). Root-hair nuclei can undergo specific forward or backward migration, depending on the developmental stage of the root hair. During differentiation, trichoblast nuclei undergo an outward polar migration (Nakamura et al. 2018). After initiation, the nucleus moves from the body of the trichoblast cell into the root hair bulge (Nakamura et al. 2018). During polar growth, the

nucleus moves toward the growing tip and maintains a fixed tip distance. Once elongation stops, the nucleus migrates to a random location. In mature root hairs, the spindle-shaped nuclei move rapidly and bidirectionally across the whole cell length (Figure 1C, panel 10) (Tamura et al. 2013). Finally, the nucleus relocates back to the root hair base (Ketelaar et al. 2002; Tan et al. 2016; Nakamura et al. 2018).

Previously it was established that the plant-specific myosin AtMyosin XI-i and the LINC complex-associated proteins AtWIT1 and AtWIT2 (Figure 2, Table 1) are involved in nuclear movement in mature root hairs (Tamura et al. 2013), but how the cytoskeleton is involved in nuclear positioning and movement during polar growth had not been characterized. In *A. thaliana*, during root hair elongation the nucleus moves forward to keep a fixed distance of about 80 μm from the apex (Ketelaar et al. 2002; Singh et al. 2021). Evidence suggests that this is essential for root hair growth because when the tip distance is disrupted by optical trapping experiments, root hair elongation is halted (Ketelaar et al. 2002).

Two new studies characterize the cytoskeletal trafficking of the nucleus during root hair polar growth. Brueggeman et al. (2022) have now shown that forward nuclear movement and tip distance regulation are independent of AtMyosin XI-i during root hair elongation (Brueggeman et al. 2022). Microtubules lessen erratic nuclear movements and are involved in backward nuclear movement, but they are not required for forward nuclear movement (Brueggeman et al. 2022). Zhang et al. (2019) found that forward migrating nuclei were accompanied by more actin bundles than backward migrating nuclei (Figure 1C, panel 10) (Zhang et al. 2019). Therefore, forward nuclear migration during root hair growth is primarily regulated by actin bundle formation. Inhibition of the actin nucleator formin (Figure 2, Table 1) prevented backward nuclear migration and caused fragmentation of actin bundles (Zhang et al. 2019). From this, backward nuclear migration during root hair growth depends specifically on formin-nucleated actin. Together, these observations indicate that the direction of nuclear migration in young root hairs is mainly regulated by perinuclear actin bundle formation, while microtubules are only involved in erratic forward and backward movements (Zhang et al. 2019; Brueggeman et al. 2022). This is similar to the observations in pollen (Wang et al. 2024), indicating that nuclear migration in Arabidopsis tip growing cells occurs through the competition of these cytoskeletal forces; with actin regulating the larger forward and backward movements, while microtubules fine-tune these movements. The importance of the fine-tuning role of microtubules during nuclear migration events in tip growing cells is an area for further growth.

In the evolution of plants, the microtubule minus end directed transporter found in animals, dynein, was lost. Dynein is required for cargo transport, microtubule-based force generation (Grill and Hyman 2005; Gönczy 2008; McNally 2013), and cytoskeletal cross-linking in animals (Grabham et al. 2007; Ferenz et al. 2009; Perlson et al. 2013; Tanenbaum et al. 2013; Coles and Bradke 2015), yet plants still perform these functions without dynein. *Physcomitrium patens* have tip-growing filamentous extensions from their spores, called protonema. The protonemal apical cells have microtubule tracks along which the nucleus is transported as cargo (Yamada et al. 2017). It was found that several Kinesin 14-IIs, which contain calponin homology domains (PpKCHs), control minus end-directed nuclear transport away from the cell tip and cell tip growth in *P. patens* (Figure 1A, panel 2, Figure 2, Table 1) (Yamada and Goshima 2018). PpKCHs were found to be comparable to animal dynein as long-distance backwards moving transporters (Yamada and Goshima 2018). Nuclear movement in this tip-growing cell type, unlike in Arabidopsis root hairs, is dominated by microtubules. It would be interesting to investigate further tip-growing cell types across plant species to see what patterns emerge and if other cytoskeletal structures and interactors are utilized.

2.3 | Nucleo-Cytoskeletal Interface in Leaf Stimulus Responses

Nuclei are mobile in leaf mesophyll and epidermal cells in response to a variety of stimuli, including light, darkness, and pathogen responses. Under high-light conditions, nuclei are positioned along the anticlinal cell walls, in what is likely a light-avoidance response. In dim light and darkness, they move to the periclinal cell walls, parallel to the surface of the leaf. Both processes are actin dependent, but the detailed mechanisms differ. During light-induced nuclear positioning, chloroplasts attach to the nucleus to carry it to the anticlinal cell walls (Higa et al. 2014). Light-induced nuclear positioning is well characterized, and the mechanism has been well studied (Wada 2013, 2016; Suetsugu et al. 2017). In contrast, the mechanism of dark-induced nuclear positioning is not well understood. During dark-induced nuclear positioning, leaf nuclei migrate toward the center of the leaf and become positioned at the inner periclinal cell walls (Figure 1C, panel 3) (Iwabuchi et al. 2016). Centripetal nuclear positioning suggests a cell polarity exists within leaves, but this mechanism has not been characterized.

The actin cytoskeleton and AtMyosin XI-i are required for dark-induced nuclear positioning (Tamura et al. 2013; Iwabuchi et al. 2016). In screening for novel mutants defective in dark-induced nuclear positioning, two mutants, termed *unusual nuclear positioning 1* and *2* (*unp1/2*), were identified and determined to be a dominant negative mutant of *ACTIN7* (*unp1*) and a recessive mutant of the Arabidopsis gene *ANGUSTOFOLIA* (*AtAN*) (*unp2*) (Figure 2, Table 1) (Iwabuchi et al. 2019). The authors determined that AtACTIN7 is involved in dark-induced nuclear positioning in mesophyll cells, and is required to maintain the structural integrity and number of actin filaments in pavement cells (Iwabuchi et al. 2019). AtAN is a cytosolic protein required for dark nuclear positioning in both pavement and mesophyll cells. It acts through positioning actin filaments associated with nuclei at the inner periclinal wall; loss of AtAN function results in actin positioning along anticlinal walls, perpendicular to the leaf surface (Iwabuchi et al. 2019). This actin filament regulation is through an interaction with dual-specificity tyrosine phosphorylation-regulated kinases. This suggests that actin filament organization in mesophyll and pavement cells is critical for dark-induced nuclear migration. Further elucidation of these actin regulatory mechanisms may provide a

better understanding of the importance of dark-induced nuclear migration.

During pathogenesis in plants, the host nucleus first moves toward a fungal infection site (Figure 1C, panel 1) (Heath et al. 1997; Genre et al. 2005; Griffis et al. 2014). In response to powdery mildew invasion, the nucleus of a pea pavement cell then migrates away from the infection site as the infection enters the colony expansion and sporulation phase (Sharma and Chandran 2022). Powdery mildew infection depends on actin, but not microtubules (Sharma and Chandran 2022). This actin-mediated nuclear movement response by the host is conserved across attacks from diverse pathogens (Sharma and Chandran 2022). The actin cytoskeleton itself plays a critical role in plant immunity, including its rearrangement in response to pathogen attack, involvement in defense signaling, transcription activation, secretion of defense proteins, and cell wall modification (Li and Staiger 2018). In Arabidopsis, during powdery mildew attack an actin patch is formed beneath the fungal invasion site, mediated by the ARP2/3 complex and Class I formins (Figure 2, Table 1) (Qin et al. 2021). Investigating if and how the nucleus interacts with this actin patch and whether such an interaction drives nuclear migration would further illuminate the host cytoskeletal response to pathogen attack.

During the plant effector-triggered immune response, chloroplasts migrate to the nucleus along actin filaments with the aid of stromules (Figure 1C, panel 2), which are stroma-filled tubule-like structures that extend from the chloroplast envelope (Hanson and Conklin 2020). These structures extend along microtubules, anchoring to actin filaments along nuclei, and promote perinuclear chloroplast clustering during effector-triggered immunity (Kumar et al. 2018). A KCH-type kinesin which is required for inducing stromule formation (Kinesin Inducing Stromule formation 1, AtKIS1) was identified and characterized as critical for this perinuclear clustering through the induction of stromules (Figure 2, Table 1) (Meier et al. 2023). The microtubule-binding motor domain and the tail domain of AtKIS1 are required for stromule formation (Meier et al. 2023). Stromule formation induced by AtKIS1 only requires microtubules and not actin filaments (Meier et al. 2023). The actin-binding calponin homology domain, motor domain, and tail domain are all involved in perinuclear chloroplast clustering (Meier et al. 2023). AtACTIN7, the most abundant isoform of actin, is also critical for perinuclear chloroplast clustering in Arabidopsis mesophyll chloroplasts (Sheahan et al. 2020). Stromule formation and an abundance of actin filaments are required for perinuclear chloroplast clustering to occur (Sheahan et al. 2020; Meier et al. 2023).

The importance of both AtKIS1 and actin in the movement of chloroplasts to the nucleus further expands our understanding of the relationship between the nucleus and cytoskeleton during stimulus responses; here we have a movement toward the nucleus via the cytoskeleton. Greater understanding of the links between the cytoskeleton, nucleus, and chloroplasts would provide a broader insight into the importance of this movement during immunity. Together, the role of the nucleo-cytoskeletal interface in responses to stimuli depends greatly on actin networks, with contributions from microtubules. The connection of these cytoskeletal networks to the nucleus, as well as a broader understanding of the regulation of these networks, promises to greatly expand our understanding of these phenomena.

3 | Interface Between Nucleus and Cytoskeleton

3.1 | Role of Nuclear Migration and Cytoskeletal Organization During Asymmetric Cell Division

During asymmetric cell division (ACD), the nucleus migrates to the site of division, using different combinations of F-actin and microtubules, and this migration is often required for pre-prophase band and cortical division zone formation (Yi and Goshima 2022; Ashraf et al. 2023; Attrill et al. 2024; Yi and Goshima 2020; Kimata et al. 2016; Yi et al. 2025). Recent work has begun to dissect the relationship between the cytoskeleton and nuclear migration in patterning asymmetric cell division.

Arabidopsis guard cells form stomatal pores, which allow plants to undergo gas exchange, and have a tightly regulated spacing to prevent water loss. During guard cell development, a meristemoid mother cell divides asymmetrically to form a stomatal lineage ground cell, which will undergo further divisions to develop into a stomatal pore (Pillitteri and Torii 2012; Torii 2021). Two nuclear migrations occur during these divisions: one pre-mitotic microtubule-dependent nuclear migration and one post-mitotic actin- and AtMyosin XI-i dependent migration toward a second division site, which can create a second stomatal-lineage ground cell (Figure 1C, panel 8, Figure 2, Table 1) (Muroyama et al. 2020). Both of these divisions are regulated by a polarity crescent of the proteins BASL and Brxf, which orients the nuclear migration (Muroyama et al. 2020).

In haploid *Marchantia polymorpha* spores, asymmetric microtubule and actin arrays, including acentrosomal microtubule organizing centers (MTOCs) around the nucleus, coordinate to move the nucleus to the basal end of the spore before the first cell division (Figure 1A, panel 1) (Attrill et al. 2024). The number and orientation of the polar organizers are regulated by MpKatanin, a protein involved in microtubule severing, the internal "breaking" of a microtubule (Figure 2, Table 1) (Attrill and Dolan 2024). The basal polar organizer leads the migration, with a dense astral array of microtubule filaments extending from it and determines the nuclear and organizer position. Actin filaments are additionally reorganized into a filament patch at the basal pole during and after cytokinesis. Here, microtubules and actin play different roles in the pre-ACD nuclear migration compared with the asymmetric divisions in the Arabidopsis stomatal lineage, with both microtubules and actin involved in the same nuclear migration. Actin filaments are required for migration of the nucleus to the basal pole, while microtubules have a more expansive role; they are required for migration and orientation of the nucleus to the basal pole and retention of the nucleus at the basal pole after it has migrated (Attrill et al. 2024).

Both F-actin and microtubules are also required for nuclear migration during asymmetric subapical cell branching in *Physcomitrium patens* protonema (Figure 1A, panel 2) (Yi and Goshima 2020). Following apical cell division, the actin cytoskeleton, together with Rho of plants (ROP) GTPases (Figure 2, Table 1), regulates the bulging of a membrane subdomain in

the subapical cell. This bulge then regulates the microtubules connected to its base, which are required for the long-distance transport of the nucleus to the division site. From an evolutionary perspective, this suggests that the involvement of both F-actin and microtubules for nuclear migration during land plant asymmetric cell divisions is well conserved, but that the specific roles of the two cytoskeletal systems vary.

The nature of the connection of the nucleus to the cytoskeleton during asymmetric cell division has only recently begun to be examined. LINC complexes, which consist of an inner nuclear membrane SUN protein and an outer nuclear membrane KASH protein, have been shown to be important in connecting the nucleus to the cytoskeleton throughout opisthokonts (Starr and Fridolfsson 2010; Meier et al. 2017; Groves et al. 2020). During the asymmetric subapical branching in *Physcomitrium patens*, PpSUN2 (Figure 2, Table 1) was identified as a factor required for nuclear movement, MTOC formation, and the onset of mitosis (Yoshida et al. 2023). In a *Ppsun2*-KO line, fewer microtubule bundles around the nucleus were seen, suggesting that PpSUN2 is required for the association of microtubules with the NE during mitosis. Loss of PpSUN2 further impacted chromosome alignment, spindle orientation, and MTOC positioning and attachment to the NE (Yoshida et al. 2023). This is the first report implicating a plant SUN protein in nuclear migration during asymmetric cell division; previously, SUN proteins were shown to be involved in nuclear migration in tip-growing pollen tubes (Zhou et al. 2015).

The role of KASH proteins in nuclear positioning during asymmetric cell division has also been recently examined. In maize, ZmMLKS2, a *Zea mays* SINE1-like KASH protein containing an ARMADILLO-repeat region (Figure 2, Table 1) (Gumber et al. 2019), is required for maize subsidiary cell division (Gumber et al. 2019; Ashraf et al. 2023). During maize stomatal development, an asymmetric cell division establishes a guard mother cell (GMC) and a subsidiary mother cell (SMC). The SMC then divides asymmetrically again to form two subsidiary cells (Figure 1B, panel 3). During the SMC division, the nucleus migrates toward the GMC using actin filaments and is then anchored at the division site via microtubules (Panteris et al. 2006). *mlks2-1* has pre-mitotic nuclear positioning defects during SMC division, which result in mispositioned division sites. Nuclear migration in *zmmlks2* mutants was misdirected more often and had less stable post-PPB band formation (Ashraf et al. 2023). Overall, this suggests that ZmMLKS2 is important for the stability and directionality of nuclear migration during subsidiary cell formation. The importance of maize SUN proteins during nuclear migration has not been examined; however, loss of the nuclear lamina component ZmKAKU4 (Figure 2, Table 1) results in similar subsidiary cell defects (McKenna et al. 2021), suggesting that the connection of ZmMLKS2 to the INM and possibly the nuclear lamina plays a role during subsidiary cell asymmetric cell division.

LINC complex proteins are thus important for nuclear migrations in asymmetric cell division, from *Physcomitrium* to maize, but the exact nature of the nucleo-cytoskeletal interface and the contribution of each type of cytoskeleton can vary significantly across species. Further investigation of the impacts of LINC complexes on the cytoskeleton during these nuclear migrations may contribute to a better understanding of the role of the nucleo-cytoskeletal interface during asymmetric cell division. The role of actin and microtubules can vary significantly between species, with separate, opposing, or synergistic effects of actin and microtubules on nuclear migration. Understanding this interface may thus provide greater insights into the importance of these cytoskeletal contributions, and into the reasons for their variability.

3.2 | Nuclear Envelope and the Nucleus in Meiosis

During meiosis, like during mitosis, plant LINC complexes have been suggested to form a bridge between the NE and the cytoskeleton. Previous work in Arabidopsis and maize showed that SUN proteins are required for synapsis, crossover events, and telomere dynamics, along with the Arabidopsis kinesin Pollen Semi-Sterility 1 (AtPSS1). AtPSS1 can interact with the KASH proteins AtWIP1 and AtWIP2, although whether this interaction is important during meiosis has not been examined (Duroc et al. 2014; Varas et al. 2015; Pradillo et al. 2019). In maize, both SUN proteins and the KASH protein ZmMLKS2 have been shown to play roles in telomere dynamics, bouquet formation, and chromosome segregation (Murphy et al. 2014; Gumber et al. 2019; Pradillo et al. 2019). This suggests that a bridge between SUN proteins, KASH proteins, and the cytoskeleton is required for several steps during meiosis.

In animals, LINC complexes are important to link the cytoskeleton to centromeres during centromeric rapid movement during prophase, which might contribute to homologous pairing; but this connection has not been established in plants (Burke 2018; Zeng et al. 2018). In Arabidopsis, SUN proteins have recently been linked to these rapid movement events (Figure 1C, panel 5, Figure 2, Table 1) (Cromer et al. 2024). Meiotic recombination proteins are not required for this process, but loss of AtSUN1 and AtSUN2 resulted in a substantially lower speed of movement. During meiotic prophase I, the nuclear envelope undergoes a massive rearrangement where SUN proteins polarize during zygotene and pachytene, while the nuclear lamina disappears (Cromer et al. 2024). SUN proteins additionally help to anchor telomeres to the nuclear envelope (Cromer et al. 2024). Together, this is the first establishment of LINC complex protein involvement in centromeric rapid movements in plants and further increases our understanding of the role of nuclear envelope and nucleoskeletal proteins during plant meiosis.

Our understanding of plant LINC complexes during meiosis has also been recently expanded to *Oryza sativa* (rice), where, similar to Arabidopsis, OsSUN1 and OsSUN2 localize to the NE during meiosis, and their loss results in fewer crossover events (Figure 1B, panel 2, Figure 2, Table 1) (Zhang et al. 2020). OsSUN2 can complement OsSUN1 in rice, but the reverse is not true. Both OsSINE1 and OsWIP1 can interact with OsSUN1 and OsSUN2, as well as OsPSS1 (Zhang et al. 2020), suggesting that multiple LINC complexes may be involved in linking chromosomes to microtubules. OsPSS1 (Figure 2, Table 1) is recruited to the NE and is required for normal meiotic behavior through its involvement in spindle assembly and microtubule bundling, homologous pairing and synapsis, and reduced crossovers (Zhou et al. 2024). Due to the interaction of OsPSS1 with multiple

KASH proteins, multiple mutants may need to be examined to elucidate the importance of KASH proteins during meiosis. Further study of LINC complex roles during meiosis promises to greatly expand our understanding of both cytoskeletal and chromatin dynamics during meiosis.

3.3 | The Nucleo-Cytoskeletal Interface in ABA-Induced Stomatal Closure

LINC complexes have previously largely been studied in the context of nuclear shape and positioning (Meier et al. 2017). Recent work, however, has begun to examine the impact of KASH proteins, and therefore the nucleus, on the cytoskeleton. Two Arabidopsis KASH proteins, AtSINE1 and AtSINE2 (Figure 2, Table 1), have been shown to play important roles in stomatal cytoskeletal regulation (Biel et al. 2020a, 2020b, 2022; Moser et al. 2024). Stomata consist of two guard cells that together form a stomatal pore, which allows for gas exchange. The apertures of stomata are tightly regulated to prevent water loss, and the hormone Abscisic Acid (ABA) is produced during drought and begins a signaling cascade that results in stomatal closure. Stomatal closure is accompanied by a fundamental reorganization of the cytoskeleton. While microtubules are radially arrayed in fully open stomata and depolymerize during closure, actin filaments reorganize from radial filaments to longitudinal actin cables, going through an intermediate depolymerization step (Figure 1C, panel 9) (Eun and Lee 1997; Gao et al. 2008, 2009; Eisinger et al. 2012; Jiang et al. 2014).

AtSINE1 and AtSINE2 are paralogous proteins containing an ARMADILLO (ARM)-repeat domain, a transmembrane domain, and a KASH tail, which interacts with AtSUN1 and AtSUN2, together forming a LINC complex (Zhou et al. 2014). The ARM domain of AtSINE1 co-localizes with actin filaments, suggesting a direct or indirect interaction (Zhou et al. 2014). Loss of AtSINE1 or AtSINE2 results in reduced stomatal closure in response to ABA (Biel et al. 2020a). Without AtSINE1 or AtSINE2, microtubule arrays in fully open stomata consist of fewer and more disarrayed filaments, which show very little change during stomatal closing, suggesting a role for both AtSINE1 and AtSINE2 in regulation of the microtubule cytoskeleton (Biel et al. 2020b). While AtSINE1 and AtSINE2 play similar roles in microtubule organization, they play opposing roles during actin cytoskeletal reorganization. AtSINE2 contributes to the depolymerization of the radially arranged actin cytoskeleton, while AtSINE1 contributes to the repolymerization of the actin cytoskeleton to longitudinal actin cables (Biel et al. 2022).

The pathways previously shown to regulate actin reorganization involve a complex signaling cascade through a PYR1-like/protein phosphatase type 2C signaling module, a variety of kinases, SCAR/WAVE, and finally the ARP2/3 complex (Figure 2, Table 1). Additionally, several actin depolymerizing factors and the guard-cell specific actin-reorganizing factor SCAB1 (Figure 2, Table 1) regulate the cytoskeleton during ABA-induced stomatal closure (Qian et al. 2019, 2019; Zheng et al. 2019; Li et al. 2022; Shi et al. 2022). The pathways regulating microtubule reorganization are less well characterized but involve several E3 ubiquitin ligases, MAPs, WDL7, phosphatidic acid signaling, and an Open Stomata1–SPIRAL1 module (Yu et al. 2020; Dou et al. 2021, 2023; Li et al. 2022; Wang et al. 2022).

AtSCAB1 is a plant-specific protein involved in actin bundling. It is regulated during stomatal closure by phosphorylation and phosphoinositide binding, and regulates Ca^{2+} and ABA signaling during osmotic-induced stomatal closure (Zhao et al. 2011; Yang et al. 2021; Fu et al. 2022; Zhang et al. 2023). Double mutants between AtSCAB1 and AtSINE1 suggest that AtSCAB1 is epistatic to AtSINE1, and AtSINE2 is epistatic to AtSCAB1, confirming that AtSINE1 and AtSINE2 regulate actin at different steps of stomatal closure, and suggesting roles for AtSINE1 in actin bundling (Moser et al. 2024).

The ARP2/3 complex is a well-characterized actin-binding complex involved in branching, which is required for the formation of longitudinal filaments during stomatal closure (Jiang et al. 2012). Double mutants between the ARP2/3 complex and AtSINE1 demonstrated the role of the ARP2/3 complex in the same pathway as AtSINE1 during ABA-induced stomatal closure, whereas the ARP2/3 complex and AtSINE2 are in opposing pathways (Moser et al. 2024).

Together, this suggests that the nuclear envelope plays an important role in cytoskeletal regulation during stomatal closure, which has previously been unexamined. The nature of this regulation, and whether it occurs by a direct or indirect effect of AtSINE1 and AtSINE2 on the proteins involved in actin or microtubule reorganization or in an indirect way through changes in gene expression, awaits further investigation.

4 | Connection Between the Nucleoskeleton and the INM

4.1 | Composition of the Plant Nucleoskeleton

In animals, the inner nuclear membrane (INM) is supported by the nuclear lamina, a network of filaments that are significant components of the animal nucleoskeleton (Starr and Fridolfsson 2010). The animal nuclear lamina is composed of lamins, which are type V intermediate filament proteins (Aebi et al. 1986; Burke and Stewart 2013). Lamins connect to the INM through interactions with SUN proteins and therefore are connected to the cytoskeleton through LINC complexes. Through this connection to LINC complexes, lamins are vital for nuclear shape determination, nuclear movement, and mechanical signal transduction (Burke and Stewart 2013). Additionally, lamins interface with chromatin, both directly and indirectly (Mattout et al. 2015).

Plants lack homologs of animal lamins and do not contain intermediate filament proteins. Nonetheless, a similar structure of electron dense nucleoskeleton has been described (Ciska et al. 2013), and proteins proposed to make up the plant nucleoskeleton have been identified (Meier et al. 2017). The first plant lamins were identified in *Daucus carota* as Nuclear Matrix Constituent Proteins (NMCPs) (Figure 2, Table 1) (Masuda et al. 1993; Ciska et al. 2013; Kimura et al. 2014). In Arabidopsis, the plant lamin homologs of NMCPs are named CROWDED

NUCLEI (CRWN) 1–4 (first identified as LITTLE NUCLEI/LINC) (Figure 2, Table 1) (Dittmer et al. 2007; Sakamoto and Takagi 2013; Wang et al. 2013). NMCP/CRWNs do not have sequence similarity to animal lamins, but do share some structural features, such as a tripartite structure and extended coiled-coil domain (Ciska et al. 2013).

Two classes of NMCP/CRWNs have been identified: NMCP1-type and NMCP2-type plant lamins (Ciska et al. 2013; Wang et al. 2013). Arabidopsis has three NMCP1-type proteins in AtCRWN1-3 and one NMCP2-type protein, AtCRWN4 (Sakamoto and Takagi 2013; Wang et al. 2013; Poulet et al. 2017b). AtCRWN1 and AtCRWN4 are localized to the nuclear periphery and are key determinants of nuclear shape (Dittmer et al. 2007; Sakamoto and Takagi 2013; Wang et al. 2013). AtCRWN2 and AtCRWN3 have been reported to localize in the nucleoplasm, but recent evidence suggests that under native expression, both proteins localize to the nuclear periphery, indicating that the subcellular localization of AtCRWN2 and AtCRWN3 may be closely linked to expression level (Sakamoto et al. 2020).

AtCRWN1 has been shown to interact with AtCRWN2, AtCRWN3, and AtCRWN4, while AtCRWN4 only interacts with AtCRWN1 (Sakamoto et al. 2020). Yin et al. (2024) explored which AtCRWN1 domains are required for interaction with the other NMCP1-type CRWNs, AtCRWN2 and AtCRWN3. The AtCRWN1 N-terminus, containing both coiled-coil domains, is sufficient to rescue a nuclear shape defect in Arabidopsis *crwn1 crwn2* guard cells (Yin et al. 2024). As shown by both yeast 2-hybrid and co-immunoprecipitation, the AtCRWN1 coiled-coil domain 1, but not coiled-coil domain 2, is required for interaction with AtCRWN2, AtCRWN3, and AtCRWN1 self-interaction (Yin et al. 2024). Furthermore, Blunt et al. (2020) examined interdependence between AtCRWN1 and AtCRWN4. AtCRWN1 protein abundance does not decrease in *crwn2*, *crwn3*, or *crwn4* mutants. In contrast, AtCRWN4 protein levels are drastically decreased in *crwn1-1* and partially decreased in *crwn3-1* (Blunt et al. 2020). The AtCRWN4 dependence on AtCRWN1 and NMCP1-type CRWNs in general is independent of transcript level, suggesting the interaction between CRWNs may be important for protein stability (Blunt et al. 2020). Taken together, this suggests that individual NMCPs/CRWNs are dependent on an intact lamina meshwork for their stability.

Recent studies have focused on the plant lamin network, using superresolution microscopy to visualize the meshwork. Sakamoto et al. (2020) utilized STED to examine the NMCP1-type CRWNs (AtCRWN1-3), while Masuda et al. (2021) used STED to examine the plant lamins ApNMCP1 and ApNMCP2 in *Apium graveolens*. The NMCP1-type CRWNs form continuous networks at the nuclear periphery (Sakamoto et al. 2020). Masuda et al. (2021) visualized ApNMCP1 and ApNMCP2, allowing for examination of the interconnected network. The two types of plant lamins both localized to the nuclear periphery, and skeletonization of the fluorescent signal revealed that the individual networks overlapped and were associated (Masuda et al. 2021). ApNMCP1 was additionally shown to overlap with chromatin. *Daucus carota* NMCP1 and NMCP2 were purified and tested for their ability to self-assemble into filaments. Both DcNMCP1 and DcNMCP2 were able to form filaments in vitro, with DcNMCP1 dimers able to readily form long filaments (Masuda et al. 2021). These data represent the first evidence for individual NMCPs forming a lamin-like meshwork in vivo, and NMCPs assembling into filaments in vitro. It further validates NMCPs/CRWNs as the functional analogs of animal lamins.

A recent study reported changes in nucleoskeleton structure in response to abiotic stress. Following heat stress, AtCRWN1, AtCRWN4, and AtKAKU4 are localized in the nucleoplasm, rather than at the nuclear periphery (Wang et al. 2023). This change in localization was nucleoskeleton-specific, as SUN1 and the nucleoporin NUP1 did not change localization. Genomic loci with plant nuclear lamina-associated domains also lost their nuclear periphery association under heat stress (Wang et al. 2023). This indicates that the plant nuclear lamina disassembles in response to heat, as well as several other abiotic stresses (Wang et al. 2023). The nature of lamina disassembly in response to stimuli remains to be elucidated. Assembly and disassembly of the plant lamina are emerging fields of study, and the recent advances in understanding the plant lamina meshwork will create a platform for advancements on that front.

4.2 | Nucleoskeletal Connections With the Inner Nuclear Membrane and Nuclear Pore Complex

In plants, the connection between the INM and nuclear lamina remains to be thoroughly investigated. In animals, the nucleoskeleton is physically connected to the INM through interactions with several proteins, including Lamin B Receptor, MANI, Emerin, and SUNs (Starr and Fridolfsson 2010). SUN proteins and LEM domain proteins tether the lamina to the INM in animals (Starr and Fridolfsson 2010; Mirza et al. 2021; Sobo et al. 2024). Some classes of LEM domain proteins interact with chromatin via an intermediate, barrier-to-autointegration factor (BAF), which is not present in plants (Mirza et al. 2021). Many animal INM proteins do not have functional homologs in plants, including LEM domain proteins, with the exception of SUN proteins (Graumann et al. 2010). SUN proteins and LEM domain proteins tether the lamina to the INM in animals. There is evidence for an Arabidopsis SUN-CRWN1 interaction, via the nucleoplasmic domain of AtSUN1 and AtSUN2 (Graumann 2014). Recent work from Tang et al. (2022a) has identified a novel Arabidopsis INM protein that interacts with the nucleoskeleton, PLANT NUCLEAR ENVELOPE TRANSMEMBRANE PROTEIN 2 (PNET2) (Figure 2, Table 1). AtPNET2 was identified from two independent proteomic screens, a subtractive proteomic screen and a proximity labeling screen, using the Arabidopsis homolog of an animal INM protein as bait (Tang et al. 2020, 2022a). Three PNET2 proteins are encoded in the Arabidopsis genome, AtPNET2_A, AtPNET2_B, and AtPNET2_C, which have been proposed as Arabidopsis homologs of the opisthokont INM protein NempA (Tang et al. 2022a). The N-terminal, nucleoplasmic domain of AtPNET2_A and AtPNET2_B interacts with AtCRWN1. AtPNET2_A immunoprecipitated the histone H2A, and AtPNET2_B can interact with the histone acetylase HTA6, via bimolecular fluorescence complementation, indicating the AtPNET2-nucleoskeleton association may play a role in

chromatin regulation (Tang et al. 2022a). PNET2s are therefore good candidates to be the functional analogs of LEM domain proteins in plants, connecting to both the plant nuclear lamina and chromatin. Further study will be required to elucidate the role of these proteins in the lamina-chromatin interface.

In addition to AtCRWNs, another protein at the nuclear periphery has been identified and characterized. AtKAKU4 is an angiosperm-specific protein and was initially identified in a mutagenesis screen for nuclear shape determinants (Goto et al. 2014; Poulet et al. 2017b). AtKAKU4 has been reported to interact with AtCRWN1 (Goto et al. 2014). Absence of AtKAKU4 results in round nuclei, in line with phenotypes reported for other nucleoskeleton mutants (*crwn* mutants) (Wang et al. 2013; Goto et al. 2014). AtKAKU4 has been proposed to be a member of the plant lamina because of several factors: it localizes to the nuclear periphery, *kaku4* mutants phenocopy the nuclear size and shape defects reported in *crwn* mutants, and AtKAKU4 physically interacts with AtCRWNs. However, AtKAKU4 lacks the structural features that make AtCRWNs attractive candidates to be the functional analogs of animal lamins. Additionally, overexpression of AtKAKU4 results in nuclear invaginations and deformities, which are more extensive than nuclear deformities reported for other nucleoskeletal proteins, leading to the possibility that AtKAKU4 is involved in a different aspect of nuclear shape and size determination (Goto et al. 2014).

A recent study from Mermet et al. (2023) endeavored to identify the specific regions in AtKAKU4 required for its nuclear peripheral localization. They show that AtKAKU4 interacts with all three NMCP1-type AtCRWNs (AtCRWN1-AtCRWN3), through the N-terminus (Mermet et al. 2023). Three conserved motifs within the N-terminus were identified, with M1 and M2 shown to be involved in the interaction with CRWNs, while all three motifs (M1-M3) were required for nuclear peripheral localization (Mermet et al. 2023). These protein motifs were also identified in two Arabidopsis nuclear basket nucleoporins, Nup82 and Nup136 (Figure 2). AtKAKU4, AtNup82, and AtNup136 were shown to interact with NMCP1-type CRWNs (AtCRWN1-3), and AtKAKU4 interacted with AtNup82 and AtNup136 in a Bimolecular Fluorescence Complementation assay (Mermet et al. 2023). Similar to AtKAKU4, the M1 and M2 motifs were sufficient for AtNup82 and AtNup136 interactions with CRWNs. This suggests that KAKU4 is closely associated with both nuclear pores and the nuclear lamina.

A novel nucleoporin was recently identified, guanylate-binding protein-like GTPase (GBPL3) (Figure 2), through a series of proximity labeling screens (Tang et al. 2022b). AtGBPL3 interacts with nuclear basket nucleoporins (AtNup136, AtNup82) and NMCP1-type CRWNs (AtCRWN1-CRWN3), similar to KAKU4 (Tang et al. 2022b). AtGBPL3 can also recruit and co-localize with proteins performing a variety of roles, including mRNA processing, transcription regulation, and chromatin remodeling. Taken together, the plant nucleoskeleton connection to the nuclear pore complex includes KAKU4 and GBPL3. These studies have furthered our understanding of the connections of the nucleoskeleton with the INM, both directly (SUN and PNET2) and through interactions with the nuclear pore. Many of these proteins lack homologous animal counterparts, suggesting that the nature of this connection is different from animals and that there may be more proteins yet to be identified.

4.3 | Physiological Role of the Plant Nucleoskeleton

In animals, the nucleoskeleton is important for mechanosensing, as well as maintaining nuclear shape and nuclear integrity (Hatch 2018; McPhee et al. 2024; Sobo et al. 2024). Much of the characterization of the biological role of the plant nucleoskeleton to this point has been done in Arabidopsis. CRWNs (NMCPs) are required for nuclear shape and size control in a variety of tissues including leaves, guard cells, root hairs, and trichomes (Dittmer et al. 2007; Wang et al. 2013; Sakamoto and Takagi 2013; Zhou et al. 2015; Poulet et al. 2017a, 2017b). In addition to the decrease in nuclear size, loss of AtCRWNs results in a decrease in chromocenter number (Wang et al. 2013). For all these phenotypes, AtCRWN1 and AtCRWN4 appear to play a predominant role, with loss of AtCRWN2 or AtCRWN3 alone insufficient to trigger a defect. The significant reduction in nuclear size has an impact on the whole plant level, with double mutants of NMCP1-type CRWNs (*crwn1 crwn2*, *crwn1 crwn3*) presenting a significant vegetative growth defect, with a large reduction in rosette size (Wang et al. 2013). Triple mutants with no NMCP1-type CRWNs are inviable, and the *crwn1 crwn2 crwn4* and *crwn1 crwn3 crwn4* triple mutants have a severe vegetative growth defect (Wang et al. 2013).

A recent study examined the role the plant lamina plays in reproduction. Silique length and seed set were significantly reduced in the *crwn1 crwn2* double mutant, and the severity of the defects was increased in the *crwn1 crwn2 crwn4* and *crwn1 crwn3 crwn4* triple mutants (Choi and Gehring 2024). All three *crwn* multiple mutants displayed pollen defects, and aborted seeds were present in all three mutants (Choi and Gehring 2024). Aberrant seeds were reported, and seed germination rates in the *crwn* mutants were reduced. These data together indicate the nuclear shape and size defects observed in *crwn* mutants have an impact on development.

Additionally, the role the nuclear lamina plays in global histone methylation has been an area of active study. Choi and Gehring (2024) determined that H3K27me3 was reduced in *crwn1 crwn2* mutants, consistent with prior studies that reported loci that lost the same methylation state (Choi et al. 2019; Choi and Richards 2020). In addition to CRWNs, Cao et al. (2024) examined the histone methylation state in the presence and absence of AtKAKU4. In a knockdown of AtKAKU4, H3K27me3 levels were also decreased, as were those of H3K9me2 (Cao et al. 2024). These data indicate that the plant lamina plays a role in maintaining the epigenetic state at the nuclear periphery, but more studies will be required to elucidate the mechanism of this regulation.

In addition to its role in global histone methylation, the plant nucleoskeleton has been shown to play a role in 3D genome organization (Wang et al. 2013; Poulet et al. 2017a). Several studies have shown that CRWNs are required for a variety of stress responses (Groves et al. 2020). A recent study from Sakamoto

et al. (2020) has reported a role for CRWNs in maintaining copper tolerance. In wild type, under excess copper conditions, the Copper Associated (CA) gene locus moves from the center of the nucleus to the nuclear periphery (Sakamoto et al. 2020). In the *crwn1 crwn4* mutant, the CA locus fails to relocate to the nuclear periphery (Sakamoto et al. 2020). Following copper-induced relocation, expression of several of the CA genes increases in WT, but not in the *crwn1 crwn4* mutant (Sakamoto et al. 2020). These data are the first evidence in plants for the plant lamina being required for locus repositioning, and that movement being linked to expression. This indicates that in the absence of a fully intact nucleoskeleton, 3D genome reorganization in response to stress is impaired.

Recent studies have begun to expand our knowledge of the role of NMCPs in other species. NMCPs have been previously identified in a variety of species, including *Daucus carota*, *Oryza sativa*, and *Allium cepa* (Masuda et al. 1993, 1997; Ciska et al. 2018; Yang et al. 2020). In *Solanum lycopersicum*, the genome encodes for two NMCP1-type proteins (SlNMCP1A & SlNMCP1B), and one NMCP2-type protein (SlNMCP2) (Figure 2, Table 1) (Blunt et al. 2023). Loss of NMCP2 in *Solanum lycopersicum* was lethal, whereas in Arabidopsis, loss of CRWN4 has no observable whole plant phenotypes (Wang et al. 2013; Blunt et al. 2023). Loss of SlNMCP1A or SlNMCP1B resulted in a nuclear size and shape defect in guard cells, but only in *nmcp1b* mutants was a whole plant phenotype observed (Figure 1C, panel 11) (Blunt et al. 2023). In *nmcp1b* mutants, the growth rate was decreased, leading to a decrease in fresh weight at the same time point, compared to wild type and *nmcp1a* mutants. Loss of nucleoskeleton components in *Solanum lycopersicum* produced a different set of developmental defects compared to Arabidopsis, but similar cellular level defects (Sakamoto and Takagi 2013; Wang et al. 2013; Blunt et al. 2023). This indicates that the composition of the *Solanum lycopersicum* nuclear lamina may be different from Arabidopsis, and that the dynamics between SlNMCP1 and SlNMCP2-type proteins may be different between species.

In *Zea mays*, two NMCP homologs have been identified, ZmNCH1 (NMCP1-type) and NCH2 (NMCP2-type) (Gumber et al. 2019; McKenna et al. 2021). In addition, homologs of the Arabidopsis nucleoskeleton protein AtKAKU4 have been identified, ZmMKAKU41 and ZmKAKU42 (McKenna et al. 2021). Similar to Arabidopsis, overexpression of ZmKAKU41 in the heterologous system *Nicotiana benthamiana* resulted in nuclear invaginations and other nuclear abnormalities. Additionally, co-expression of ZmKAKU41 with ZmNCH1 or ZmNCH2 resulted in a marked increase in severe nuclear abnormalities (McKenna et al. 2021). Following treatment with Latrunculin B, the number of nuclear abnormalities increased (McKenna et al. 2021). These data suggest that actin plays a role in stabilizing nuclear shape and is required for the induction of the nuclear invaginations observed in AtKAKU4 overexpression.

In the liverwort *Marchantia polymorpha*, the genome only encodes for a single NMCP, *MpNMCP* (Figure 2, Table 1) (Wang et al. 2021). In angiosperms, null mutants for CRWNs/NMCPs have not been recovered, indicating they may be required for viability (Wang et al. 2013; Blunt et al. 2023) Unlike angiosperms, the absence of NMCPs is not lethal, but *mpnmcp1* mutants were dwarfed compared to wild type (Wang et al. 2021). However, *mpnmcp1* mutants did not display nuclear morphology defects, and *MpNMCP1* could not complement the Arabidopsis *crwn1 crwn2* mutant, in either nuclear morphology or dwarfed growth (Wang et al. 2021). This indicates that NMCP function may have diverged, in both form and function of the nuclear lamina and its constituent proteins, between vascular and non-vascular land plants.

Taken together, recent work highlights the vital importance of the plant lamina for growth and development throughout the plant kingdom. These studies have further elucidated the role of the plant lamina in genome organization, as well as expanded our knowledge into new species.

5 | Summary and Outlook

A great deal of progress has been made in characterizing the players and roles of the nucleo-cytoskeletal interface in different cell types and in new species. The migrations of the sperm cell nucleus in fertilized *A. inaequidens* central cells (González-Gutiérrez et al. 2021), prior to asymmetric cell division in *M. polymorpha* spores (Attrill et al. 2024), and in response to fungal attack in *P. sativum* (Sharma and Chandran 2022) have been newly characterized and provide some of the first examinations of the intersection of the cytoskeleton with nuclear migrations in these species. Future work to dissect the components of these nucleo-cytoskeletal interfaces, along with comparisons to their Arabidopsis counterparts, will enhance our understanding of the mechanisms and evolution of nuclear migration.

Actin and microtubule dynamics have begun to be co-examined during a wide variety of nuclear migrations across cell types and species. In order to move the nucleus, a number of different patterns emerge: microtubule or actin filaments can form platforms for the other filament (Yi and Goshima 2020; Ali et al. 2023), coordinate nuclear migration in opposing directions (Zhang et al. 2019; Muroyama et al. 2020; Brueggeman et al. 2022) or the same direction (Attrill et al. 2024; Wang et al. 2024), or act alone (Ali et al. 2020; Sharma and Chandran 2022). Of experimental interest will be whether these patterns of nuclear migration share additional characteristics across disparate contexts, such as regulators of actin or microtubule organization, or interfacing proteins between the nucleus and cytoskeleton. Additionally, while nuclear positioning and migrations are important for cellular growth and function in many of these processes, why nuclear migrations must occur during tip growth and stimulus response is largely unknown and is a site for future experimentation.

Calponin-homology kinesins emerge here as new players at the nucleo-cytoskeletal interface across tissues and species (Yamada and Goshima 2018; Schattner et al. 2021; Meier et al. 2023; Wang et al. 2024). KCHs have been previously shown to be involved in nuclear movement in tobacco (Frey et al. 2010), and as cross-linkers of actin and microtubules (Klotz and Nick 2012; Walter et al. 2015), and it will be exciting to see if they emerge as factors in any of the less characterized nuclear migration events as well.

A major site of future investigation will be the molecular nature of the connection of the nucleus to the cytoskeleton. While LINC complex proteins have been shown to impact nuclear movement (Tamura et al. 2013; Zhou et al. 2015; Ashraf et al. 2023; Yoshida et al. 2023) and cytoskeletal organization (Biel et al. 2020b, 2022; Yoshida et al. 2023), whether and how LINC complexes interface with the cytoskeleton in many of these processes is an open question. Recent work suggests that the LINC complex coordinates between microtubules and chromosomes during meiosis (Zhang et al. 2020; Zhou et al. 2024), but whether LINC complexes might play a role in any of these newly characterized nuclear migrations, either in cytoskeletal organization or in connecting the nucleus to the cytoskeleton during movement, remains to be considered.

While many plant nucleoskeletal proteins have previously been identified, new work has begun to characterize the interactions and protein stability dependencies between different nuclear lamina proteins in Arabidopsis (Blunt et al. 2020; Sakamoto et al. 2020; Masuda et al. 2021; Yin et al. 2024). NMCPs have newly been established as forming a filamentous network at the nuclear periphery and self-assembling into filaments in vitro (Masuda et al. 2021). Disassembly of the nuclear lamina has also been shown to be involved in abiotic stress responses (Wang et al. 2023). This provides a basis for future experiments to begin querying the in vivo formation and disassembly of the lamina network, which could provide better insights into how the nuclear lamina regulates genome organization, particularly during stress responses.

Nucleoskeleton components have now been identified in many new species, such as *S. lycopersicum*, *Z. mays*, and *M. polymorpha* (McKenna et al. 2021; Wang et al. 2021; Blunt et al. 2023). Examination of NMCPs in new plant species has found significantly different roles and compositions of NMCP1- and NMCP2-type proteins across species. This suggests that understanding the evolution of the nucleoskeleton is of interest, especially as work on NMCP proteins originated in disparate systems. Understanding the filament dynamics and network structures of NMCP1 and NMCP2 across species may give greater insight into the nature, formation, and composition of this filamentous network.

At the interface between the nucleus and nucleoskeleton, new players tether the nuclear lamina to the nuclear envelope in Arabidopsis. These proteins lack close animal homologs, suggesting that, as the plant nuclear lamina is not homologous to the animal nuclear lamina, the proteins required to interface between the plant nuclear envelope and lamina may be significantly different from those in animals (Tang et al. 2022a, 2022b; Mermet et al. 2023). This leaves open the possibility that there are more players interfacing between the nuclear envelope and lamina; additionally, given the different lamina compositions between plant species, there may be significantly different tethering proteins across plant species as well. Identifying these will require identifying both new INM proteins as well as proteins that could serve as intermediaries between INM proteins and the nuclear lamina.

Together, characterization of the interface between the nucleus and cytoskeleton has barely scratched the surface, but there is exciting potential for new molecular mechanisms in a variety of critical plant processes, which will further serve to expand our understanding of the possibilities of this interface throughout life.

Author Contributions

N.R.G. and K.A. conceived and researched the topic; N.R.G. structured the manuscript and oversaw the writing; N.R.G., K.A., and L.A.S. researched, wrote, and edited the topic; K.A. designed the figures; I.M. researched, wrote, and edited the topic, and provided funding.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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