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Review

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Cytoskeletal and membrane dynamics during higher plant cytokinesis

Author for correspondence:
Sebastian Y. Bednarek
Tel: +1 608 2630309
Email: sybednar@wisc.edu

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Colleen M. McMichael and Sebastian Y. Bednarek

Department of Biochemistry, University of Wisconsin-Madison, 433 Babcock Dr, Madison, WI, 53713, USA

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Summary

Following mitosis, cytoplasm, organelles and genetic material are partitioned into daughter cells through the process of cytokinesis. In somatic cells of higher plants, two cytoskeletal arrays, the preprophase band and the phragmoplast, facilitate the positioning and *de novo* assembly of the plant-specific cytokinetic organelle, the cell plate, which develops across the division plane and fuses with the parental plasma membrane to yield distinct new cells. The coordination of cytoskeletal and membrane dynamics required to initiate, assemble and shape the cell plate as it grows toward the mother cell cortex is dependent upon a large array of proteins, including molecular motors, membrane tethering, fusion and restructuring factors and biosynthetic, structural and regulatory elements. This review focuses on the temporal and molecular requirements of cytokinesis in somatic cells of higher plants gleaned from recent studies using cell biology, genetics, pharmacology and biochemistry.

I. Introduction

Cytokinesis, the final step of cell division, results in the partitioning of cellular components to form distinct daughter cells. In animals, cytokinesis begins at the cell periphery where an actinomyosin contractile ring drives invagination of the plasma membrane (PM) as new membrane is added to the growing furrow to facilitate abscission (Neto *et al.*, 2011). By contrast, higher plant cytokinesis is an inside-out process mediated by the cell plate (CP), whose orientation and assembly is orchestrated by the plant-specific cytoskeletal preprophase band (PPB) and phragmoplast (Samuels *et al.*, 1995; Jürgens, 2005; Backues *et al.*, 2007). In this review we highlight and focus on recent advances in our understanding of the cytoskeletal and membrane dynamics that mediate cytokinesis in somatic plant cells. For additional background on this subject, the reader is referred to several previous reviews concerning plant cytokinesis: Samuels *et al.* (1995); Otegui & Staehelin (2000); Verma (2001); Seguí-Simarro *et al.* (2004); Jürgens (2005); and Backues *et al.* (2007). For convenience, the proteins mentioned in this review are summarized in Tables 1 and 2.

Table 1 Cytoskeleton-associated proteins involved in plant cytokinesis

Proteins	AGI Accession Numbers	Orthologs[a]	Localization[b,c]	Function[b,c]	Reference(s)
TON1a, TON1b	At3g55000, At3g55005		PPB MTs	Organize/stabilize PPB MTs	Azimzadeh *et al.* (2008); Malcos & Cyr (2011)
MOR1/GEM1	At2g35630		PPB MTs	Organize/stabilize PPB MTs	Whittington *et al.* (2001); Kawamura *et al.* (2006)
AtKINUa/ ARK3/PAK	At1g12430		PPB MTs	Organize/stabilize PPB MTs	Sakai *et al.* (2008)
TON2/FASS/ EMB40	At5g18580	(Zm) DCD1, ADD1	PPB MTs	Regulate TON1a/b, MOR1, TAN1	Camilleri *et al.* (2002); Wright *et al.* (2009)
TAN1	At3g05330	(Zm) TAN1	PPB; CDZ	PPB memory	Walker *et al.* (2007)
RanGAP1	At3g63130		PPB; CDZ	PPB memory	Xu *et al.* (2008)
POK1, POK2	At3g17360, At3g19050		PPB; CDZ	Regulate TAN1, RanGAP1	Müller *et al.* (2006)
AIR9	At2g34680		PPB; CP leading edge; CW	CP recognition/ maturation	Buschmann *et al.* (2006)
KCA1/KAC1	At5g10470		Non-CDZ cortical MTs; phragmoplast midzone	(–)-end-directed kinesin	Vanstraelen *et al.* (2004, 2006); Malcos & Cyr (2011)
EB1a/EB1H2, EB1b, EB1c/ EB1H1	At3g47690, At5g62500, At5g67270		Phragmoplast MTs	MT (+)-end tracking protein	Chan *et al.* (2003); Van Damme *et al.* (2004); Bisgrove *et al.* (2008)
NEDD1	At5g05970		Spindle and phragmoplast MTs	γ-TuRC: nucleate/organize MTs	Zeng *et al.* (2009)
γ-tubulin/ TUBG1	At3g61650		Spindle and phragmoplast MTs	γ-TuRC: nucleate/organize MTs	Van Damme *et al.* (2004)
GCP2/TUBG2	At5g05620		Spindle and phragmoplast MTs	γ-TuRC: nucleate/organize MTs	Nakamura *et al.* (2010)
AUG1/ EMB2819, AUG3	At2g41350, At5g48520		Spindle and phragmoplast MTs	Augmin complex: recruit γ-tubulin and γ-TuRC	Ho *et al.* (2011)
AtFH5, AtFH8, AtFH14	At5g54650, At1g70140, At1g31810		PPB, spindle and phragmoplast MFs and MTs	Align phragmoplast MFs and MTs	Li *et al.* (2010b); Wang *et al.* (2012)
PAKRP2	At4g14330		Phragmoplast	Vesicle transport on MTs	Lee *et al.* (2001)
AtNACK1/ HIK, AtNACK2/ TES/STD	At1g18370, At3g43210	(Nt) NACK1, NACK2; (Os) DBS1/ OsNACK	Phragmoplast MTs; phragmoplast midzone	Phragmoplast organization/ dynamics; kinesin; activate MAPK cascade (NACK-PQR)	Nishihama *et al.* (2002); Strompen *et al.* (2002); Tanaka *et al.* (2004); Takahashi *et al.* (2010)
AtPAKRP1/ Kin-12a, AtPAKRP1L/ Kin-12b	At4g14150, At3g23670		Phragmoplast midzone	(+)-end-directed kinesin	Lee & Liu (2000); Pan *et al.* (2004)
AtKRP125c/ AtKin5C/ LPH/RSW7	At2g28620	(Nt) TKRP125, (Dc) KRP120	Phragmoplast MTs	(+)-end-directed kinesin	Asada *et al.* (1997); Barroso *et al.* (2000); Bannigan *et al.* (2007)
ATK5/Kin-5	At4g05190		Spindle MTs; phragmoplast midzone	(-)-end-directed kinesin; MT (+)-end tracking protein	Ambrose *et al.* (2005)
KCA2/KAC2	At5g65460		Phragmoplast midzone	(-)-end-directed kinesin	Vanstraelen *et al.* (2004, 2006); Malcos & Cyr (2011)
AtKCBP/ZWI	At5g65930	NtKCBP, TvKCBP, GhKCBP, HvKCBP	PPB MTs; phragmoplast MTs	(-)-end-directed kinesin; Ca^{2+}-calmodulin-regulated MT bundling	Bowser & Reddy (1997); Smirnova *et al.* (1998); Vos *et al.* (2000); Preuss *et al.* (2003)
AtKinG	At1g63640	NtKCH, OsKCH, GhKCH	PPB MTs; phragmoplast MTs and MFs	(-)-end-directed kinesin; KCH domain-mediated MF binding	Xu *et al.* (2009); Frey *et al.* (2010); Buschmann *et al.* (2011); Klotz & Nick (2012)
ANP1, ANP2, ANP3	At1g09000, At1g54960, At3g06030	(Nt) NPK1	Phragmoplast MTs; phragmoplast midzone	MAPKKK; activates ANQ1/ MKK6	Nishihama *et al.* (2001); Krysan *et al.* (2002)

Table 1 (Continued)

Proteins	AGI Accession Numbers	Orthologs[a]	Localization[b,c]	Function[b,c]	Reference(s)
ANQ1/MKK6	At5g56580	(Nt) NQK1/ NtMEK1	Phragmoplast MTs; phragmoplast midzone	MAPKK; activates MPK4 and MPK6	Soyano *et al.* (2003); Beck *et al.* (2010, 2011)
MPK4, MPK6	At4g01370, At2g43790	(Nt) NRK1/ NTF6	PPB MTs (MPK6); phragmoplast MTs; phragmoplast midzone (MPK4)	MAPK; activates MAP65-1, MAP65-2 and MAP65-3/PLE	Calderini *et al.* (1998); Beck *et al.* (2010, 2011); Kosetsu *et al.* (2010); Müller *et al.* (2010); Takahashi *et al.* (2010);
MAP65-1, MAP65-2, MAP65-3/ PLE	At5g55230, At4g26760, At5g51600	(Nt) MAP65-1a/b	PPB MTs; phragmoplast MTs (MAP65-1, -2); phragmoplast midzone (MAP65-3)	Phosphorylation-mediated regulation of NACK-PQR-targeted substrates; bundle MTs	Müller *et al.* (2004); Sasabe *et al.* (2006, 2011); Beck *et al.* (2010)
TIO/AtFU	At1g50240		Phragmoplast midzone	Kinase; regulates PAKRP1 and PAKRP1L	Oh *et al.* (2005, 2012)
RUK/ EMB3013	At5g18700		PPB; phragmoplast	Phragmoplast organization/ dynamics	Krupnova *et al.* (2009)
AUR1, AUR2	At4g32830, At2g25880		CP	Kinase	Van Damme *et al.* (2011b)

[a]Homologous localization and/or function; Zm, *Zea mays* (corn); Nt, *Nicotiana tabacum* (tobacco); Os, *Oryza sativa* (rice); Dc, *Daucus carota* (carrot); Tv, *Tradescantia virginiana* (spiderwort); Gs, *Gossypium hirsutum* (cotton); Hk, *Haemanthus katherinae* (blood lily).
[b]Known or predicted.
[c]PPB, preprophase band; CDZ, cortical division zone; CP, cell plate; CW, cell wall; MTs, microtubules; MF, actin microfilament.

II. The role of the cytoskeleton in cytokinesis

1. The preprophase band

Preprophase bands (Fig. 1a) form in somatic cells before mitosis through the selective depolymerization of non-PPB cortical microtubules (MTs), leaving behind a MT belt that surrounds the nucleus (Dhonukshe & Gadella, 2003). As the cell cycle progresses, cortical actin filaments assemble alongside PPB MTs and help condense and narrow the PPB into an area called the cortical division zone (CDZ) (Liu *et al.*, 2011b); however, PPB narrowing is not absolutely required for cytokinesis (Eleftheriou & Palevitz, 1992; Yoneda *et al.*, 2004). In fact, PPBs are not essential for cell division, as somatic cells can progress through mitosis and complete cytokinesis following experimental ablation of PPBs, albeit with misoriented spindles and misaligned CPs (Mineyuki *et al.*, 1991; Murata & Wada, 1991; Marcus *et al.*, 2005). Furthermore, PPBs are not required for endosperm cellularization or for meiotic and subsequent generative divisions during gametogenesis (Otegui & Staehelin, 2000; Azimzadeh *et al.*, 2008).

Proteins shown to localize to and promote the formation of PPBs include the Arabidopsis proteins TONNEAU1a (TON1a), TON1b, TON2, MICROTUBULE ORGANIZATION 1 (MOR1) and *Arabidopsis thaliana* KINESIN ungrouped clade, gene A (AtKINUa) (Traas *et al.*, 1995; Whittington *et al.*, 2001; Camilleri *et al.*, 2002; Kawamura *et al.*, 2006; Sakai *et al.*, 2008; Azimzadeh *et al.*, 2008; Malcos & Cyr, 2011). TON2/FASS and maize orthologs DISCORDIA1 (DCD1) and ALTERNATIVE DISCORDIA1 (ADD1) are putative regulatory subunits of PROTEIN PHOSPHATASE 2A (PP2A) (Camilleri *et al.*, 2002; Wright *et al.*, 2009), and TON2 genetically interacts with the PPB MT-binding proteins TON1a/b and MOR1 (Kirik *et al.*, 2012). A possible model is that the putative phosphatase activity of TON2-associated PP2A may function to positively regulate TON1 and MOR1 binding to and stabilization of PPB MTs, wheras phosphorylation of TON1 and MOR1 by the kinase CDKA/ CDC2aAt, which, following its activation by B-type cyclins in late prophase, associates with and promotes disassembly of mature PPBs (Imajuku *et al.*, 2001; Weingartner *et al.*, 2001), may inhibit their function. Similarly, PPB association of the Arabidopsis kinesin, AtKINUa, which contains a CDKA phosphorylation site (Azimzadeh *et al.*, 2008; Malcos & Cyr, 2011), may be regulated by TON2-PP2A and CDKA activities. Additionally, AtKINUa contains a D-BOX motif, and thus regulation of its PPB association may also be dependent upon ubiquitination and proteasome-mediated degradation (Malcos & Cyr, 2011).

The PPB disassembles at late prophase/early prometaphase, well in advance of mitotic nuclear breakdown, yet its former position accurately foretells the site of the growing CP. The Arabidopsis TANGLED 1 (TAN1) MT-associated protein and Ran GTPase ACTIVATING PROTEIN 1 (RanGAP1) localize to the PPB and remain at the CDZ after PPB breakdown, serving as a persistent spatial marker throughout mitosis and cytokinesis (Walker *et al.*, 2007; Xu *et al.*, 2008). Although PPBs form in *tan1* mutants and RanGAP1 RNAi lines, they are misoriented, resulting in distorted CPs and cell walls (CWs) (Smith *et al.*, 1996; Cleary & Smith, 1998; Walker *et al.*, 2007; Xu *et al.*, 2008). Localization of TAN1 and RanGAP1 depends upon TON2 and the redundant pseudokinesins PHRAGMOPLAST-ORIENTING KINESIN1 (POK1) and POK2 (Müller *et al.*, 2006; Walker *et al.*, 2007; Xu *et al.*, 2008). POK1 interacts with TAN1 and RanGAP1, and, consistent with this, *pok1 pok2* double mutants mimic *tan1* and RanGAP1 RNAi phenotypes (Müller *et al.*, 2006; Walker *et al.*, 2007; Xu *et al.*, 2008).

Table 2 Proteins involved in membrane dynamics during plant cytokinesis

Protein	AGI	Localization[a,b]	Function[a,b]	Reference(s)
KN/SYP111	At1g08560	Golgi; TGN/EE; CP vesicles; CP leading edge	t-SNARE: regulate vesicle and target membrane fusion	Waizenegger *et al.* (2000); Chow *et al.* (2008)
ECH	At1g09330	TGN/EE	Maintain TGN/EE structure/function	Gendre *et al.* (2011)
ELC	At3g12400	TGN/EE; endosome	Endosomal sorting; stabilize MTs	Spitzer *et al.* (2006)
RABA1b/BEX5	At1g16920	TGN/EE	GTPase: regulate TGN/EE-to-CP vesicle transport/fusion	Feraru *et al.* (2012)
RABA2a/AtRAB11c, RABA2b, RABA3	At1g09630, At1g07410, At1g01200	TGN/EE; CP leading edge	GTPase: regulate TGN/EE-to-CP vesicle transport/fusion	Chow *et al.* (2008)
RABA4b	At4g39990	TGN/EE	GTPase: regulate TGN/EE-to-PM vesicle transport/fusion	Preuss *et al.* (2004, 2006)
RABF1/ARA6,RABF2b/ARA7	At3g54840, At4g19640	TGN/EE; MVB/PVC; CP; CP vesicles	GTPase: regulate TGN/EE-to-CP/PM vesicle transport/fusion	Ueda *et al.* (2004); Dhonukshe *et al.* (2006)
GN/VAN7/EMB30	At1g13980	TGN/EE; CP	Regulate TGN/EE-to-CP vesicle transport/fusion	Dhonukshe *et al.* (2006)
SCD1	At1g49040	CCVs; CP	CCV-associated Rab GEF	Falbel *et al.* (2003); Korasick *et al.* (2010)
AtTRS33, AtTRS120, AtTRS130/CLUB (and others)	At3g05000, At5g11040, At5g54440	TGN/EE; CP	TRAPPII (GEF for RabAs; i.e. regulate TGN/EE-to-CP trafficking) subunits	Jaber *et al.* (2010); Thellmann *et al.* (2010); Qi *et al.* (2011); Qi & Zheng (2011)
EXO70A1 (and others)	At5g03540	CP; CDS; CW	Exocyst complex (vesicle-PM or vesicle-CP tether) subunit	Synek *et al.* (2006); Fendrych *et al.* (2010)
SNAP33/SNP33	At5g61210	CP	KN/VAMP721/722-interacting t-SNARE	Heese *et al.* (2001)
VAMP721/VAMP7b, VAMP722/SAR1	At1g04750, At2g33120	CP	Redundant, KN/SNP33-interacting v-SNAREs	Zhang *et al.* (2011)
NSPN11	At2g35190	CP	KN-interacting v-SNARE	Zheng *et al.* (2002)
NSF, αSNAP1	At4g04910, At3g56450	CP	KN/SNP33/VAMP721/722 trans-SNARE disassembly	Rancour *et al.* (2002)
KEU	At1g12360	CP	Promote KN/SNP33/VAMP721/722 trans-SNARE complex	Assaad *et al.* (2001);Heese *et al.* (2001)
CHC1, CHC2	At3g08530, At3g11130	CP	w/CLC, forms clathrin coat	Van Damme *et al.* (2011a)
CLC1, CLC2, CLC3	At2g40060, At2g20760, At3g51890	CP	w/CHC, forms clathrin coat	Konopka *et al.* (2008); Van Damme *et al.* (2011a,b); Ito *et al.* (2012); Fig. 2

Table 2 (Continued)

Protein	AGI	Localization[a,b]	Function[a,b]	Reference(s)
AP180/Epsin (and other A/ENTH proteins)	At1g05020	CP	Promote assembly of clathrin membrane patches	Barth & Holstein (2004);Ito *et al.* (2012); Song *et al.* (2012)
TPLATE	At3g01780	CP; CDS flanks of PM	AP-/COP1-like complex subunit; interacts with CHC1 and CLC2	Van Damme *et al.* (2006, 2011a,b)
DRP1A/ADL1A/RSW9, DRP1C/ADL1C, DRP1E/ADL1E/EDR3, DRP2A/DLP6, DRP2B/ADL3	At5g42080, At1g14830, At3g60190, At1g10290, At1g59610	Sites of CME at PM; CP leading edge	GTPases: clathrin vesicle scission and CP membrane tubulation	Fujimoto *et al.* (2008, 2010); Konopka & Bednarek *et al.* (2008); Ito *et al.* (2012); Fig. 2
AtCDC48	At3g09840	CP	AAA-ATPase chaperone	Rancour *et al.* (2002)
SYP31/SED5	At5g05760	ER; Golgi, CP	t-ER formation w/in CDZ	Rancour *et al.* (2002)
RHD3/GOM8	At3g13870	ER	GTPase: ER formation/ dynamics	Chen *et al.* (2011b)
PATL1	At1g72150	CP	TGN/EE-derived vesicle formation	Peterman et al. (2004)
PAS2/PEP	At5g10480	CP	Elongate membrane phospholipids	Bach et al. (2011)
FK/HYD2/ELL1, CPH/SMT1, HYD1/ MAD4	At3g52940, At5g13710, At1g20050	CP	Biosynthesize sterols	Diener et al. (2000); Jang et al. (2000); Schrick et al. (2000); Souter et al. (2002)
GSL8/MAS/CHOR	At2g36850	CP	Synthesize callose	Chen et al. (2009); Guseman et al. (2010);
GCS1/KNF, RSW3/PSL5, CYT1/GMP1/ SOZ1/VTC1, KOR/RSW2/IRX2/DEC/ GH9a1/TSD1, PRC1/CESA6/IXR2, CESA1/RSW1, CSLD/SOS6	At1g67490, At5g63840, At2g39770, At5g49720, At5g64740, At4g32410, At1g02730	CP; CW	Sugar modification necessary to build CWs	Fagard et al. (2000); Boisson et al. (2001); Lane et al. (2001); Lukowitz et al. (2001); Burn et al. (2002); Gillmor et al. (2002); Hunter et al. (2012)

[a]Known or predicted.
[b]TGN/EE, trans-Golgi network/early endosome; CP, cell plate; MVB/PVC, multivesicular body/prevacuolar compartment; CDS, cortical division site; CW, cell wall; CME, clathrin-mediated endocytosis; PM, plasma membrane; ER, endoplasmic reticulum; MTs, microtubules; CCV, clathrin-coated vesicle; CDZ, cortical division zone.

The Arabidopsis AUXIN-INDUCED IN ROOT 9 (AIR9) protein localizes to PPBs, but this localization is not maintained throughout mitosis. Yet, at late stages of cytokinesis, AIR9 reappears at the leading edge of the CP, and, following CP insertion at the cortical division site (CDS; i.e. the site within the CDZ where the CP attaches to the parental CW), redistributes along the new CW (Buschmann *et al.*, 2006). Callose, which is removed and replaced by cellulose in mature CWs (Samuels *et al.*, 1995), is absent in the AIR9-positive, newly formed CWs (Buschmann *et al.*, 2006), suggesting a role for AIR9 in recognition and maturation of CPs and CWs that join the parental PM at the CDS, which presumably possesses memory cues that mark the former PPB position.

Preprophase band memory cues are likely established and maintained through the selective removal and/or exclusion of proteins from the CDZ. Despite their role in PPB formation, actin microfilaments (MFs) diminish at the CDZ as the PPB disassembles, and this actin-depleted zone persists throughout mitosis and cytokinesis (Hoshino *et al.*, 2003; Panteris, 2008). In some cells, cortical actin accumulations are evident on either side of the CDZ, forming the so-called MF twin peaks, which is proposed to provide structural support to guide the expanding phragmoplast and growing CP toward the CDS (Cleary *et al.*, 1992; Sano *et al.*, 2005; Panteris, 2008). Consistent with this idea, depolymerization of cortical MFs before the appearance of the actin-depleted zone results in the formation of distorted CPs (Hoshino *et al.*, 2003). The kinesin motor protein KINESIN CDKA-ASSOCIATED1 (KCA1) is excluded from the CDZ throughout mitosis and cytokinesis. This KCA-depleted zone forms only if intact PPB MTs are present; however, its maintenance following PPB disappearance is not MT- or MF-dependent (Vanstraelen *et al.*, 2006). The localization of KCA1, like TON1 and AtKINUa, is negatively regulated by CDKA (Imajuku *et al.*, 2001; Vanstraelen *et al.*, 2006). Sustained exclusion of MFs and/or KCA1 from the CDZ throughout mitosis and cytokinesis suggests the cell has the ability to remember the former position of the PPB so that, later on, it can properly position the phragmoplast and CP.

2. The phragmoplast

Following completion of nuclear division in somatic plant cells, MFs and MT remnants of the mitotic spindle grow and reassemble into the phragmoplast, an antiparallel cytoskeletal array oriented perpendicular to the division plane, centered within the CDZ

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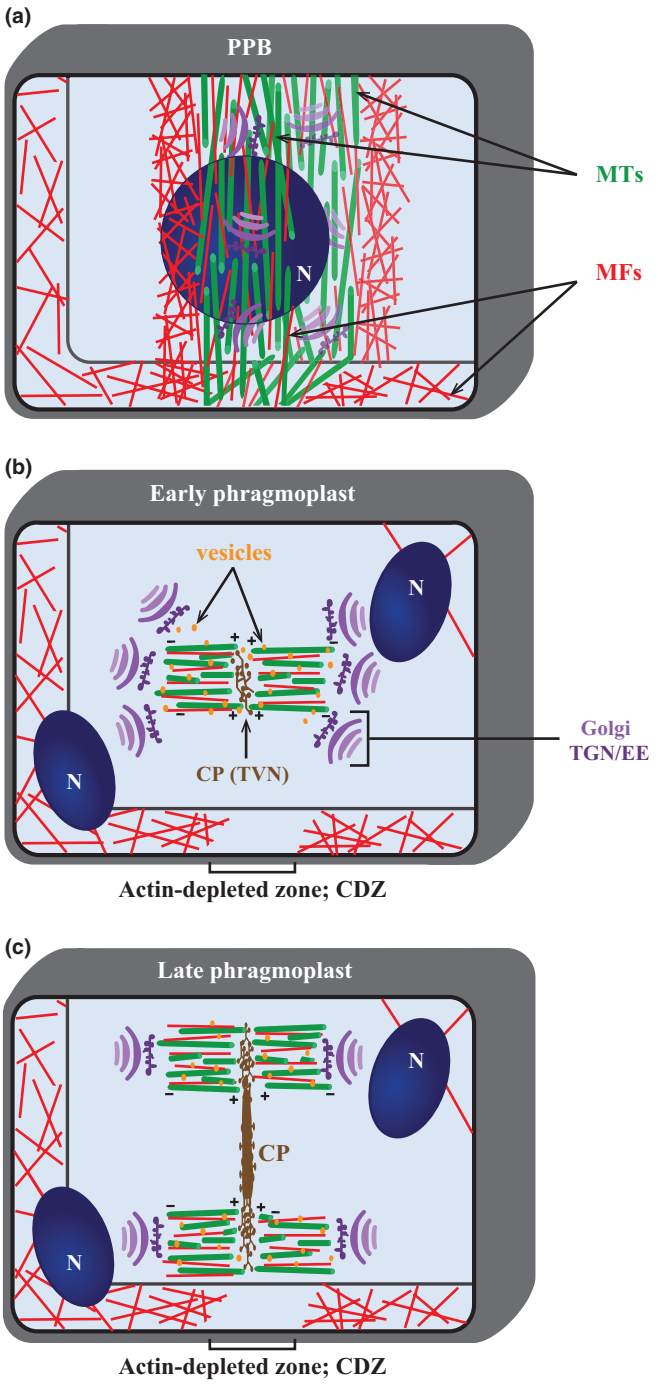

Fig. 1 The arrangement of the cytoskeleton, Golgi apparatus and trans-Golgi network/early endosome (TGN/EE) during cytokinesis. (a) In late G2, microtubules (MTs; green) and actin microfilaments (MFs; red) surround the nucleus (N; blue) to form the Preprophase band (PPB), which predicts the future division plane (i.e. the cortical division zone, CDZ). The preprophase band (PPB) is disassembled in late prophase/early prometaphase. Cortical microfilaments are enriched alongside the PPB, forming the 'MF twin peaks', which will persist throughout mitosis and cytokinesis. Golgi (lavender-to-purple) also encircles the nucleus to form the 'Golgi belt'. (b) Cytokinesis follows nuclear reformation and is initiated by the assembly of the phragmoplast perpendicular to the CDZ from MT and MF remnants of the mitotic spindle. Vesicles (Golgi-derived and recycled; orange) travel along the phragmoplast and fuse at its center to form the tubular-vesicular network (TVN) stage of the young cell plate (CP; brown, center). (c) In late cytokinesis, the cell plate (CP) and the phragmoplast have expanded toward the cortical division site of the parental plasma membrane. MT polarity within the phragmoplast is indicated by + (plus end) and – (minus end) signs in panels (b) and (c). Brackets in panels (b) and (c) denote the actin-depleted zone, which persists throughout mitosis and cytokinesis and marks the CDZ. (Note: proteins, most organelles and portions of the MF twin peaks have been omitted for clarity).

(Fig. 1b,c). Phragmoplast MTs and MFs coalign into a bipolar arrangement with their plus ends toward the phragmoplast midzone. It is upon this cytoskeletal scaffolding that vesicles are guided to the phragmoplast midzone wherein they fuse to build the CP. The phragmoplast is dynamic and must expand toward the cell cortex to allow the CP growing within it to expand centrifugally. This is accomplished as MTs and MFs depolymerize at the center of the phragmoplast and assemble at its leading edge (Liu *et al.*, 2011a).

Early *in vitro* studies showing that fluorescently labeled tubulin polymerized onto extant MT plus ends, resulting in the appearance of a fluorescent band at the phragmoplast midzone, indicated that phragmoplast MTs are dynamic. This band widened and moved away from the midzone in the presence of excess unlabeled tubulin, suggesting that phragmoplast MT dynamics resulted from MT treadmilling and putative GTPase-dependent mechanoenzyme-mediated MT translocation toward the distal ends of the phragmoplast (Asada *et al.*, 1991). However, subsequent studies examining phragmoplast MT turnover rates, and localization of EB1, a MT plus-end tracking protein, and various subunits of the negative-end-binding γ-tubulin ring complex (γ-TuRC) throughout the phragmoplast, were inconsistent with the phragmoplast MT treadmilling and translocation model (Liu *et al.*, 1994; Hush *et al.*, 1994; Dryková *et al.*, 2003; Kumagai *et al.*, 2003; Chan *et al.*, 2003; Van Damme *et al.*, 2004; Bisgrove *et al.*, 2008; Zeng *et al.*, 2009; Kong *et al.*, 2010; Nakamura *et al.*, 2010). Live cell imaging of EB1-GFP dynamics indicated that growing MT plus ends do not exclusively reside at the phragmoplast midzone, and phragmoplast MTs elongate both away from and toward the midzone (Ho *et al.*, 2011). Furthermore, fluorescence recovery after photobleaching experiments and computer modeling using YFP-tubulin indicated that MT dynamic instability predominantly drives phragmoplast morphology, and that phragmoplast MT asymmetry is achieved by an increase in the number and rate of MTs that polymerize toward the CP rather than away (Smertenko *et al.*, 2011).

Microtubule nucleation and growth are promoted by γ-TuRC, a complex of γ-tubulin and several γ-tubulin complex proteins, including GCP2 (Nakamura *et al.*, 2010) and the GCP-WD ortholog NEDD1 (Zhu *et al.*, 2008; Zeng *et al.*, 2009). In animals and fungi, the γ-TuRC stabilizes MT minus ends to form the functional core of MT organizing centers (centrosomes and spindle pole bodies, respectively; Lüders & Stearns, 2007), assemblies that plant cells lack. Nonetheless, plant γ-TuRCs are capable of nucleating MTs on the sides of extant MTs (Murata *et al.*, 2005). In *nedd1* mutants, MTs fail to organize into a proper phragmoplast, leading to defective CP consolidation (Zeng *et al.*, 2009). Plant

orthologs of augmin complex subunits, which promote recruitment of γ-TuRC to spindles and polymerization of MTs in mammals (Zhu *et al.*, 2008), are required for γ-tubulin recruitment, phragmoplast MT organization and CP formation (Zeng *et al.*, 2009; Nakamura *et al.*, 2010; Ho *et al.*, 2011; Hotta *et al.*, 2012). Thus, at least one way in which acentrosomal plant cells nucleate and organize mitotic MT arrays is through augmin-mediated association of γ-TuRC and MTs.

While MTs are the predominant cytoskeletal elements comprising the phragmoplast, MFs are also present (Hepler *et al.*, 2002; Sano *et al.*, 2005; Yu *et al.*, 2006). Live cell imaging has shown that actin polymerization occurs at MF plus ends just outside the phragmoplast midzone and at the CP leading edge (Smertenko *et al.*, 2010). The specific role of MFs in cytokinesis is unclear. Drug treatments that promote MF disassembly delay or inhibit CP formation (Schmit & Lambert, 1988; Valster *et al.*, 1997; Kovar *et al.*, 2006), whereas *act2* and *act2 act7* mutants have unaltered cell division (Baluška *et al.*, 2001; Gilliland *et al.*, 2002; Nishimura *et al.*, 2003). However, it is difficult to assess the role of a particular population of MFs during cell division since actin mutants and MF-depolymerizing drugs have the potential to disrupt all actin-dependent cellular processes. Characterization of the formin proteins, which facilitate nucleation, capping, bundling and severing to regulate MF polymerization/depolymerization rates that influence MF dynamics (Staiger & Blanchoin, 2006; Blanchoin & Staiger, 2010), has been more informative of the role of actin in cytokinesis. The Arabidopsis formins AtFH5, AtFH8 and AFH14 are required for cytokinesis, but possess diverse MF-regulating activities necessary for CP formation (Ingouff *et al.*, 2005; Kovar *et al.*, 2006), mitotic progression (Xue *et al.*, 2011), and phragmoplast MT and MF alignment (Li *et al.*, 2010b; Wang *et al.*, 2012), and thus may differentially regulate MF organization and/or function of during cytokinesis.

3. Cytoskeletal motor proteins

Higher plants use kinesin and myosin cytoskeletal motor proteins for ATP-dependent movement along MTs and MFs, respectively (Hepler *et al.*, 2002). Relative to other eukaryotes, there appears to have been a major expansion in the number of kinesins encoded by plants (61 in Arabidopsis vs 45 in humans; Zhu & Dixit, 2011; Li *et al.*, 2012; Hotta *et al.*, 2012), many of which may serve plant-specific functions at the PPB or phragmoplast for short-range movement of organelles and vesicles (Cai & Cresti, 2012). Myosins have been shown to drive the long-distance movement and repositioning of endomembrane compartments, including Golgi and Golgi-derived vesicles, during polar cell expansion; however, the role of myosins in plant cytokinesis is less clear. Studies using myosin-inhibiting drugs indicated that myosins influence phragmoplast alignment and CP expansion (Hepler *et al.*, 2002), yet plant myosins are thought to preferentially associate with bundled MF cables, which are not prevalent during plant cell division (Smith & Oppenheimer, 2005; Thomas, 2012), raising questions about the necessity of myosins during cytokinesis.

Consistent with the arrangement of antiparallel MT plus ends at the phragmoplast midzone, it has been hypothesized that MT plus-end-directed kinesins facilitate the transport of vesicles along phragmoplast MTs to the midzone to deliver material for CP construction. Immunolocalization and live cell imaging of fluorescent fusion proteins have shown that many of the kinesins encoded by Arabidopsis (Li *et al.*, 2012), tobacco (Asada *et al.*, 1997), rice (Lee & Liu, 2000), cotton (Preuss *et al.*, 2003; Xu *et al.*, 2009), and carrot (Barroso *et al.*, 2000) localize to the phragmoplast *in vivo*. Of these, however, only the Arabidopsis PHRAGMOPLAST-ASSOCIATED KINESIN-RELATED MOTOR PROTEIN 2 (PAKRP2) decorates phragmoplast MTs in a punctate fashion, consistent with localization on CP transport vesicles (Lee *et al.*, 2001).

Other plus-end-directed kinesins have been shown to localize to and/or be required for the construction, maintenance or dynamics of the phragmoplast. The tobacco NPK1-ACTIVATING KINESIN-LIKE PROTEIN 1 (NACK1) and NACK2 (Nishihama *et al.*, 2002), Arabidopsis AtNACK1/HIK and AtNACK2/STD/TES (Strompen *et al.*, 2002; Tanaka *et al.*, 2004) and rice DBS1/OsNACK (Sazuka *et al.*, 2005), as well as the Arabidopsis PHRAGMOPLAST-ASSOCIATED KINESIN-RELATED PROTEIN 1 (AtPAKRP1) and AtPAKRP1L (Lee & Liu, 2000; Pan *et al.*, 2004; Lee *et al.*, 2007), localize to the phragmoplast midzone and are directly implicated in phragmoplast organization and/or dynamics necessary for CP expansion. However, the function of the TOBACCO KINESIN-RELATED PROTEIN 125 (TKRP125) protein, and its orthologs in carrot, DcKRP120, and Arabidopsis, AtKRP125c, which localize along phragmoplast MTs (Asada *et al.*, 1997; Barroso *et al.*, 2000; Bannigan *et al.*, 2007), remains to be determined.

Arabidopsis MT minus-end-directed ATK5, KCA1 and KCA2 localize to the phragmoplast midzone (Vanstraelen *et al.*, 2004, 2006; Ambrose *et al.*, 2005), which seems paradoxical as this site was thought to be occupied exclusively by MT plus ends. However, according to the dynamic instability model for phragmoplast MT dynamics, MT minus ends also likely reside at the phragmoplast midzone (Smertenko *et al.*, 2011). Furthermore, kinesins not only function in directional transport, but can regulate organization of MT arrays through translocation, depolymerization, bundling or crosslinking to other cellular components (Zhu & Dixit, 2011). Consistent with this, localization of ATK5 and KCA1 at or near the phragmoplast midzone is independent of motor domain activity (Vanstraelen *et al.*, 2004, 2006; Ambrose *et al.*, 2005). The distribution, levels and localization of KCA1 and KCA2 are also likely mediated by their phosphorylation status (Vanstraelen *et al.*, 2004, 2006), and ubiquitin-mediated degradation (Malcos & Cyr, 2011).

Various other minus-end-directed plant-specific kinesins that function in cytokinesis contain domains that modulate their activity during cell division such as calpain homology and calmodulin-binding protein domains. KINESIN-LIKE CALMODULIN-BINDING PROTEINs (KCBPs) from various plant species, including Arabidopsis, tobacco, spiderwort, cotton, and blood lily, localize to the PPB and phragmoplast where they likely mediate Ca^{2+}-calmodulin-regulated MT bundling (Bowser & Reddy, 1997; Smirnova *et al.*, 1998; Vos *et al.*, 2000; Preuss *et al.*, 2003). Arabidopsis, tobacco and rice members of the KINESIN

WITH CALPAIN HOMOLOGY DOMAIN (KCH) family associate along the entire length of phragmoplast MTs (Frey *et al.*, 2010; Buschmann *et al.*, 2011), or the phragmoplast midzone (Xu *et al.*, 2009), and can bind and bundle both MTs and MFs (Preuss *et al.*, 2004; Xu *et al.*, 2009; Umezu *et al.*, 2011; Klotz & Nick, 2012), likely coupling these two cytoskeletal networks during cytokinesis.

Given the importance and number of kinesins involved in phragmoplast cytoskeletal dynamics and vesicle transport, it is not surprising that there exist numerous diverse potential modes of kinesin regulation, including the action of kinases. As discussed earlier, the kinase CDKA regulates the activity of a number of proteins, including PPB- and phragmoplast-associated kinesins. Kinesins themselves also regulate kinase signaling cascades. In tobacco, NACK1 and/or NACK2 kinesin motor proteins activate the NACK-PQR kinase cascade, comprising the mitogen-activated protein kinase kinase kinase (MAPKKK), NUCLEUS-AND PHRAGMOPLAST-LOCALIZING KINASE 1 (NPK1), the MAPKK, NQK1, and the MAPK, NRK1 (Calderini *et al.*, 1998; Nishihama *et al.*, 2001, 2002; Soyano *et al.*, 2003; Takahashi *et al.*, 2004; Komis *et al.*, 2011). NRK1 in turn regulates a number of substrates; including the MT bundling protein MAP65-1, which is inactivated by phosphorylation, allowing for phragmoplast and CP expansion (Sasabe *et al.*, 2006; Smertenko *et al.*, 2006). In Arabidopsis, AtNACK1 and AtNACK2 kinesins activate an orthologous NACK-PQR cascade, which is required for cytokinesis, consisting of the MAPKKKs, ANP1, ANP2 and ANP3 (Krysan *et al.*, 2002), the MAPKK ANQ1 (Beck *et al.*, 2010, 2011), and several downstream MAPKs, including MPK4a and MPK6, and target substrates, including MAP65-1, -2, and -3 (Müller *et al.*, 2004, 2010; Smertenko *et al.*, 2004; Sasabe *et al.*, 2006, 2011; Sasabe & Machida, 2006; Beck *et al.*, 2010, 2011; Takahashi *et al.*, 2010; Kosetsu *et al.*, 2010; Komis *et al.*, 2011; Bögre, 2011).

The TWO-IN-ONE (TIO) kinase interacts with the kinesins PAKRP1 and PAKRP1L and likely modulates their localization and/or activity at the phragmoplast midzone via phosphorylation (Oh *et al.*, 2012). RUNKEL (RUK), a MT-associated protein with a putative kinase domain, localizes to PPBs, phragmoplast midzones and the expanding CP. However, the kinase activity of RUK is not required for cytokinesis (Krupnova *et al.*, 2009), thus its function during cytokinesis is unclear. There are several additional kinases that influence cell division through their regulation of cell cycle progression or of cell polarity to regulate asymmetric divisions necessary for proper tissue patterning, including Arabidopsis AURORA 1 (AUR1); however, this kinase affects cytokinesis only indirectly, perhaps through its ability to phosphorylate HISTONE H3 (Kurihara *et al.*, 2006; Demidov *et al.*, 2009; Van Damme *et al.*, 2011b).

III. Membrane dynamics during cytokinesis

1. Endomembrane organization

During division, the plant secretory pathway undergoes numerous organizational changes to facilitate the initiation, consolidation and maturation of the CP and segregation of endomembranes into daughter cells. The trans-Golgi network (TGN) and endosomes are the major compartments through which newly synthesized and endocytosed proteins, lipids and CW polysaccharides traffic to and from the CDZ and developing CP. In plants, the TGN, also known as the partially coated reticulum (Pesacreta & Lucas, 1984; Tanchak *et al.*, 1988), mediates delivery of secretory proteins to the PM and vacuole. Originally thought to be distinct from early endosomes (EEs), more recent studies demonstrate that the TGN can move independently of the Golgi apparatus (Staehelin & Kang, 2008; Toyooka *et al.*, 2009; Viotti *et al.*, 2010), and is the initial compartment to which endocytosed PM proteins and the dye FM4-64, a marker of bulk PM endocytosis, are delivered (Dettmer *et al.*, 2006; Lam *et al.*, 2007; Chow *et al.*, 2008; Viotti *et al.*, 2010). Together these data support the current view of the TGN as a transiently mobile TGN/EE hybrid compartment through which PM- and vacuole-destined secretory and endocytic cargo pass.

In early mitosis, Golgi and TGN/EEs accumulate near the PPB (Dixit & Cyr, 2002) and in a subcortical ring, the 'Golgi belt', surrounding the future site of CP formation (Nebenführ *et al.*, 2000) (Fig. 1a). Subsequently, vesicles carrying newly synthesized proteins and polysaccharides, including xyloglucans and arabinogalactans (Samuels *et al.*, 1995; Seguí-Simarro *et al.*, 2004), traffic along phragmoplast MTs to initiate and provide material for CP construction. In particular, the cytokinesis-specific syntaxin-related SNARE, KNOLLE (KN), which is required for CP formation (Lauber *et al.*, 1997), traffics through the Golgi and TGN/EE before appearing at the division plane (Chow *et al.*, 2008). Similarly, newly synthesized PM syntaxins, SYP121, SYP112, and SYP132, are targeted to the CP when expressed under control of the M-phase-specific KN promoter (Müller *et al.*, 2003; Reichardt *et al.*, 2007, 2011), indicating that trafficking of biosynthetic secretory cargo from the TGN/EE is, perhaps by default (Touihri *et al.*, 2011), polarized toward the division plane rather than the PM during cytokinesis.

In addition to the delivery of newly synthesized cargo, mature CW-derived pectins and xyloglucans (Baluška *et al.*, 2005), and FM4-64 (Dhonukshe *et al.*, 2006; Dettmer *et al.*, 2006; Reichardt *et al.*, 2007) localize to the CP during cytokinesis. Direct fusion of late endosomes (i.e. multivesicular bodies/prevacuolar compartments; MVBs/PVCs) with the CP was postulated to mediate delivery of this internalized material to the CP (Dhonukshe *et al.*, 2006). However, the TGN/EE marker vacuolar H(+)-ATPase subunit a1 (VHA-a1), and markers of the late endocytic MVB/PVC compartments, do not localize to the CP, bringing into question the generality of this model (Dettmer *et al.*, 2006; Chow *et al.*, 2008; Lam *et al.*, 2008). Indeed, *echidna* (*ech*) mutants, defective for a protein required for proper TGN/EE structure and function, show mislocalization of VHA-a1 to the CP and tonoplast (Gendre *et al.*, 2011), suggesting that endosomes may fuse with CPs, albeit under abnormal conditions. More likely, internalized CW components and proteins reach the CP during cytokinesis following their endocytosis and delivery to the TGN/EE. Analysis of other PM proteins that undergo constitutive or regulated endocytosis and cycling between the PM and TGN/EE, and the use

of the inhibitor, Endosidin1, which selectively affects the recycling of PM proteins (e.g. the brassinosteroid receptor BRI1 and the auxin carriers PIN-FORMED 2 (PIN2) and AUX1, but not PIN1; Robert *et al.*, 2008) could be used to further address this. Such studies may also address the question of whether newly synthesized and recycled CW components and PM proteins are delivered to the CP via a distinct or a common class of TGN/EE-derived vesicles.

Although endocytic cargo localizes to developing CPs, whether its delivery to the division plane is essential for cytokinesis is controversial. Based on the finding that the late endosomal trafficking inhibitor, wortmannin, did not affect CP formation, it was concluded that endocytosis was not required for cytokinesis (Reichardt *et al.*, 2007). However, wortmannin has other less well-defined effects, including inhibition of clathrin dynamics (Ito et al., 2012), and thus it is best to exercise caution when interpreting its effects on CP formation. By contrast, *elch* mutants, defective in a subunit of the MVB ESCRT-I sorting complex (Spitzer *et al.*, 2006), and expression of a dominant negative form of the MVB/PVC Rab GTPase, RABF2b(S24N) (Dhonukshe *et al.*, 2006), result in cytokinesis defects. Further experiments are therefore necessary to reconcile these contradictory findings about the necessity for delivery of internalized CW components and PM proteins to CP formation.

2. Cell plate vesicle trafficking machinery

The formation, targeting and fusion of transport vesicles within each branch of the plant exocytic and endocytic secretory pathway are regulated by a large number of evolutionarily conserved cytosolic and membrane-associated factors (Bassham *et al.*, 2008). Formation of secretory and endocytic vesicles involves the assembly of distinct coat protein complexes (e.g. COPII, COPI and clathrin) that drive membrane budding and the selection of cargo proteins (Hwang & Robinson, 2009). Despite the morphological data that indicate that CP- and PM-destined vesicles are transported from the Golgi and TGN/EE, the molecular machinery involved in their formation and loading with cargo remains to be more clearly defined. Clathrin-coated vesicles (CCVs) have been implicated in the transport of proteins, including vacuolar proteins (Harley & Beevers, 1989; Song *et al.*, 2006), from the Golgi and TGN/EE; however, this view was recently challenged (Scheuring *et al.*, 2011). Perhaps CCVs may thus function in the trafficking of newly synthesized and/or recycled material from the TGN/EE to the PM and CP. In addition to CCVs, other vesicle types have also been observed to form from the TGN/EE, including dense vesicles containing vacuolar storage proteins (Hohl *et al.*, 1996; Hinz *et al.*, 1999), and secretory vesicles (Staehelin & Kang, 2008). TGN/EE-derived secretory vesicle clusters have been implicated in the delivery of proteins and polysaccharides (Toyooka *et al.*, 2009) to the PM and CP; however, their formation remains to be determined.

While limited understanding of their formation exists, we have a better understanding of the cadre of proteins involved in directional transport, docking and fusion of CP-destined vesicles. Rab/Ypt proteins are monomeric small GTPases, which, in their GTP-bound form, recruit divergent effectors to coordinate the formation, transport, tethering and fusion of secretory and endocytic vesicles and organelles throughout the biosynthetic and endocytic trafficking pathways (Nielsen *et al.*, 2008; Woollard & Moore, 2008; Hutagalung & Novick, 2011). Of the 57 Rabs encoded by Arabidopsis, 26 have been annotated to encode RabA-type GTPases, which are most closely related to members of the mammalian Rab11 subclass that function at recycling endosomes (Van Ijzendoorn, 2006) and are critical for later stages of cytokinesis (Skop *et al.*, 2001). Likewise, in *Saccharomyces cerevisiae*, the Ypt31/Ypt32 pair of RabA/Rab11-related proteins are required for polarized secretion of TGN-derived vesicles (Jedd *et al.*, 1997; Lipatova *et al.*, 2008) and recycling from the PM through EEs to the Golgi (Chen *et al.*, 2011a).

Plant RabA proteins have been divided into six subclasses (RABA1-6) (Rutherford & Moore, 2002), with various members, including NtRAB11, RABA1b, RABA2a and RABA4b, functioning in the delivery of material from the TGN/EE to the PM (Preuss *et al.*, 2004, 2006; De Graaf *et al.*, 2005; Chow *et al.*, 2008; Feraru *et al.*, 2012). Similarly, RABA2 and RABA3 colocalize with VHAa1 and internalized FM4-64 within a subcompartment of the TGN/EE and are PM-associated, suggesting that they function in exocytosis as well (Chow *et al.*, 2008). During cytokinesis, RABA2 and RABA3 colocalize extensively with KN in both the TGN/EE and at the CP leading edge, which is embedded within a ribosome-excluding CP assembly matrix (CPAM) (Otegui & Staehelin, 2004) and is the site to which CP-destined vesicles are delivered and fuse with the expanding CP. GTPase-inactive or GTP-bound-mimic mutant RABA2 proteins also accumulate at the CP (Chow *et al.*, 2008) and result in cytokinesis defects, including abnormal cell files and multinucleated cells with incomplete CWs. Together these data indicate that RabAs likely regulate the trafficking of TGN/EE-derived vesicles containing newly synthesized, and possibly recycled, material to the division plane.

In addition to the RabA GTPases, the MVB/PVC Rabs, RABF1 and RABF2b (Ueda *et al.*, 2004), localize to CPs, and expression of a GTPase mutant form of RABF2b results in cytokinesis defects (Dhonukshe *et al.*, 2006). However, localization of RABF2b and other late edosomal/MVB/PVC markers, for example, BP80 and the ARF guanine nucleotide exchange factor (GEF), GNOM, to the CP was notconfirmed (Chow *et al.*, 2008). Furthermore, in contrast to the preferential association of RABA2a/A2b/A3 and KN with the CP leading edge (Chow *et al.*, 2008), RABF1 and RABF2b were distributed throughout the division plane (Dhonukshe *et al.*, 2006), inconsistent with a role in membrane delivery and addition to the growing CP. Thus further work is necessary to understand whether there is a direct role for late endocytic Rabs in CP formation.

Rabs are activated by RabGEFs, inactivated by GTPase activating proteins (RabGAPs), and recycled by GDP dissociation inhibitors (RabGDIs). At the present time, little is known about the identity and function of plant RabGAPs and RabGDIs in membrane trafficking to the PM and CP. However, the putative late secretory pathway RabGEFs, TRAPPII (discussed later) and SCD1, are required for CP formation and cell expansion. Loss-of-function and missense mutations in the SCD1 N-terminal DENN

domain cause defects in cytokinesis, cell expansion and innate immunity responses to pathogens (Falbel *et al.*, 2003; Korasick *et al.*, 2010). DENN domains are constituents of proteins that associate with Rabs (Levivier *et al.*, 2001) and function as animal Rab GEFs (Sato *et al.*, 2008; Allaire *et al.*, 2010; Yoshimura *et al.*, 2010). In particular, Connecdenn/DENND1A/RME-4 functions as a CCV-associated GEF for Rab35 (Allaire *et al.*, 2010), a Rab required for CCV trafficking, endosomal recycling and cytokinesis in mammalian cells (Kouranti *et al.*, 2006; Patino-Lopez *et al.*, 2008). As plants lack Rab35 homologs, SCD1 may function as a GEF for members of the significantly expanded and divergent plant RabA/Rab11 family (Rutherford & Moore, 2002) or other Rab(s) that function in late secretory membrane trafficking during cytokinesis and cell expansion.

Following their formation and trafficking to their final destination, vesicles are brought into close proximity to their target membrane through the action of Rabs and cognate tethering factors. In yeast, the multisubunit TRAPPII and exocyst tethering complexes function in the late Golgi and mediate TGN/EE to PM trafficking, respectively (Cai *et al.*, 2007). TRAPPII consists of the seven subunits of the TRAPPI complex, which is required for endoplasmic reticulum (ER) to Golgi transport, and three additional subunits, Trs65, Trs120, and Trs130 (Sciorra *et al.*, 2005). Both yeast TRAPPI and TRAPPII function as Rab GEFs. TRAPPII serves as a GEF for Ypt31/32, the yeast Rab11 orthologs, and is required for Rab11 localization and cleavage furrow ingression during cytokinesis in Drosophila (Robinett *et al.*, 2009). Mammalian TRAPPII, however, localizes to the early Golgi and activates the early secretory pathway Rab protein, Rab1 (Yamasaki *et al.*, 2009).

By electron microscopic (EM) tomography, putative tethering factors have been observed to be associated with fusing CP vesicles (Otegui & Staehelin, 2004; Seguí-Simarro *et al.*, 2004) and recent studies reveal that TRAPPI, TRAPPII, and the exocyst are required for cytokinesis (Fendrych *et al.*, 2010; Thellmann *et al.*, 2010; Qi *et al.*, 2011). Disruption of the Arabidopsis TRAPPI/TRAPPII-subunit-encoding *AtTRS33*, *AtTRS120* or *AtTRS130* genes results in defective CP formation and cell expansion (Jaber *et al.*, 2010; Thellmann *et al.*, 2010; Qi *et al.*, 2011). Further localization and genetic interaction studies suggest that the Arabidopsis TRAPPII complex likely serves as a GEF for RabAs in the trafficking of TGN/EE-derived vesicles containing newly synthesized and endocytosed proteins to the PM and CP (Qi *et al.*, 2011; Qi & Zheng, 2011).

Vesicle fusion at the PM and developing CP is aided by the exocyst complex, an evolutionarily conserved assembly that is localized to sites of active exocytosis on the PM in polarized mammalian cells (Cai *et al.*, 2007). Plants encode multiple genes for each of the exocyst subunits, the most extreme example being the Arabidopsis Exo70 subunit, which is encoded by a family of 23 genes (Synek *et al.*, 2006) that are primarily expressed in cells that require active exocytosis (Hála *et al.*, 2008; Li *et al.*, 2010a). Arabidopsis and maize exocyst subunit mutants display multiple defects in plant growth and development, cell expansion, and incomplete epidermal cytokinesis (Wen *et al.*, 2005; Cole *et al.*, 2005; Hála *et al.*, 2008; Fendrych *et al.*, 2010; Li *et al.*, 2010a). The exocyst complex is associated with the leading edge, maturing regions and parental PM fusion sites of the CP (Fendrych *et al.*, 2010), suggesting that the exocyst mediates the addition and consolidation of CP membrane at all stages of CP formation.

Whether additional tethering complexes function directly in the tethering of transport vesicles required for CP assembly remains to be determined. Characterization of Arabidopsis mutants expressing defective genes for subunits of the GARP complex, which functions in endosome to late-Golgi trafficking in yeast (Cai *et al.*, 2007) and is required for pollen tube elongation (Wang *et al.*, 2008), did not reveal a role for this tethering complex in CP formation (Thellmann *et al.*, 2010); however, it cannot be ruled out that other tethering complexes (e.g. TRAPPII) could compensate for the role of GARP in membrane retrieval from the developing CP.

Ultimately it is the assembly of specific trans-SNARE protein complexes between transport vesicles and target membranes that drives membrane bilayer fusion. These complexes comprise four α-helical SNARE domains that are contributed by multiple (Q-type) target membrane t-SNAREs and one (R-type) v-SNARE on the vesicle/donor membrane (Südhof & Rothman, 2009). Formation of the initial trans-SNARE complex between opposing membranes is regulated by a host of proteins, including their activation by Sec1/Munc18-like (SM) proteins, and N-ethylmaleimide sensitive factor (NSF)- and α-SNAP-mediated ATP-dependent disassembly. The most likely SNARE complex involved in CP vesicle fusion comprises the t-SNAREs, KN (Lauber *et al.*, 1997) and SNAP33 (Heese *et al.*, 2001), and the functionally redundant t-SNAREs, VAMP721 and VAMP722, all of which localize to and are required for the formation of the CP (Kwon *et al.*, 2008; Zhang *et al.*, 2011). Another t-SNARE, NSPN11, shows CP localization and KN interaction (Zheng *et al.*, 2002); however, as *nspn11* mutants show no detectable cytokinesis defects, it is unknown whether this SNARE is involved in CP membrane fusion. KN interacts with NSF/α-SNAP (Rancour *et al.*, 2002) and the Arabidopsis SM protein, KEULE, which is essential for CP formation (Waizenegger *et al.*, 2000; Assaad *et al.*, 2001; Park *et al.*, 2012). Although SM proteins are generally thought to interact with the closed/inactive form of syntaxin-type SNAREs to promote SNARE complex formation (Südhof & Rothman, 2009), KEULE appears to interact preferentially with a fusion-competent form of KN (Park *et al.*, 2012), raising the interesting question of whether CP vesicle fusion is mechanistically similar to, or distinct from, other SNARE-mediated membrane fusion processes.

Of the SNAREs shown to be required for CP vesicle fusion, only KN specifically functions in cytokinesis. In nondividing cells, SNAP33 and VAMP721/722 interact with other members of the SYP1 t-SNARE family in the trafficking of CW material and PM proteins (Kwon *et al.*, 2008; Zhang *et al.*, 2011). In particular, VAMP721 and VAMP722, which localize to the VHA-a1-positive TGN/EE, function as v-SNAREs in the targeting and fusion of exocytic TGN/EE-derived vesicles with the PM (Zhang *et al.*, 2011).

3. Cell plate membrane recycling

The flux of membrane to the division plane during cytokinesis is balanced by retrograde transport. Based on changes to the

surface area of the CP throughout cytokinesis, it is estimated that *c.* 70% of the membrane delivered to the division plane is ultimately recycled (Samuels *et al.*, 1995; Otegui *et al.*, 2001). Recent studies have implicated clathrin-dependent membrane transport in the recycling of proteins and lipids during positioning, maturation and fusion of the CP with the parental membrane, as well as their redistribution following cytokinesis. While MFs have been shown to be integral to clathrin-mediated endocytosis (CME) in mammals and yeast (Mooren *et al.*, 2012), the role of MFs and/or MTs in clathrin-dependent endocytosis from the PM or membrane recycling from the CP is not well understood.

Clathrin-dependent membrane transport is likely required for localized changes in the protein and/or lipid composition of the PPB-associated PM/CW domain before mitosis, which serve as cortical memory cues for CP fusion with the CDS. Support for this hypothesis came from EM analysis of chemically fixed dividing guard mother cells, which showed prominent CW thickenings, indicative of polarized secretion of PM and CW material to the CDS, and the presence of coated vesicles at the CDZ (Galatis *et al.*, 1984). Although these thickenings are likely a unique aspect of guard cell cytokinesis, the use of electron tomographic analysis of high-pressure frozen/freeze-substituted samples and live cell imaging has provided convincing evidence for the enrichment of endosomes, endocytic clathrin-coated pits and CCVs at the CDZ in other cell types (Dhonukshe *et al.*, 2005; Karahara *et al.*, 2009; Van Damme *et al.*, 2011a).

Electron microscopic studies of high-pressure frozen/freeze-substituted plant cells undergoing cytokinesis have also highlighted the importance of clathrin in the recycling of CP membranes during CP maturation. CCVs have been detected budding from maturing regions of the CP concomitant with the appearance of MVB/PVCs, organelles to which the CCVs are believed to deliver recycled membrane and cargo from the CP (Samuels *et al.*, 1995; Otegui *et al.*, 2001; Otegui & Staehelin, 2004; Seguí-Simarro *et al.*, 2004; Dhonukshe *et al.*, 2005; Seguí-Simarro & Staehelin, 2006; Tahara *et al.*, 2007). Indeed, KN is recycled from the CP as it matures, and accumulates in MVBs/PVCs before being degraded in the vacuole (Tse *et al.*, 2004; Reichardt *et al.*, 2007; Boutté *et al.*, 2010). Also, the PIN proteins are targeted to developing CPs during cytokinesis and recycled via clathrin-dependent membrane trafficking during CP maturation (Baluška *et al.*, 2005; Dhonukshe *et al.*, 2006, 2007; Mravec *et al.*, 2011).

Recent studies have demonstrated that endocytosis, and particularly CME, is essential for plant growth, development and signaling (Dhonukshe *et al.*, 2007; Robert *et al.*, 2010; Kitakura *et al.*, 2011; Adam *et al.*, 2012). In mammalian cells, CME and the formation of CCVs at the TGN involves the coordinated interplay of accessory and regulatory proteins that is initiated by binding of the cargo adaptor protein (AP) complexes, AP-2 and AP-1, at the PM and TGN, respectively. Subsequently, the polymerization of clathrin triskelia, composed of heavy chain (CHC) and light chain (CLC) subunits, and the membrane remodeling activities of accessory proteins, are necessary for the invagination and release of the budding CCVs (Kirchhausen, 2000). Many evolutionarily conserved structural and regulatory proteins involved in CCV formation, such as CLC, CHC, AP-2 adaptins, dynamins and AP180/Epsin N-terminal homology (A/ENTH) domain-containing proteins (involved in membrane curvature), have been identified in plants (Blackbourn & Jackson, 1996; Holstein, 2002; Barth & Holstein, 2004; Kotchoni *et al.*, 2009; Bednarek & Backues, 2010; Song *et al.*, 2012). Live cell imaging has also demonstrated that clathrin, the adaptin-like TPLATE, the plant dynamin-related proteins and A/ENTH proteins localize to the CP (Konopka *et al.*, 2008; Konopka & Bednarek, 2008; Fujimoto *et al.*, 2010; Van Damme *et al.*, 2011a; Ito *et al.*, 2012; Song *et al.*, 2012), suggesting that clathrin-mediated CP membrane recycling is mechanistically related to CCV formation at the TGN and during CME.

Dynamin and DYNAMIN-RELATED PROTEINS (DRPs) are a structurally similar but functionally diverse group of large GTPases. In plants, two distinct DRP families, DRP1 and DRP2, play essential and nonredundant roles in plant endomembrane trafficking and dynamics (Gu & Verma, 1997; Kang *et al.*, 2003a, b; Collings *et al.*, 2008; Backues *et al.*, 2010; Taylor, 2011; Mravec *et al.*, 2011). DRP1 and DRP2 colocalize together with CLC2 at the PM in dynamic foci that likely correspond to sites of CME (Konopka *et al.*, 2008; Konopka & Bednarek, 2008; Fujimoto *et al.*, 2010) and within maturing regions of the expanding CP (Fig. 2; S. K. Backues & S. Y. Bednarek, unpublished) (Kang *et al.*, 2003a; Konopka *et al.*, 2008; Fujimoto *et al.*, 2008, 2010). *drp1* and *drp2* mutants also display defects in CP formation, such as incomplete CWs (Gu & Verma, 1997; Kang *et al.*, 2003a; Collings *et al.*, 2008; Mravec *et al.*, 2011) or highly convoluted CP membranes (Backues *et al.*, 2010), respectively. More specifically, in *drp1* mutants, KN is mislocalized to the PM following completion of CP formation (Boutté *et al.*, 2010), and clathrin-mediated recycling of PIN proteins from the developing CP is defective (Mravec *et al.*, 2011).

Imaging studies reveal that DRP1/2 also localize to the leading edge of the forming CP (Kang *et al.*, 2003a; Konopka *et al.*, 2008; Fujimoto *et al.*, 2010) before the appearance of clathrin and A/ENTH proteins (Ito *et al.*, 2012; Song *et al.*, 2012) (Fig. 2; S. K. Backues & S. Y. Bednarek, unpublished). Indeed, DRP1 and possibly DRP2 ring complexes have been observed by EM to form constrictions in the early syncytial-type and somatic CP tubular networks in the absence of clathrin-coated buds (Otegui *et al.*, 2001; Seguí-Simarro *et al.*, 2004). Based on current models, dynamins are recruited to sites of CCV formation via their interaction with clathrin, lipids, the AP complex and A/ENTH proteins. Hence the localization of DRPs to the CP leading edge in the absence of clathrin and A/ENTH domain-containing proteins (Ito *et al.*, 2012; Song *et al.*, 2012) is likely to be distinct from their recruitment in CCV formation. Putative functions for the DRP rings at the CP leading edge include membrane tubulation, which may promote CP tubule fusion through the generation of regions of high curvature, and tethering or restricting the lateral diffusion of enzymes (e.g. callose synthases) and other proteins required for CP formation and maturation.

The plant-specific TPLATE protein contains a domain similar to regions found within the large subunit of the AP complexes and the β, γ1 and γ2 subunits of the COP1 coatamer protein complex

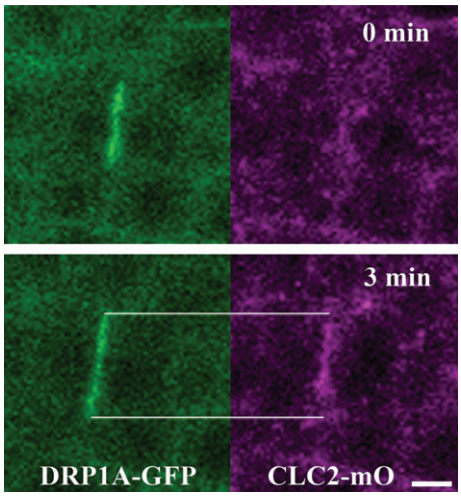

Fig. 2 Time-lapse laser scanning confocal microscopy images of DYNAMIN-RELATED PROTEIN 1A (DRP1A)-GFP (left panels; green) and CLATHRIN LIGHT CHAIN 2 (CLC2)-mOrange (right panels; magenta) at the cell plate. Horizontal lines indicate the leading edges of the cell plate. Bar, 5 μm.

(Van Damme *et al.*, 2006), suggesting it functions in membrane dynamics. TPLATE colocalizes with CLC2 to growing CPs and later to the flanks of the CDS as the CP attaches to the parental PM (Van Damme *et al.*, 2011a). RNAi-mediated knockdown of TPLATE perturbs this attachment, resulting in incomplete CWs (Van Damme *et al.*, 2006). TPLATE was also shown to interact with CHC1 and CLC2. Together these data implicate TPLATE in clathrin-mediated membrane reorganization/recycling at the CP and/or parental PM necessary for integration of the CP at the CDS (Van Damme *et al.*, 2011a).

4. The endoplasmic reticulum

In addition to the close association of Golgi, TGN/EE and MVBs with the division plane, maturation and fusion of the CP at the CDS are accompanied by the recruitment of ER membranes to the CDZ and the formation of a tightly associated reticular network surrounding the CP (Hepler, 1982; Schopfer & Hepler, 1991; Cutler & Ehrhardt, 2002; Otegui & Staehelin, 2004; Seguí-Simarro *et al.*, 2004). This ER network may be the precursor to the cortical ER network that lies in close proximity to the PM in all plant cells (Lichtscheidl & Hepler, 1996; Staehelin, 1997).

Potential roles for the CP-associated ER are direct lipid transfer to the CP and/or establishment and maintenance of an appropriate ionic environment (e.g. supplying Ca^{2+}) (Lichtscheidl & Hepler, 1996; Otegui & Staehelin, 2004; Seguí-Simarro *et al.*, 2004) to support CW biosynthesis and CP membrane fusion and consolidation. Tubular elements of the CP-associated ER network also fuse and become entrapped, forming the desmotubule that traverses plasmodesmata (Hepler, 1982) between adjacent daughter cells. Coordinate assembly of the CP and expanding PM with ER membrane networks likely involves active membrane trafficking and fusion within the division plane.

Endoplasmic reticulum formation within the CDZ may be mediated by the abundant and conserved hexameric AAA (ATPases associated with diverse cellular activities) molecular chaperone, CDC48/p97, which is structurally related to NSF (Hanson & Whiteheart, 2005). Like NSF, CDC48/p97 functions in a variety of SNARE-dependent membrane fusion pathways including homotypic fusion of ER, transitional-ER (t-ER), and mitotic Golgi fragments (Latterich *et al.*, 1995; Rabouille *et al.*, 1995; Patel *et al.*, 1998; Roy *et al.*, 2000).

In plant cells, CDC48/p97 localizes to the cytoplasm, nucleus, PM and ER during interphase (Aker *et al.*, 2007; Park *et al.*, 2008) and at the phragmoplast midzone during late cytokinesis, and its function is required for cytokinesis (Park *et al.*, 2008). However, unlike NSF, AtCDC48 does not interact with KN (Rancour *et al.*, 2002), indicating that its chaperone activity is not required for the initiation of CP membrane fusion. Rather, based on its colocalization and interaction with the Golgi/ER t-SNARE, SYP31 (Rancour *et al.*, 2002; Bubeck *et al.*, 2008), an ortholog of the syntaxin5 SNARE protein required for assembly of t-ER (Roy *et al.*, 2000) and ER network formation in mammals (Uchiyama *et al.*, 2002), AtCDC48 and SYP31 may be required for ER formation within the CDZ critical for CP maturation. However, as CDC48/p97 activity is required for many other cellular processes, including ER-associated protein degradation (Meyer *et al.*, 2012) and endocytosis (Ritz *et al.*, 2011; Ramanathan & Ye, 2012), other roles for AtCDC48 in cytokinesis cannot be ruled out. Further characterization of ER membrane reticulons (Sparkes *et al.*, 2010) and the GTPase RHD3 (Chen *et al.*, 2011b), which mediate tubular ER membrane formation and dynamics, may provide additional insight into the dynamics and role of ER membrane assembly in CP formation.

5. Cell wall and lipid requirements

In addition to their structural roles in cellular membranes, phosphotidylinositides (PIs) function as signaling molecules and influence the localization of PI-binding proteins. In dividing cells, the PI3P-specific probe YFP-2xFYVE localizes in punctate structures at or near the CP leading edge (Vermeer *et al.*, 2006), while the PI4P marker, YFP-PHFAPP1, labels the growing CP and STmd-positive TGN/EEs (Vermeer *et al.*, 2009), suggesting a role in CP expansion/maturation. PI3P/PI4P may facilitate the localization of factors required for CP formation, such as the DRP2 proteins, which contain a PI3P-/PI4P-binding PH domain (Bednarek & Backues, 2010). Similarly, Arabidopsis PATELLIN (PATL) localizes to growing CPs and contains a PI3P-binding domain homologous to that of Sec14, which functions in the formation of TGN-derived vesicles (Peterman *et al.*, 2004).

Other lipids, including very long fatty acyl chain (VLFA) of phospholipids and sterols, are required for cytokinesis. Mutations within the Arabidopsis *PASTICCINO2 (PAS2)* gene, which encodes an elongase necessary for synthesis of VLFAs, delays or halts CP expansion concomitant with mislocalization of KN and RABA2a (Bach *et al.*, 2011). The CP membrane sterol composition is also critical for maintenance of KN within the CDZ via endocytosis during late, but not early, cytokinesis (Boutté *et al.*, 2010) and for the repolarization of PIN2 proteins after cytokinesis that localize to the CP during division (Men *et al.*, 2008). Sterol-

rich microdomains, which are crucial for cellulose biosynthesis (Schrick *et al.*, 2000, 2002, 2004, 2012), may also be critical for maintaining the structural integrity and enzyme activities involved in CW formation within the developing CP. Sterol biosynthesis mutants *fackel* (*fk*), *cephalopod1* (*cph1*) and *hydra1* (*hyd1*) display cell division, cell expansion and embryonic patterning defects; specifically, typical cellulose-deficient phenotypes are observed, including multinucleated cells, incomplete CWs and CW thickenings as a result of ectopic callose and lignin deposition (Diener *et al.*, 2000; Jang *et al.*, 2000; Schrick *et al.*, 2000, 2002; Souter *et al.*, 2002).

During cytokinesis, vesicles carrying newly synthesized and recycled pectic polysaccharides, hemicelluloses, arabinogalactan proteins, and biosynthetic enzymes are delivered to the lumen of the growing CP to initiate CW formation (Staehelin & Moore, 1995; Baluška *et al.*, 2005). Callose is the major CW material found in young CPs, and is later replaced by cellulose in the mature primary CW (Samuels *et al.*, 1995). The Arabidopsis callose synthase mutant *gsl8* displays multinucleated epidermal cells with incomplete CWs, implicating the necessity of GSL8 for successful cytokinesis (Töller *et al.*, 2008; Chen *et al.*, 2009; Guseman *et al.*, 2010). These phenotypes are shared by many sugar modification mutants, such as *knopf* (*knf*), *radially swollen 3* (*rsw3*), *cytokinesis-defective1* (*cyt1*), and *korrigan* (*kor*), and by several cellulose biosynthetic mutants, such as *procuste1* (*prc1*), *cellulose synthase A1* (*cesA1*) and *cellulose synthase-like D1* (*cslD*), implying that their wild-type gene products may contribute to late CP formation and/or strengthening of the daughter CW (Zuo *et al.*, 2000; Fagard *et al.*, 2000; Lukowitz *et al.*, 2001; Boisson *et al.*, 2001; Lane *et al.*, 2001; Gillmor *et al.*, 2002; Burn *et al.*, 2002; Hunter *et al.*, 2012).

IV. Conclusion

Higher plant cytokinesis depends upon cytoskeletal dynamics and membrane trafficking for the demarcation of division orientation and the temporally and spatially distinct processes required for CP initiation, maturation and integration with the CDS. As highlighted in this review, in recent years there has been a vast increase of our knowledge of the molecular players and their roles in PPB formation, phragmoplast MT and MF dynamics, and CP membrane trafficking and fusion. However, there remains a number of significant questions regarding the mechanisms by which cytoskeletal dynamics and membrane trafficking are coordinated across time and space during cell division to execute cytokinesis. In particular, major questions to be addressed are how the PPB is initially defined and what molecular cues reside at or are excluded from the CDZ that direct CP fusion at the CDS. Likewise, the specific phragmoplast cytoskeletal dynamics required for, and the roles of endosomes and endocytic trafficking in, delivery and recycling of protein, lipid and CW material to and from the CP are poorly understood. As our inventory of the molecular players involved in cytoskeletal and membrane dynamics necessary for cytokinesis continues to increase, additional imaging and biochemical approaches, including the use of *in vitro* system(s) that reconstitute various stages of phragmoplast and CP biogenesis and function, will likely address some of the controversial issues and questions that we raised in this review and provide a more comprehensive understanding of plant cytokinesis.

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