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Rab GTPases, tethers, and SNAREs work together to regulate *Arabidopsis* cell plate formation

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Cell plates are transient structures formed by the fusion of vesicles at the center of the dividing plane; furthermore, these are precursors to new cell walls and are essential for cytokinesis. Cell plate formation requires a highly coordinated process of cytoskeletal rearrangement, vesicle accumulation and fusion, and membrane maturation. Tethering factors have been shown to interact with the Ras superfamily of small GTP binding proteins (Rab GTPases) and soluble N-ethylmaleimide-sensitive factor attachment protein receptors (SNAREs), which are essential for cell plate formation during cytokinesis and are fundamental for maintaining normal plant growth and development. In *Arabidopsis thaliana*, members of the Rab GTPases, tethers, and SNAREs are localized in cell plates, and mutations in the genes encoding these proteins result in typical cytokinesis-defective phenotypes, such as the formation of abnormal cell plates, multinucleated cells, and incomplete cell walls. This review highlights recent findings on vesicle trafficking during cell plate formation mediated by Rab GTPases, tethers, and SNAREs.

KEYWORDS
***Arabidopsis*, vesicle trafficking, Rab GTPases, tethers, SNAREs, cytokinesis, cell plate**

1 Introduction

Cell division is fundamental to plant growth, development, and reproduction, including the processes of DNA replication, nuclear division, and cytokinesis (Tulin and Cross, 2014). Cytokinesis is the final step in cell division, which involves the process of separating a mother cell into two daughter cells by forming a new compartment between two newly formed daughter nuclei. This is a highly coordinated spatiotemporal event that involves specialized rearrangements of the cytoskeleton during cell division and a series of vesicle transport activities (Müller, 2019; Yi and Goshima, 2022). During cytokinesis, the aggregation and alignment of microtubules forms the phragmoplast, which promotes the orderly delivery of vesicles at the plane of cell division; furthermore, the fusion and fission of aggregated vesicles in the center of dividing cells promotes early cell plate formation (Euteneuer and McIntosh, 1980; Lee et al., 2001; Jürgens, 2005).

The formation of the cell plate goes through the following four distinct stages (Figure 1): (i) The Golgi-derived vesicles are guided to the cell division plane by the phragmoplast, and vesicles aggregate and fuse to form dumbbell structures. (ii) The initial collection of fused tubes at the center of the segmentation plane undergo a series of morphological changes, resulting in a tubulo-vesicular network, depolymerization of the microtubules underlying the tubulo-vesicle network, and stabilization of the microtubules adjacent to the edge of the fusion channel (Nishihama and Machida, 2001; Seguí-Simarro et al., 2004). (iii) Gradual merging into a tubular network form, which is a membrane morphology that subsequently forms into a smoother structure largely through network expansion. (iv) Formation of a fenestrated sheet that fuses with the parental plasma membrane (PM) (Samuels et al., 1995; Sinclair et al., 2022). This process involves various actions such as closing the plate fenestrae, adding pectin and xyloglucan, removing excess membranes, and replacing callose with cellulose. Eventually, the cell plate fuses with the mother cell wall, and the process ends with a transition to an entirely new lateral wall that separates the daughter cells (Samuels et al., 1995; Seguí-Simarro et al., 2004; Baluska et al., 2005).

During cell plate biogenesis, cytokinetic vesicles deliver cargo and contribute membrane material. Cytokinetic vesicles are primarily derived from the Golgi/*trans*-Golgi network (TGN) and are contributed by endosomal populations. ARF guanine exchange factors (ARF GEFs) BIG1-4 assist in the transport of newly synthesized proteins and endocytic products to the formed cell plate (Seguí-Simarro et al., 2004; Richter et al., 2014). Intracellular membrane fusion generally depends on Rab GTPases, tethering factors, and SNARE proteins (Jahn et al., 2003; Jahn and Scheller, 2006; Stenmark, 2009; Hong and Lev, 2014). Rab GTPases are master regulators of membrane trafficking, regulating the transport of vesicles during cell plate formation (Davis et al., 2016; Minamino and Ueda, 2019). Activation of Rab GTPases by GEFs promotes recruitment of tethering factors to the membranes (Stenmark, 2009). Tethering proteins provide specificity for targeting, and vesicle tethering initiates SNARE-dependent fusion of membrane vesicles to form cell plates (Yu and Hughson, 2010) (Figure 2). Some Rab GTPases, tethers, and SNAREs are localized to the cell plate during cytokinesis, and some of these mutations lead to typical cytokinesis-defective phenotypes, such as the formation of abnormal cell plates, binucleated or multinucleated cells, and cell wall stubs (Chow et al., 2008; Jaber et al., 2010; Qi et al., 2011; Zhang et al., 2011) (Figure 3).

2 The Rab family of small GTPase proteins are involved in plant cell plate formation

Rab GTPases are members of the Ras-like small GTP-binding protein superfamily, which are guanine nucleotide-binding proteins that act as molecular switches that can alternate between the following two conformations: the inactive form (GDP-bound) and the active form (GTP-bound). The conversion of Rab GTPases from a GDP-bound to a GTP-bound form requires a GEF (Cui et al., 2014; Rosquete et al., 2019). The Rab GTPase plays an important role in various forms of membrane transport, by activating and/or recruiting various membrane traffic regulators (also known as Rab effector proteins) (Prekeris, 2003; Sohn et al., 2003; Hutagalung and Novick, 2011). Rab GTPases are involved in the regulation of multiple cellular processes, including endosome organization, PM recycling, phagocytosis, cytokinesis and so on (Pereira-Leal and Seabra, 2001;

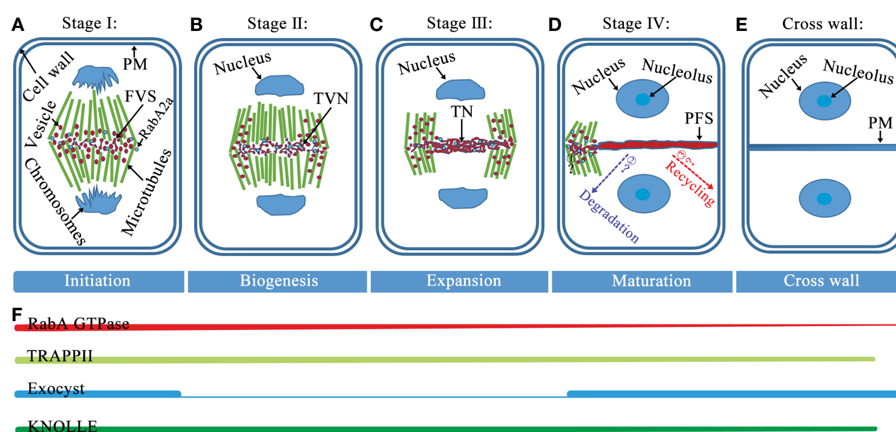

FIGURE 1
Model of cell plate formation stages and spatiotemporal distribution of Rab GTPases, tethers, and SNAREs. **(A)** Stage I, at this fusion of vesicles stage (FVS), during the initial fusion and fission of the bladder, the dumbbell structure forms. **(B)** Stage II, vesicles undergo fusion, fission, and conformational changes to form a tubulo-vesicular network (TVN). **(C)** Stage III, the TVN gradually merges into a tubular network (TN). **(D)** Stage IV, as the cell plate continues to smoothen and expand, the formation of a planar fenestrated sheet (PFS). The cell plate extends fusion tube connecting to the cell plate fusion site with PM and fuses with PM (Step1), and the black question mark indicates an unknown mechanism. After the cell plate is anchored to PM, the proteins diffused from the cell plate would be recycled and/or degraded (Step2 and 3), and dashed arrows with question marks indicate where these proteins are likely to go. **(E)** At the end of cytokinesis, the cell plate enters maturation when the new primary cross wall and daughter cells separate. **(F)** The association of RabA GTPase with the membrane provides cargo for cell plate formation and remains present throughout cell plate formation. Both TRAPPII and exocyst complexes are present at the onset of cytokinesis. Thereafter, the TRAPPII complex consistently marks the cell plate from cytoplasmic division and it is required for its biogenesis, while the outer capsule is primarily required for the maturation of the cell plate. Throughout the cell plate formation phase, SNARE-dependent membrane vesicles fuse to form the cell plate. Abbreviations: PM, plasma membrane; FVS, fusion of vesicles stage; TVN, tubulo-vesicular network; TN, tubular network; and PFS, planar fenestrated sheet.

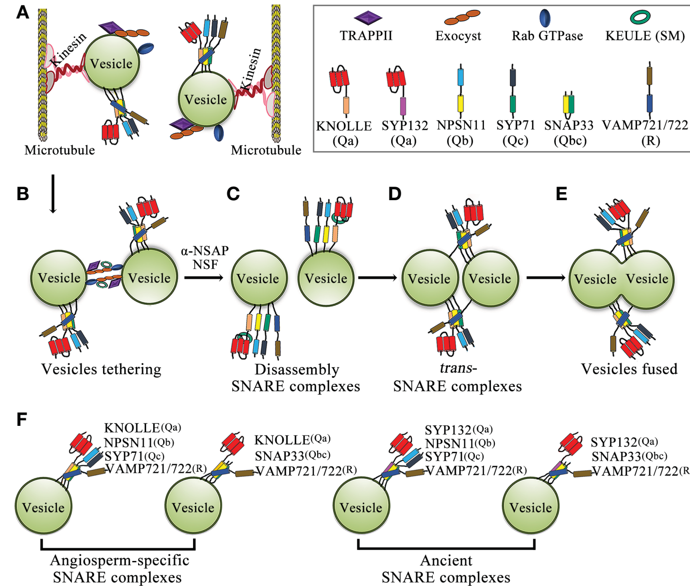

FIGURE 2
Schematic model of membrane-vesicle fusion during cytokinesis. **(A)** Vesicles carry Rab GTPase, two types of tethering complexes, TRAPPII and exocyst, and the KNOLLE-containing *cis*-SNARE complex through kinesin transport along microtubules to the plane of cell division. **(B)** Rab GTPases promote the tethering of two adjacent vesicles by tethering complexes (TRAPPII and exocyst). **(C)** The *cis*-SNARE complex is disassembled by NSF-ATPase and α-SNAP, and the Qa-SNARE KNOLLE interacts with the Sec/Munc18 protein KEULE to keep the KNOLLE in an open conformation. **(D)** KNOLLE interacts with SNARE partners of adjacent vesicles to form *trans*-SNARE complexes. **(E)** Two adjacent vesicles fused together. **(F)** Model of the SNARE complex in cytokinesis. The cytokinesis-specific Qa-SNARE KNOLLE forms two types of SNARE complexes. In addition, the evolutionarily ancient Qa-SNARE SYP132 forms two types of SNARE complexes. Abbreviations: SM, Sec1p/Munc18; α-SNAP, α-soluble NSF attachment protein; and NSF, n-ethylmaleimide-sensitive factor.

Woollard and Moore, 2008). Cytokinesis requires the activity of Rab GTPase to regulate vesicle-mediated material contributions to the developing cell plate (Chow et al., 2008). The *Arabidopsis* genome encodes at least 57 members of the Rab GTPases, which are grouped into eight subfamilies (RabA GTPase to RabH GTPase) (Vernoud et al., 2003; Woollard and Moore, 2008). Four subfamilies of Rab GTPases (RabA, RabE, RabF and RabH) are involved in the formation of the cell plate during cytokinesis (Table 1).

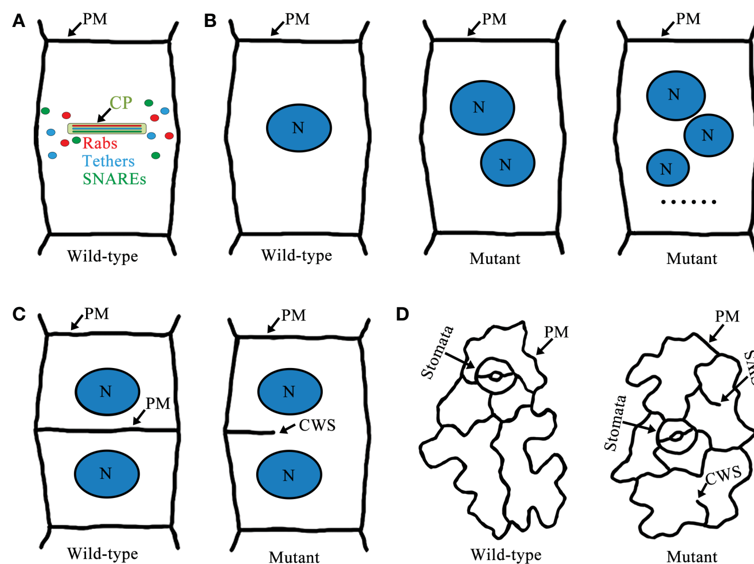

FIGURE 3
A schematic model of Rab GTPases, tethers, SNAREs cell plate localization and cytokinesis-defective mutants in *Arabidopsis*. **(A)** Localization of Rab GTPases, tethers, and SNAREs in the cell plate. **(B)** Wild-type root epidermal cells of *Arabidopsis* have normal cytokinesis and only one nucleus per cell. In cytokinesis-defective mutants there are two or more nuclei per cell. **(C)** Wild-type root epidermal cells have intact cell walls, but defects in cell plate formation in cytokinesis-defective mutants lead to the formation of cell wall stubs. **(D)** Wild-type cotyledon epidermal cells are intact cells with clear outlines. However, cytokinesis-defective mutants often have cell wall stubs. Abbreviations: CP, cell plate; N, nucleus; PM, plasma membrane; and CWS, cell wall stubs.

Ten RabA GTPases (RabA1b, RabA1c, RabA1d, RabA1e, RabA2a, RabA2b, RabA2c, RabA2d, RabA3, and RabA5c) are localized to the cell plate (Table 1). The gene BEX5 encodes RabA1b, which localizes to the TGN/EE, PM, and cell plates, and it functions in protein trafficking in *Arabidopsis* roots, presumably by regulating vesicle formation, budding, and trafficking from the TGN/EE to the PM/cell wall (Geldner et al., 2009; Feraru et al., 2012; Asaoka et al., 2013). *Bex5* mutants display the following defects: increased protein accumulation in abnormal trafficking inhibitor brefeldin A (BFA) compartments, abnormal endosomes, and defects in both exocytosis and transcytosis of PM proteins (Feraru et al., 2012). During cell division, RabA1c is relocated to the cell plate, and this process can be interrupted by the chemical compound endosidin 1 (ES1). In addition, RabA1c defines a group of TGNs that are related to VHA-a1-tagged TGN but only partially overlap with them (Qi and Zheng, 2013). RabA1c (S27N) and RabA1c (Q72L), which are dominant inhibitory mutants, are impaired in root growth and show severe cytokinesis defects (Qi and Zheng, 2013). In addition, root growth and cytokinesis in root cells of *raba1a/b/c* triple mutant seedlings are sensitive to low levels of ES1 (Kotzer et al., 2004; Lee et al., 2004; Qi and Zheng, 2013). RabA1d is localized at the TGN/EE and cell plates and is involved in vesicle trafficking and cell plate formation. The accumulation pattern of RabA1d is consistent with regions of active vesicle fusion during cell plate formation and cell growth, which suggests that it plays an important role in cell plate formation and membrane/cargo trafficking for membrane recycling (Takáč et al., 2012; Berson et al., 2014). RabA1e appears on the cell plate in cytokinesis and it may mediate vesicle transport during cytokinesis. In early-stage cell plates, YFP-RabA1e and YFP-RabA2a were consistently localized to a disk-shaped structure at the center of the dividing cell. In late-stage cell plates, the localization patterns of the two proteins were different, in which YFP-RabA2a were mainly localized to ring-shaped structures across the cell division plane, whereas YFP-RabA1e were mainly localized to both ring-shaped structures and disk-shaped structures. In addition, in late-stage cell plates, differences between YFP-RabA2a and YFP-RabA1e were more pronounced after treatment of cytokinesis inhibitor endosidin 7. RabA1e and RabA2a exhibit different

TABLE 1 Characteristics of Rab GTPases located in cell plates.

Type	Gene	AGI Gene	Localization	Function	Reference
RabA	RabA1b/ BET5	AT1g16920	TGN/EE, PM, CP	Secretory pathway from TGN to PM; exocytic trafficking; recycling pathways.	Feraru et al., 2012 ; Asaoka et al., 2013
	RabA1c	At5g45750	TGN/EE, CP	Involved in cytokinesis; the polar secretion and circulation of PM proteins.	Qi et al., 2011; Qi and Zheng, 2013
	RabA1d	At4g18800	TGN/EE, CP	Cell plate formation and polarized cell expansion of root hairs; regulates vesicular trafficking at TGN.	Takáč et al., 2012; Berson et al., 2014
	RabA1e	At4g18430	E, RE, CP	Vesicle-mediated cargo delivery during cytokinesis and root hair elongation.	Geldner et al., 2009; Berson et al., 2014; Davis et al., 2016
	RabA2a	At1g09630	TGN/EE, CP	Involved in cytokinesis; vesicle secretion regulates vesicle trafficking from the TGN to the PM; regulation of K^+ homeostasis.	Chow et al., 2008; Park et al., 2014; Davis et al., 2016; Pang et al., 2022
	RabA2b	At1g07410	TGN/EE, PM, CP	Mediated PM trafficking to improve drought tolerance.	Chow et al., 2008; Ambastha et al., 2021
	RabA2c	At3g46830	TGN/EE, CP	Vesicle secretion and vesicle trafficking.	Chow et al., 2008
	RabA2d	At5g59150	TGN/EE, CP	Vesicle secretion and vesicle trafficking.	Chow et al., 2008
	RabA3	At1g01200	TGN/EE, CP	Vesicle secretion and vesicle trafficking.	Chow et al., 2008
	RabA5c	At2g43130	TGN/EE, CP	Involved in cytokinesis; regulates the specification of geometric edges in directional cell growth lateral roots; specifies a secretory pathway from the TGN/EE to the PM.	Rahni and Birnbaum, 2016; Kirchhelle et al., 2016; Kirchhelle et al., 2019; Elliott et al., 2020
RabE	RabE1c	At3g46060	Golgi, PM, CP	Post-Golgi trafficking to the PM; involved in the degradation of the peroxisomal protein receptor peroxin 7.	Speth et al., 2009; Ahn et al., 2013; Cui et al., 2013; Mayers et al., 2017
	RabE1d	At5g03520	Golgi, PM, CP	Response to pathogen; secretory pathways from the Golgi to the PM.	Zheng et al., 2005; Chow et al., 2008; Speth et al., 2009
RabF	RabF1/ ARA6	At3g54840	PM, MVEs, RE, CP	Trafficking pathway from endosomes to the PM; may be involved in recycling and degradation.	Dhonukshe et al., 2006; Bottanelli et al., 2011; Ebine et al., 2011; Ebine et al., 2012; Inada et al., 2017
	RabF2b/ ARA7	At4g19640	LE, PVC, TGN/EE, CP	Involved in cytokinesis; endocytosis; vesicle transport between the PVC and the vacuole.	Dhonukshe et al., 2006; Jia et al., 2013; Ito et al., 2016
RabH	RabH1b	At2g44610	Golgi, TGN/EE, CP	Influences cell elongation/growth and cellulose biosynthesis in hypocotyl growth; regulating the transport of cellulose synthase proteins between the Golgi apparatus and PM.	Chow et al., 2008; Johansen et al., 2009; He et al., 2018; Jia et al., 2018

E, endosome; TGN, trans-Golgi network; EE, early endosome; LE, late endosome; RE, recycling endosome; PVC, pre-vacuolar compartment; PM, plasma membrane; MVEs, multivesicular endosomes; and CP, cell plate.

subcellular behaviors, which implies that their localization and transport functions may involve different cellular components (Chow et al., 2008; Berson et al., 2014; Davis et al., 2016). In *Arabidopsis*, the small GTPases RabA2 (RabA2a, RabA2b, RabA2c, and RabA2d) and RabA3 are preferentially localized to the leading edge of the cell plate, implying that RabA2 and RabA3 play a role in the delivery and incorporation of novel substances into the assembled cell plate (Chow et al., 2008; Park et al., 2014; Mayers et al., 2017). Inducible expression of dominant inhibitory mutants of RabA2a (S26N), RabA2a (Q71L), and RabA2a (N125I) results in severely disrupted cell division patterns, binucleate and multinucleate cells, and significant inhibition of cytokinesis (Söllner et al., 2002; Chow et al., 2008). These results demonstrate that RabA2a is required for cytokinesis and transport to the cell plate *via* the Golgi and TGN, possibly by regulating secretion or endocytosis associated with cell plate development. RabA5c accumulates in unique vesicles and sometimes in the TGN, resides at the cell plate, and promotes cytokinesis (Kirchhelle et al., 2016; Kirchhelle et al., 2019; Elliott et al., 2020). Inducible expression of RabA5c (N25I) resulted in severe restriction of root growth, grossly abnormal cell geometries, and incomplete and misaligned cytokinesis in lateral roots (Kirchhelle et al., 2016).

In addition to RabA GTPases, there are five other subfamilies of Rab GTPases located in the cell plate of dividing cells, including two RabE GTPases (RabE1c and RabE1d), two RabF GTPases (RabF1 and RabF2b), and one RabH GTPase (RabH1b) (Table 1). Five members of the RabE subfamily (RabE1a to RabE1e) are believed to regulate post-Golgi trafficking to the PM, and live cell imaging shows that RabE1d and RabE1c localize to the Golgi apparatus, PM, and cell plate of dividing cells (Vernoud et al., 2003; Zheng et al., 2005; Chow et al., 2008; Speth et al., 2009). RabE1 interacts with the stomatal cytokinesis defect (SCD) complex, a multiprotein complex that in turn interacts with exocyst components to jointly promote secretion and endocytosis during cytokinesis; furthermore, overexpression of RabE1c rescues the growth and guard cell cytokinesis phenotypes of the temperature-sensitive mutant *scd1-1* (Mayers et al., 2017). In fixed *Arabidopsis* roots, RabF1 (Ara6) and RabF2b (Ara7) are localized to the cell plate and they are involved in the formation of cell plates during cytokinesis. *Arabidopsis* seedlings expressing dominant-negative RabF2b (Ara7 S24N) show stunted growth, root tip structure disorder, abnormal cytokinesis with multinucleated cells and incomplete cell walls (Dhonukshe et al., 2006). Interestingly, weak fluorescence is generally observed for YFP: RabH1b on the cell plate in addition to the Golgi localization signal, but the intensity of YFP: RabH1b signaling on the cell plate never exceeds the intensity in the same Golgi stack cells (Chow et al., 2008; He et al., 2018; Renna et al., 2018). These findings show that Rab GTPase plays an important role in vesicle trafficking during cell plate formation.

3 Tethering complexes involved in cell plate formation

Tethers refer to the initial contact between the donor and acceptor membranes, which is a highly selective transport process that facilitates vesicle docking and fusion. The initial connection between the carrier vesicle and its target membrane requires tethers, but not all putative tethers can bind the vesicle (Cai et al., 2007). Tethering factors fall into the following two main categories: long putative coiled-coil proteins and multisubunit tethering complexes (Cai et al., 2007; Koumandou et al., 2007; Ravikumar et al., 2017). Tethering complexes act by capturing vesicles and holding them in the vicinity of the target membrane, thereby they play an important role in cell plate assembly (Vukašinović and Žárský, 2016). Of these tethering factors, two important classes of tethering complexes, TRAPPII and exocysts, are required for plant cytokinesis (Rybak et al., 2014). In *Arabidopsis*, the TRAPPII complex consists of ten subunits, including the previously discovered TRAPPII subunits (Bet3, Bet5, Trs20, Trs23, Trs31, Trs33, Tca17, Trs120, and Trs130) and the recently reported plant-specific component TRAPP-interacting plant protein (TRIPP) (Zhang et al., 2018; Garcia et al., 2020). The *Arabidopsis* TRAPPII complex was discovered by screening cytokinesis-defective mutants and it is required for cell plate biogenesis (Jaber et al., 2010; Rybak et al., 2014). The exocyst is an evolutionarily conserved tethered complex consisting of eight subunits (Sec3, Sec5, Sec6, Sec8, Sec10, Sec15, Exo70, and Exo84). The exocyst and other regulatory proteins tether secretory vesicles to the cell membrane prior to membrane fusion, and the exocyst is necessary for the maturation of the cell plate during cytokinesis (He and Guo, 2009; Heider and Munson, 2012; Rybak et al., 2014). Two tethering complexes, TRAPPII and the exocyst, physically interact with each other and coordinate the spatiotemporal regulation of cell plate initiation (Rybak et al., 2014; Müller and Jürgens, 2016). During the initiation and maturation of the cell plate, TRAPPII colocalizes with exocysts and persists there during cell plate assembly. Switching between these tethering complexes is associated with changes in the membrane properties and mediates the biogenesis of the cell plate through distinct stages (Figure 1) (Rybak et al., 2014).

Four TRAPPII subunits (TRS120/VAN4, TRS130/CLUB, TPIPP and TRS33) are essential for cell plate formation (Table 2). TRS120 and TRS130 are localized in the TGN/EE and cell plate, and they are required for cell plate biogenesis (Ravikumar et al., 2017, 2018). Mutations in TRS120 or TRS130 result in a lethal and typical cytoplasmic defect in seedlings, including cell wall stubs, multinucleate cells, and incomplete connective walls. In addition, in both mutants, vesicles aggregate at the division plane but fail to assemble into the cell plate (Jaber et al., 2010; Thellmann et al., 2010; Qi et al., 2011; Ravikumar et al., 2017; Ravikumar et al., 2018). Interestingly, organization and trafficking of the endoplasmic reticulum (ER)-Golgi interface are normal in *trs120* and *trs130* mutants; however, trafficking from the post-Golgi to the cell plate and cell wall, but not to the vacuole, is impaired (Qi et al., 2011). Recently, TRIPP was found to be a plant-specific member of the highly conserved TRAPPII complex, which is localized to TGN/EE in interphase cells, and localized to the cell plate during both early and late cytokinesis; furthermore, the TRAPPII complex is involved in the formation of the cell plate in cytokinesis (Smertenko et al., 2017; Garcia et al., 2020). Loss-of-function *tripp* mutants exhibit infertility, dwarfism, and partial photomorphogenesis in the dark, and the *tripp* mutant has reduced polarity of the auxin transporter PIN2, incomplete transverse cell wall formation, and disordered localization of TRAPPII-specific component formation (Garcia et al., 2020; Hughes, 2020). In addition, TRS33 is required for the

TABLE 2 Characteristics of tethers located in cell plates.

Type	Gene	AGI Gene	Localization	Function	Reference
TRAPPII	TRS120/ VAN4	AT5g11040	TGN/EE, CP	Required for cell plate biogenesis during cytokinesis; polar localization of PIN2; mediated exocytosis at the TGN; regulated the post-Golgi trafficking.	Qi et al., 2011; Naramoto et al., 2014; Rybak et al., 2014; Ravikumar et al., 2018; Kalde et al., 2019
	TRS130/ CLUB	AT5g54440	TGN/EE, CP	Required for cell plate biogenesis during cytokinesis; regulating intracellular trafficking; polar localization of PIN2; regulates the post-Golgi trafficking.	Jaber et al., 2010; Qi et al., 2011; Rybak et al., 2014; Ravikumar et al., 2017; Kalde et al., 2019
	TRIPP	AT3g17900	TGN/EE, CP	Involved in cytokinesis; polar localization of PIN2; plant specific component of TRAPPII vesicle transport complex.	Garcia et al., 2020
	TRS33	AT3g05000	TGN/EE, Golgi	Involved in cytokinesis; auxin distribution; polar localization of both PIN1 and PIN2.	Kalde et al., 2019; Garcia et al., 2020; Zhang et al., 2020
Exocyst	SEC3A	AT1g47550	PM, CP, Cytoplasm	As a polarity determinant that links between polarized exocytosis and cell morphogenesis; tethers secretory vesicles to specific domains of the PM.	Zhang et al., 2013; Bloch et al., 2016; Li et al., 2017
	SEC6	AT1g71820	PM, CP, Cytoplasm	Involved in vesicle tethering during cell plate formation; regulate membrane fusion; help to tether the vesicles before fusion; polar auxin transport and PIN protein recycling.	Fendrych et al., 2010; Wu et al., 2013; Tan et al., 2016; Tan et al., 2022
	SEC8	AT3g10380	CP, PM, Cytoplasm	Involved in cytokinesis; involved in recycling of PIN1, PIN2 and the brassinosteroid receptor BRI1 to the PM; involved in the localized deposition of seed coat pectin.	Kulich et al., 2010; Drdová et al., 2013; Janková Drdová et al., 2019
	SEC10	AT5g12370	PM, CP, Cytoplasm	Involved in exocytotic vesicle fusion; PIN protein recycling and polar auxin transport.	Drdová et al., 2013; Zmienko et al., 2020
	SEC15B	At4g02350	PM, CP, Cytoplasm	Involved in cytokinesis; involved in tethering vesicles to the PM.	Rybak et al., 2014; Mayers et al., 2017
	EXO70 A1	AT5g03540	PM, CP, Cytoplasm	Involved in cytokinesis; auxin efflux carrier recycling and polar auxin transport; involved in cell and organ morphogenesis; required for exocyst recruitment to the PM; secretion; EXO70A1 is required for the location of CASP1 at the Casparian Strip Domain (CSD).	Synek et al., 2006; Fendrych et al., 2010; Drdová et al., 2013; Kalmbach et al., 2017; Larson et al., 2020; Synek et al., 2021; Hématy et al., 2022
	EXO84B	At5g49830	PM, CP	Required for Cell plate maturation and cell plate to PM fusion in the final stages of cytokinesis; affects CASP1 localization in CSD and secretion of many integral membrane proteins.	Fendrych et al., 2010 Kulich et al., 2010; Cole et al., 2014; Synek et al., 2021; Hématy et al., 2022

TGN, trans-Golgi network; EE, early endosome; PM, plasma membrane; and CP, cell plate.

membrane association of TRS120 and for its localization during cytokinesis (Garcia et al., 2020). The *trs33-1* mutant exhibited shorter roots, stunted growth, and sterility, due to impaired cytokinesis, similar to *trappii* mutants (Thellmann et al., 2010; Garcia et al., 2020). Furthermore, TRAPPII is functionally upstream of several RabA GTPases in *Arabidopsis*, indicating that it can also function as a Rab GEF (Qi et al., 2011; Kalde et al., 2019). These studies indicate that TRAPPII regulates vesicle trafficking and the assembly of cell plates, and it is essential for plant growth and development.

Seven exocyst subunits (SEC3A, SEC6, SEC8, SEC10, SEC15, EXO70A1, and EXO84B) are localized to the cell plate (Table 2). SEC3A is preferentially expressed in tissues containing dividing and expanding cells (Zhang et al., 2013; Bloch et al., 2016; Li et al., 2017). Moreover, SEC3A-GFP is temporarily located in the early cell plate, disappears during cell plate elongation and reappears in the division wall. In interphase cells, SEC3A-GFP is localized in the cytoplasm and PM, where it forms solid punctate structures (Zhang et al., 2013; Li et al., 2017). At the start of cytokinesis, SEC6-GFP, GFP-SEC8, GFP-SEC15b, and EXO70A1-GFP were tightly associated with the cell plate at the moment of its emergence and were localized to the cell plate as determined by fluorescence; then, during the formation of the cell plate, the signal diminished until it reappeared at the time of cell plate insertion (Fendrych et al., 2010; Rybak et al., 2014; Gu and Rasmussen, 2022). SEC6 localizes to the cell plate, cytoplasm, post-cytokinetic wall, and somewhat to PM as determined by labeling (Fendrych et al., 2010; Tan et al., 2022). Moreover, SEC6 interacts with the SM (Sec1p/Munc18) protein KEULE and may act as a novel molecular link between vesicles and the machinery for membrane fusion; alternatively, it may directly regulate membrane fusion during the formation of plant cell plates (Wu et al., 2013). In addition, pollen-rescued *sec6* mutants (*PRsec6*) form numerous binucleate cells and cell wall stubs in embryonic cells and abnormally dividing guard cells and cell wall stubs in leaf epidermal cells (Wu et al., 2013). Furthermore, the *sec6-1-/+* and *sec6-2-/+* mutants show approximately 15% of pollen grains broken in cytokinesis during pollen mitosis I (PMI) and impaired cell plate formation (Fendrych et al., 2010; Tan et al., 2022). SEC8 localizes to the nascent cell plate and later to the extension region of the cell plate, and it is involved in cytokinesis (Fendrych et al., 2010). *Sec8* mutants show severe dwarfism and male-specific transmission defects, and root cortical cells elongate at a slower rate in shorter elongation zones (Cole et al., 2005; Kulich et al., 2010; Cole et al., 2014). SEC10 is uniformly localized in the PM, cytoplasm, and cell plates; however, the T-DNA

insertion mutant of *sec10* shows no obvious phenotypic defects, possibly due to functional redundancy (Fendrych et al., 2010; Drdová et al., 2013; Vukašinović et al., 2014). RFP-SEC15B is primarily localized to the cell plate and punctate structures at or near the PM (Fendrych et al., 2010; Rybak et al., 2014; Mayers et al., 2017). EXO70A1 is involved in cell plate initiation, and the *exo70a1* mutant shows impaired initial cell plate morphology during cell plate assembly (Synek et al., 2006; Fendrych et al., 2010; Synek et al., 2021). EXO84B is required for the maturation of the cell plate, and changes in membrane properties drive the observed changes in polysaccharide composition, because tethering complexes bind distinct populations of vesicles with different cargos to the cell plate or cross wall (Fendrych et al., 2010; Cole et al., 2014). The *exo84b* mutant shows sterile dwarfs, slow growth, infrequent cell divisions, major defects with cell dynamics at the cellular level, leaf-like epidermis with cell wall stubs, highly asymmetric stomata, and incomplete division of stomatal guard cells (Fendrych et al., 2010; Hématy et al., 2022). These results show that the exocyst complex is mainly involved in the initiation and maturation of the cell plate and formation of the new primary cell wall during *Arabidopsis* cytokinesis.

4 SNAREs mediate membrane fusion during cell plate formation

SNAREs are responsible for mediating vesicle-to-target membrane fusion, and the *Arabidopsis* genome encodes at least 64 SNAREs (Sanderfoot, 2007; Luo et al., 2022). SNARE proteins are classified as Q-SNARE or R-SNARE according to the core SNARE complex residues (glutamine and arginine, respectively) that contribute to structural assembly. Q-SNAREs are further divided into Qa-, Qb-, Qc-, and Qbc-SNAREs (Fasshauer et al., 1998; Bock et al., 2001; Lipka et al., 2007; Luo et al., 2022). SNAREs are involved in a variety of biological processes such as auxin polar transport, vesicle trafficking, autophagy, gravitropism, and biotic and abiotic stress responses (Saito and Ueda, 2009; Larson et al., 2014; Won and Kim, 2020). In addition, SNARE protein-mediated membrane fusion promotes cell plate formation in dividing cells (Lukowitz et al., 1996; El Kasmi et al., 2013; Park et al., 2018). SNAREs are the core machinery mediating membrane fusion, and an important step in membrane fusion is the formation of *trans*-SNARE complexes, which connect cell membranes so that they can fuse together (Jahn and Scheller, 2006; Saito and Ueda, 2009). Each functional SNARE complex requires two or three Q-SNAREs and one R-SNARE to generate fusion complexes based on homology to synaptic SNAREs; furthermore, cell plate formation requires vesicle fusion mediated by SNAREs and their regulators (Südhof and Rothman, 2009; Luo et al., 2022). Initially, inactive cis-SNARE complexes assemble on the ER and traffic along the secretory pathway through the Golgi and TGN to the cell division plane (Karnahl et al., 2017). In the cell division plane, the *cis*-SNARE complex is broken by NSF ATPase, and Qa-SNARE KNOLLE interacts with the Sec1p/Munc18 (SM) protein KEULE to keep KNOLLE in an open conformation, thereby promoting the formation of *trans*-SNARE complexes on adjacent vesicles by KNOLLE and its SNARE partners (Waizenegger et al., 2000; Assaad et al., 2001; Südhof and Rothman, 2009; Carr and Rizo, 2010; Park et al., 2012). KEULE also interacts with the exocyst and it provides a direct link between tethering and the formation of *trans*-SNARE complexes (Wu et al., 2013). To date, four complete SNARE complexes have been found to mediate membrane fusion during *Arabidopsis* cytokinesis (Figure 2) (El Kasmi et al., 2013; Park et al., 2018).

Five Qa-SNAREs (KNOLLE, SYP132, SYP121, SYP122, and SYP31) are involved in vesicle fusion during cell plate formation (Table 3). The Qa-SNARE KNOLLE is a cytokinesis-specific Syntaxin that accumulates in the TGN during early mitosis, then localizes to the cell plate during cytokinesis, and degrades *via* multivesicular bodies (MVBs) after completion of the newly formed PM (Lauber et al., 1997; Stierhof and El Kasmi, 2010; Reichardt et al., 2011). KNOLLE is expressed in a cell cycle-dependent manner and it mediates cell plate formation through vesicle fusion in the cell division plane (Lukowitz et al., 1996; Lauber et al., 1997). Moreover, KNOLLE is required for both somatic cytokinesis and endosperm cellularization (Park et al., 2018). *Knolle* mutant embryos develop abnormally and exhibit severe cytokinesis defects, such as incomplete cell walls and two or more nuclei, leading to seedlings lacking functional meristems, forming plaques of necrotic tissue, and eventually dying (Lukowitz et al., 1996). Evolutionarily ancient and originating from the algal ancestor Qa-SNARE, SYP132 localizes to the PM and cell plate. Moreover, SYP132 is essential for secretion and it plays an important role in membrane fusion during cytokinesis. In addition, the *syp132* mutant can have cytokinesis defects, such as multinucleated cells, cell wall stubs, cell wall debris, and nonfused vesicle bands on the cell division plane (Park et al., 2018). The Qa-SNARE SYP121 is localized to the PM and TGN, accumulates strongly on the cell plate during cytokinesis, and constitutively cycles between the PM and endosomes; however, the accumulation of the Qa-SNARE SYP122 in cell plates is relatively weak compared with that of SYP121 (Reichardt et al., 2011; Karnik et al., 2015; Liu et al., 2022). The Qa-SNARE SYP31 localizes to cell plates in *Arabidopsis* suspension cells, indicating that it is involved in cell plate formation during somatic cytokinesis. Furthermore, AtCDC48 interacts specifically with SYP31 in an ATP-dependent manner, but not with KNOLLE, which may be necessary for the fusion of "other" secretory membranes in the cell division plane (Rancour et al., 2002). In addition, Qa-SNAREs SYP31 and SYP32 regulate membrane trafficking and Golgi morphology during pollen development, and *syp31/+ syp32/+* double mutants show developmental defects in pollen with abnormal cell plate formation during PMI (Rancour et al., 2002; Rui et al., 2021).

The other three SNAREs, Qb-SNARE (NPSN11), Qc-SNARE (SYP71), and Qbc-SNARE (SNAP33), are involved in vesicle fusion during cell plate formation (Table 3). NPSN11 is a novel plant-specific Qb-SNARE that is highly expressed in tissues with active cell division and localized to the cell plate during cytokinesis. SYP71 of Qc-SNARE located at the PM, endosome, endoplasmic reticulum, and cell plate (El Kasmi et al., 2013). SNAP33 of Qbc-SNARE is a widely expressed membrane-associated protein localized to the PM, endosome, and cell plates (Heese et al., 2001; El Kasmi et al., 2013). Furthermore, SNAP33 is involved in membrane fusion during cell plate formation and plays a role in cytokinesis. In addition, *snap33*

TABLE 3 Characteristics of SNAREs located in cell plates.

Type	Gene	AGI Gene	Localization	Function	Reference
Qa	KNOLLE /SYP111	AT1g08560	TGN/EE, MVB, CP	Membrane fusion during cell plate formation; secretory vesicles trafficking on PM.	Lauber et al., 1997; Völker et al., 2001; El Kasmi et al., 2013; Park et al., 2018
	SYP132	AT5g08080	PM, CP	Membrane fusion in cytokinesis; involved in secretory pathways; vesicular trafficking at the PM; promotes PM H^+-ATPase trafficking; response to bacterial pathogens.	Ichikawa et al., 2014; Park et al., 2018; Xia et al., 2019; Baena et al., 2022
	SYP121 /PEN1	AT3g11820	TGN/EE, PM, CP	As a negative regulator in innate immunity; affect K^+ channel and promote K^+ absorption; vesicular trafficking at the PM.	Honsbein et al., 2009 Reichardt et al., 2011; Liu et al., 2022; Cui et al., 2022; Rubiato et al., 2022
	SYP122	AT3g52400	PM, CP	Vesicular trafficking at the PM; involved in secretion; negative regulation of programmed cell death.	Zhang et al., 2007; Liu et al., 2022; Rubiato et al., 2022
	SYP31	At5g05760	Golgi, CP	Involved in cell division and secretion pathways; Regulation of Golgi morphology; involved in ER-Golgi trafficking.	Rancour et al., 2002; Bubeck et al., 2008; Rui et al., 2021
Qb	NPSN11	AT2g35190	CP, PM, E	Membrane fusion during cell division; involved in cell secretion.	Zheng et al., 2002; El Kasmi et al., 2013; Park et al., 2018
Qc	SYP71	At3g09740	CP, PM, E, ER	Membrane fusion during cell plate formation; involved in vesicular trafficking to ER.	Suwastika et al., 2008; El Kasmi et al., 2013; Park et al., 2018
Qbc	SNAP33	AT5g61210	Cytoplasm, E, PM, CP	Membrane fusion during cell plate formation; innate immune and abiotic stress responses; involved in the secretion process.	Heese et al., 2001; El Kasmi et al., 2013; Park et al., 2018; Won and Kim, 2020
R	VAMP721	AT1g04750	TGN/EE, E, PM, CP	Involved in cell plate formation; regulating auxin transport and auxin distribution; regulation of K^+ uptake; involved in exocytosis and response to ER stress; Regulates the cell secretory pathway.	Yun et al., 2013; Zhang et al., 2011; Zhang et al., 2020; Zhang et al., 2021; Kim et al., 2019; Larson et al., 2020
	VAMP722	AT2g33120	TGN/EE, E, PM, CP		
	SEC22	At1g11890	Nuclear envelope, ER, CP	Cytoskeleton organization and stability; works in the early secretory pathway; ER-Golgi trafficking.	Chatre et al., 2005; El-Kasmi et al., 2011; Guan et al., 2021

E, endosome; TGN, trans-Golgi network; EE, early endosome; ER, endoplasmic reticulum; MVBs, multivesicular bodies; PM, plasma membrane; and CP, cell plate.

mutant seedlings show minor cytokinesis defects, and only later cotyledon lesions lead to lethality (Heese et al., 2001). S*nap33 npsn11* double mutant embryos show severe defects in cytokinesis and impaired cell plate formation, and the *snap33 syp71* double mutant has severe cytokinesis-related phenotypes (El Kasmi et al., 2013).

Three R-SNAREs (VAMP721, VAMP722, and SEC22) are involved in vesicle fusion during cell plate formation (Table 3). VAMP721 and VAMP722 are localized to the PM, the TGN/EE, and preferentially to expanding cell plates during cytokinesis. Moreover, VAMP721 and VAMP722 mediate PM secretion and vesicle fusion on the cell plate (Zhang et al., 2011). Furthermore, the *vamp721 vamp722* mutant shows cell wall stub and delayed expansion of the cell plate, and the seedlings of the double mutant are underdeveloped and eventually show lethal dwarfing phenotypes (Zhang et al., 2011; Zhang et al., 2021). The third R-SNARE, SEC22 is visible at the plane of cell division during cytokinesis, where it colocalizes with KNOLLE and works in the early secretory pathway, which is essential for the integrity of the ER network and the Golgi complex (Chatre et al., 2005; El-Kasmi et al., 2011; Guan et al., 2021). In addition, *sec22-4* mutants have delayed germination, short primary roots, dwarfing and partial abortion, and changes in the shape of their trichomes, pavement cells, and stomatal morphology (El-Kasmi et al., 2011). Taken together, these results show that multiple types of SNAREs are required to mediate the fusion of vesicles during cell plate formation.

5 Perspective

Endomembrane trafficking undergoes various transitions during cell plate formation. During the early stages of cell plate formation, late secretory vesicles derived from the TGN migrate along the phragmoplast toward the cell equator. Dynamic reorganization of the cytoplasm drives lateral expansion of the cell plate, resulting in the shedding of vesicles at the edges of the growing cell plate. Then, the constant flow of vesicles toward the edge of the newly formed cell plate causes the cell plate to swell and eventually fuse with the original PM (Mayer and Jürgens, 2004). During cell plate formation, Rab GTPases, tethers, and SNAREs are localized to certain membranes and function in particular vesicle trafficking events; furthermore, they are crucial regulators of membrane targeting, identity, and fusion (Chow et al., 2008; Martinière and Moreau, 2020; Risselada and Mayer, 2020). Rab GTPases are master regulators of membrane trafficking, regulating the transport of vesicles during cell plate formation (Davis et al., 2016; Minamino and Ueda, 2019). The two tethering complexes (TRAPPII and exocyst) physically interact to coordinate the formation of cell plates during cytokinesis. The TRAPPII complex marks the cell plate throughout cytokinesis and is required for cell plate biogenesis; however, the exocyst is required for maturation of the cell plate (Rybak et al., 2014; Boruc and Van Damme, 2015). Tethering proteins provide specificity for targeting, and vesicle tethering initiates SNARE-dependent fusion of membrane vesicles to form cell plates (Yu and Hughson, 2010). Rab GTPases,

tethers, and SNAREs function synergistically to promote vesicle fusion, which increases the specificity and efficiency of membrane fusion (Ebine et al., 2008; Ohya et al., 2009; Boutté et al., 2010; Ebine et al., 2011).

Rab GTPases and SNARE complexes are functionally linked by tethering complexes, which mediate the tethering of these two membranes components prior to membrane fusion (Wickner and Schekman, 2008; Takemoto et al., 2018). RabF1 localizes to the PM, where it plays a regulatory role in the formation of a SNARE complex containing endosome associated VAMP727 and PM-localized SYP121 (Ebine et al., 2011). In addition, RabA, B, D, and E GTPases are identified in the TRAPPII interactome, and TRAPPII functions as the upstream of RabA2a, which is likely to behave as a GEF for the RabA2a GTPase (Kalde et al., 2019). Furthermore, tethers mediating the physical contact between vesicles and target membranes, together with Rab GTPases, play a key role in determining the specificity of vesicle targeting and fusion events (Cai et al., 2007). Therefore, Rab GTPases, tethers, and SNAREs may coordinate the regulation of the cell plate formation (Tables 1, 2, 3; Figure 3A). However, the spatialization of the three on the cell plate is not completely clear, future research should focus on determining their precise spatiotemporal location on the cell plate and the interaction network between them. Besides, cell plate formation stage IV peripheral microtubules come in contact with the cell cortex and then cell plate extends fusion tubes connecting to the cell plate fusion site at the PM, and fuses with the PM (Boruc and Van Damme, 2015; Smertenko et al., 2017; Rodriguez-Furlan et al., 2019). Thus, to reveal the fine coordination between Rab GTPases, tethers, and SNAREs, the mechanism required for fusion of the cell plate with the PM remains to be identified, and how proteins diffused from the cell plate are recovered or degraded at this stage remains to be studied (Figure 1).

The process of cell plate localization and formation is highly complicated, and some molecular mechanisms are well understood, but many questions remain to be answered. How are vesicles transported along the phragmoplast to the cell division plane for delicate tethering and fusion? Many Rab GTPases, tethers, and SNAREs members are located to the cell plate, and how do they each coordinate the regulation of cell plate formation? Is there a difference in the molecular composition and cargo of the vesicles that are involved in the assembly of cell plates? It is not clear whether vesicles carrying different cargoes destined for the cell plate are regulated by different Rab GTPases. The identification of more proteins and mechanisms involved in cell plate formation remains a goal. A better understanding of the molecular mechanism of cell plate formation will be gained over time with further research.

Author contributions

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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