The Plant Trans-Golgi Network: Not Just a Matter of Distinction[1][OPEN]

Michel Ruiz Rosquete,[2] Destiny Jade Davis, and Georgia Drakakaki[2]

Department of Plant Sciences, University of California, Davis, California 95616

ORCID IDs: 0000-0002-0373-9738 (M.R.R.); 0000-0001-6605-4755 (D.J.D.); 0000-0002-3949-8657 (G.D.).

Transport networks may be defined as sets of connected nodes or hubs where cargo from different origins are sorted to their final destinations. The trans-Golgi network (TGN) is the most discussed and arguably busiest hub operating in the cell. The versatility of the plant TGN distinguishes it from its mammalian counterpart. It is essential for the assembly of cell walls, including the cell plate, and organizes traffic of cargoes not only to but also from the plasma membrane, two pathways that animal cells separately confine to TGN and endosomes, respectively. We stand far from models that integrate the multiple trafficking functions of the plant TGN in physiologically different cellular contexts; however, with current and recent studies, we are gaining insights into the molecular determinants, trafficking routes, and functions of TGN subcompartments.

PLANT TGN BIOGENESIS

The trans-Golgi network (TGN) is defined as the membrane compartment on the trans-side of Golgi stacks responsible for the sorting and packaging of cargo molecules for delivery to the plasma membrane and vacuoles (Roth et al., 1985; Griffiths and Simons, 1986; Kang et al., 2011). In plants, the TGN not only provides a final sorting station for Golgi-derived cargoes but also is involved in trafficking/recycling of endosomal material; therefore, the term TGN/early endosome (TGN/EE) better suits its function (Fig. 1; Tanchak et al., 1988; Dettmer et al., 2006; Viotti et al., 2010). The identity of the plant TGN as a distinct organelle and not just a tubular reticulum on the trans-side of the Golgi has been supported by results from a number of experimental approaches in recent years. Cell fractionation and electron microscopy/tomography studies allowed Kang et al. (2011) to propose a model for TGN biogenesis in which the trans-most Golgi cisterna is first transformed into a TGN-type compartment that is still tightly associated with the trans-Golgi stack. Transformation of a trans-most Golgi cisterna into a TGN cisterna is accompanied by cisternae peeling, proliferation of round, secretory-type vesicle (SV) buds, and a reduction of the cisternal membrane area (Kang et al., 2011). These authors elegantly showed that there are two forms of TGN: (1) the Golgi-associated TGN (GA-TGN) cisternae attached to the trans-side of the Golgi; and (2) the detached, free TGN cisternae. The amounts of associated clathrin-coated vesicles (CCVs) and SV buds distinguished the two fractions. Both CCVs and SV buds were more abundant in the free TGN cisternae (Kang et al., 2011).

Superresolution live imaging of the TGN-localized soluble *N*-ethylmaleimide-sensitive factor attachment protein receptor (SNARE) protein SYP43 was used recently to characterize the dynamic behavior of the GA-TGN and Golgi-independent TGN (GI-TGN) populations (Uemura et al., 2014), corroborating the Golgi cisternal maturation model (Kang et al., 2011). The GA-TGNs localized on the trans-side of the Golgi apparatus, while the GI-TGNs (Golgi-released independent TGNs) were located away from the Golgi apparatus and behaved independently (Uemura et al., 2014). The authors proposed that segregation of GA-TGNs gives rise to the GI-TGNs with a core of the GA-TGN remaining after the process.

It is plausible that GA-TGN represents a population characterized by the TGN-localized COV1 and RAB GTPase-interacting YIP4A/B proteins, since both *yip4a/b*

ADVANCES

- During the past five years, several molecular players at the TGN have been uncovered, enabling the dissection of post-Golgi trafficking.
- Improved imaging and image analysis tools have enabled the separation of GA-TGN from GI-TGN and the dynamics of vesicle trafficking to the cell plate.
- Vesicle proteomics and lipid profiling have provided insights into the cargo, lipid composition, and identity of TGN populations.
- The development of pH sensors has provided insights into pH homeostasis within the secretory pathway.
- Chemical genomics has allowed the dissection of post Golgi pathways.

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[2] Address correspondence to mrrruizrosquete@ucdavis.edu and gdrakakaki@ucdavis.edu.

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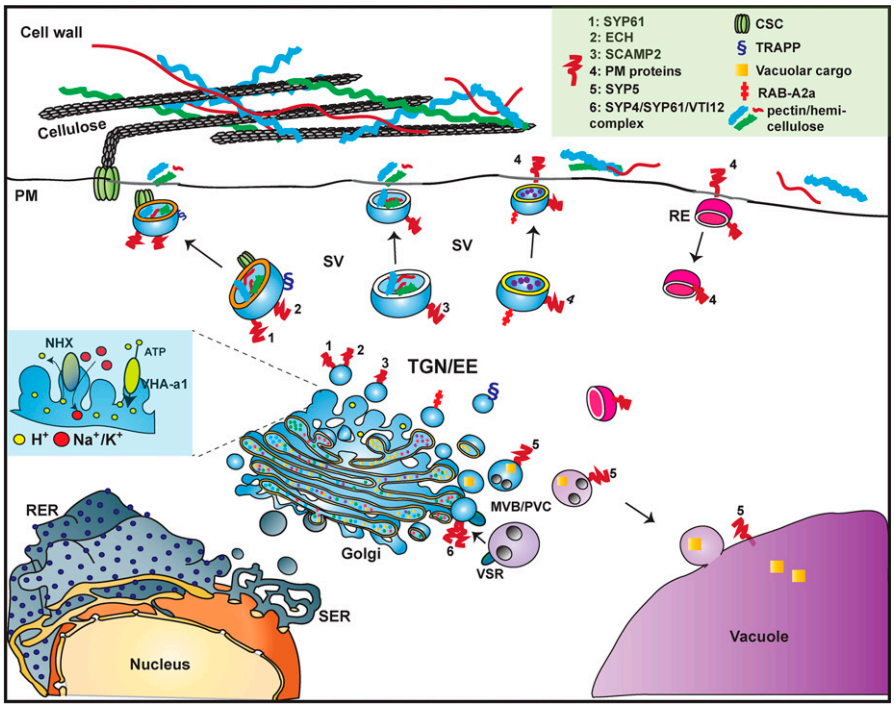

Figure 1. Simplified illustration of TGN/EE-mediated trafficking. The plant TGN comprises a very dynamic and heterogenous network of vesicles. An essential function of plant TGN is the secretion of cell wall polysaccharides and plasma membrane (PM)-associated CSC. TGN compartments defined by SYP61/ECH and SCAMP2 have been implicated in the secretory transport of CSCs, pectin, and hemicellulose (light blue vesicles). TGN also functions in the delivery of cargo to the vacuole via the multivesicular body/prevacuolar compartment (MVB/PVC; purple vesicles). Vacuolar sorting receptors (VSR) are used in this cartoon to depict the recycling of vacuolar cargo back to the TGN. In plants, TGN operates as an EE in the recycling of PM proteins (pink vesicles). Different classes of proteins regulate the trafficking functions of TGN/EE and define specific subcompartments. These include SNAREs, RAB GTPases, and tethering factors, of which examples are provided in the cartoon. The physical properties of TGN/EE are crucial for its functions. A role for vesicle lipid composition in defining TGN subcompartmentalization is emerging, here exemplified by the different lipid profiles of the SYP61 and RABA2a SVs (orange versus yellow bilayer). V-ATPase VHA-a1 and NHX antiporters are provided as examples of ion transporters involved in the critical regulation of TGN pH (see light blue-shaded inset on the left, representing a magnification of a TGN membrane fragment). The dotted interior of the Golgi represents cargo. RE, Recycling endosome; RER, rough endoplasmic reticulum; SER, smooth endoplasmic reticulum.

and *cov1* mutants affect the TGN association with Golgi (Gendre et al., 2013; Shirakawa et al., 2014). Further characterization of these proteins could reveal important, unknown elements regarding the functional connections between Golgi and GA-TGN, which appear bidirectional.

Brefeldin A (BFA) is a fungal inhibitor that causes aggregation of TGN, endosomal, and Golgi material in large intracellular bodies (Langhans et al., 2011). Regeneration of Golgi and TGN populations after the removal of BFA from treated cells proceeded independently in tobacco (*Nicotiana tabacum*) BY2 cells (Ito et al., 2017), supporting the notion that plant TGN is an independent organelle. How GI-TGN and GA-TGN functionally connect and how TGN functions feed back Golgi functions remain poorly understood. Notably, GI-TGNs were found highly abundant in the differentiation zone of the root, in contrast with the meristematic region (Uemura et al., 2014). Thus, it would be interesting to explore the likely reorganization of TGN during physiological responses, such as those evoking a more active secretory function.

PROTON PUMPS AND LEAKS: TGN PH IS ESSENTIAL

The regulation of pH homeostasis within the secretory pathway is crucial (for review, see Schumacher, 2014). An increase of only 0.2 pH units markedly impairs terminal α(2,3)-sialylation of an *N*-glycosylated reporter protein and induces mislocalization of the corresponding sialyltransferase into the endosomal compartments of mammalian cells (Rivinoja et al., 2009). Genetically encoded pH sensors targeted to specific endomembrane organelles have been engineered in an effort to establish a pH map of the plant endomembrane system. A gradual acidification from pH 7.1 in the endoplasmic reticulum (ER) to pH 5.2 in the vacuole was observed recently, with the pH of TGN at 6.3 (Shen et al., 2013). However,

lower TGN pH values of 5.6 and 6.1 have been reported by other groups (Martinière et al., 2013; Luo et al., 2015).

In eukaryotic cells, acidification of the various endomembrane compartments has been proposed to depend largely on the proton pump activity of highly conserved vacuole-type H^+-ATPases (V-ATPases; Hager and Helmle, 1981; Nishi and Forgac, 2002; Dettmer et al., 2006). V-ATPases are organized in two multisubunit domains. The peripheral V1 domain, responsible for ATP hydrolysis, is composed of eight different subunits (A–H), while the integral V0 domain forms the proton pore and includes a, c, c′, c′′, d, and e subunits (Nishi and Forgac, 2002; Toei et al., 2010). In plant cells, interfering with the TGN-resident VHA-a1 isoform causes the swelling of Golgi cisternae and inhibits cell expansion and hypocotyl growth (Dettmer et al., 2006; Brüx et al., 2008). Mutants with reduced activity of the cytosolic VHA-c subunit alter the steady-state pH in the TGN/EE, leading to reduced motility of both Golgi and TGN and defects in secretion of the brassinosteroid receptor BRI1 and Cellulose Synthase (Luo et al., 2015). Curiously, the TGN/EE-localized V-ATPase seems to contribute via an undefined mechanism to vacuolar pH (Kriegel et al., 2015). Such results suggest a rather complex interplay between different V-ATPase isoforms in the regulation of pH within each compartment of the plant endomembrane system.

Luminal pH initially determined by the activity of H^+ pumps is thought to be fine-tuned by alkalization mechanisms (Orlowski and Grinstein, 2011; Bassil and Blumwald, 2014). Exchange of luminal H^+ for Na^+ or K^+ by NHX antiporters counteracts the acidity generated by the H^+ pumps (proton leaks; Orlowski and Grinstein, 2011; Reguera et al., 2015). Two Arabidopsis (*Arabidopsis thaliana*) NHX isoforms (NHX5 and NHX6) are expressed at the TGN, where they colocalize with the H^+ pump VHA-a1 and likely counteract its activity (Bassil et al., 2011, 2012). *nhx5 nhx6* double mutants have a more acidic TGN lumen, altered trafficking to the vacuole, and are hypersensitive to salt (Bassil et al., 2012). The latter highlights the relevance of luminal pH in the orchestration of crucial adaptive responses. The transporter AtCLC-d is yet another player thought to adjust TGN's pH by mediating the transport of a counter anion such as Cl^- or NO_3^- into the TGN lumen. As NHX5/6, it colocalizes with VHA-a1 at the TGN, and the deleterious effect of inhibiting VHA-a1 was exaggerated in the *clcd-1* mutant, indicating synergistic activities between the two transporters (von der Fecht-Bartenbach et al., 2007).

LIPID COMPOSITION: AN INDEPENDENT SORTING MECHANISM?

A role for lipid rafts in the regulation of post-Golgi sorting events has received extensive attention. Lipid rafts are nanoassemblies of specific proteins and lipids that define highly dynamic membrane microdomains and influence the spatiotemporal organization of protein complexes, thereby allowing the regulation of cellular processes (Simons and Sampaio, 2011; Cacas et al., 2012; Malinsky et al., 2013). Rafts might sort proteins and lipids by clustering them together at the TGN into bigger patches, which would then pinch off as vesicles for delivery to the plasma membrane (Schuck and Simons, 2004). Using a shotgun lipidomics approach, Klemm and coworkers first demonstrated that yeast TGN selectively sorts ergosterol and sphingolipid-enriched SVs transporting plasma membrane cargo (Klemm et al., 2009; Surma et al., 2011). C-Laurdan spectrophotometry measurements revealed a higher membrane order in the immunoisolated vesicles, compared with TGN, supporting the hypothesis that lipid rafts play a role in the TGN sorting machinery (Klemm et al., 2009; Surma et al., 2011).

To our knowledge, lipid rafts have not been observed in the plant TGN, but evidence for lipid-based TGN sorting was obtained recently in Arabidopsis, where sphingolipids with α-hydroxylated acyl chains of at least 24 carbon atoms were enriched in SV subdomains of the TGN. Importantly, the authors established a novel link between α-hydroxylated acyl chain enrichment of TGN membranes and secretory trafficking, specifically in polarized transport to the apical membrane of epidermal cells (Wattelet-Boyer et al., 2016).

TGN-ASSOCIATED RABS, SNARES, TETHERS, AND ACCESSORY PROTEINS: ENSURING THE PRECISION OF DELIVERY

RAB GTPases

As a trafficking hub, one may conceive the TGN as organized into distinct domains, facilitating cargo sorting into specific vesicles to be dispatched to the next destination. In such a scenario, it is tempting to assume that different RAB GTPases (for review, see Zhen and Stenmark, 2015), a major class of cellular proteins determining membrane identity and trafficking specificity, define separate TGN sorting compartments (Grosshans et al., 2006; Woollard and Moore, 2008; Hutagalung and Novick, 2011; Bhuin and Roy, 2014). Several lines of evidence support such RAB-determined subcompartmentalization. Two subclasses within the large A group of plant RABs, RABA2 and RABA3, identify a distinct TGN/EE membrane domain that functions in cargo delivery to the cell plate during cytokinesis (Chow et al., 2008). Whereas RABA2a defines TGN domains distinct from SYP61 vesicles, evidenced by differing lipid composition, RABA4b preferentially localizes to TGN SV sites together with SYP61, where it is involved in the transport of cell wall components (Preuss et al., 2004; Kang et al., 2011; Wattelet-Boyer et al., 2016; Jonsson et al., 2017). Another TGN domain harboring the secretory SNAREs VAMP721/722 and defined by RABA1 also has been suggested (Asaoka et al., 2013).

As to members of the plant RABB and RABD clades, they have been postulated to operate in traffic between the ER and Golgi (Cheung et al., 2002; Rutherford and Moore, 2002; Zheng et al., 2005; Woollard and Moore,

2008). However, fluorescently tagged RABD1 and RABD2a localized to punctate structures associated with TGN, and both RABD2a and RABD2b were found abundantly in isolated SYP61 vesicles that define a pathway en route from TGN to the plasma membrane (Pinheiro et al., 2009; Drakakaki et al., 2012).

SNAREs

SNAREs are integral membrane proteins required for the fusion of vesicles with their target membrane (for review, see Bombardier and Munson, 2015). SNAREs can be classified based on their site of function: v (vesicle)-SNAREs are localized to the vesicle membrane, and t (target)-SNAREs are localized to the target membrane (Rothman, 1994; Søgaard et al., 1994). Syntaxins are a family of SNAREs involved in recognizing and complexing with other SNAREs on the target membrane to create a t-SNARE complex. The genome of Arabidopsis encodes 24 syntaxins or Syntaxin of Plants (SYPs; Sanderfoot et al., 2000; Bassham and Blatt, 2008).

Distinct types of Arabidopsis syntaxins reside on the various membranes of the secretory pathway. The SYP4-type syntaxins (SYP41–SYP43) and their orthologs from yeast (Tlg2p) and mammals (Syntaxin16) have all been localized to TGN (Holthuis et al., 1998; Simonsen et al., 1998; Bassham et al., 2000). SYP4 members are implicated in the transport of secretory and vacuolar cargo from the TGN. Whether SYP4s function redundantly and localize to the same TGN compartment is to be determined (Bassham et al., 2000; Uemura et al., 2012; Kim and Bassham, 2013). TNO1 (TGN-localized SYP41-interacting protein1) is a TGN-localized coiled-coil protein that interacts with the SYP41 SNARE machinery. TNO1 mutants affect TGN dynamics, vacuolar cargo sorting, and the response to salt stress (Kim and Bassham, 2011).

The Arabidopsis SYP5 family of SNAREs consists of two members, SYP51 and SYP52, which localize to tonoplast and TGN (Sanderfoot et al., 2001; Carter et al., 2004; De Benedictis et al., 2013). Both SYP5s mediate traffic to the vacuole, although they seem to differ in cargo selectivity. Intriguingly, SYP5s appear to inhibit homotypic fusion (SNARE interfering or i-SNARE) when accumulated at the tonoplast. Such an i-SNARE function could provide a control for cargo delivery to the vacuole (De Benedictis et al., 2013).

The SYP6 group is encoded by a single gene, SYP61 (Sanderfoot et al., 2000). SYP61 is proposed to form separate complexes with the SNARE VTI12 and either SYP41 or SYP42 at the TGN (Sanderfoot et al., 2001); however, some lines of evidence suggest that other members of the SYP and VTI families also could take part in these complexes. In the absence of VTI12, prevacuolar compartment-localized VTI11 is able to interact with SYP4s, and proteoliposome fusion assays demonstrated that SYP42 and SYP43 can substitute for SYP41 while VTI11 can substitute for VTI12 in driving lipid mixing (Surpin et al., 2003; Kim and Bassham, 2013). Finally, the ability of SYP41 and SYP61 to independently mediate the fusion of liposomes was shown by Chen et al. (2005), who also identified YKT61 and YKT62, two functionally interchangeable components of the SNARE complexes, required for both SYP41- and SYP61-mediated vesicle fusion

A role for the SYP4/SYP61/VTI12 complex in the recycling of vacuolar sorting receptors to the TGN has been suggested. Vacuolar Protein Sorting45, an interactor of the complex, was proposed to positively regulate this function (Zouhar et al., 2009). The role of the SYP61 compartment in post-Golgi trafficking is discussed later in this review.

Tethers

Tethering factors are traffic facilitators that function upstream of SNARE proteins in the establishment of an initial connection between an intracellular trafficking vesicle and its target membrane (Barlowe, 1997; Cao et al., 1998; for review, see Dubuke and Munson, 2016). Mechanistically, they have been suggested to mediate vesicle capturing, in virtue of their larger size compared with SNAREs, to accelerate the assembly of SNARE complexes and to provide checkpoints for SNARE specificity (Yu and Hughson, 2010). Plant tethers (for review, see Vukašinović and Žárský, 2016; Ravikumar et al., 2017) relevant to TGN-mediated trafficking include several members of the TRAPP family and the Golgi-associated retrograde protein (GARP) complex. TRAPPs assemble into fairly well-characterized multisubunit complexes in yeasts and mammals (Sacher et al., 2008; Kim et al., 2016). Our current knowledge of the function and organization of plant TRAPP homologs is extremely limited, although some lines of evidence have started to emerge with TGN-associated TRAPP involved in cytokinesis (Ravikumar et al., 2017). Several members of putative Arabidopsis TRAPP complexes were found in the proteome of TGN-associated SYP61 vesicles, suggesting a role for yet uncharacterized plant TRAPPs in the transport and/or delivery of secretory cargo to the plasma membrane (Drakakaki et al., 2012). The role of TGN-associated TRAPPs in cell plate formation and plant development (for review, see Vukašinović and Žárský, 2016; Ravikumar et al., 2017) is discussed at length in the cell plate section below.

In mammals, TGN-localized tetrameric GARP is required for retrograde trafficking from endosomes to the Golgi (Schmitt-John et al., 2005; Pérez-Victoria and Bonifacino, 2009). Mutants of Arabidopsis GARP subunits have implicated the complex in pollen tube elongation, acclimation to heat stress, and vacuolar targeting of the auxin carrier PIN1, necessary for PIN1 polar localization during the establishment of leaf vein patterning (Lobstein et al., 2004; Wang et al., 2011; Pahari et al., 2014). Interestingly, GARP shares three subunits with the Endosome-Associated Recycling Protein (EARP), which resides on recycling endosomes and is required for bringing recycling proteins/cargo to the cell surface (Schindler et al., 2015; Ravikumar et al., 2017). This

phenomenon, also characteristic in TRAPP complexes, has been referred to as modularity. Multisubunit tethering complexes can exist in a variety of modular forms as a result of subunit exchange (Desfougères et al., 2015; Ravikumar et al., 2017). The existence of an Arabidopsis homolog also for the EARP-specific subunit, syndetin, hints at GARP modularity conservation in plants.

Adaptins

While the role of CCVs in plant endocytosis is well documented (Bandmann et al., 2012; Bashline et al., 2013; Di Rubbo et al., 2013), their involvement in post-Golgi trafficking remains poorly understood. Adaptor protein complexes (AP1–AP5) consisting of four adaptin subunits select cargo proteins into CCVs (Boehm and Bonifacino, 2001; Nakatsu and Ohno, 2003; Pertl-Obermeyer et al., 2016). The Arabidopsis genome encodes putative subunits of all five AP complexes (Happel et al., 2004; Hirst et al., 2011; Park et al., 2013). Arabidopsis AP1 localizes to the TGN (Park et al., 2013; Wang et al., 2014), and mutants of the AP1M2 subunit are affected in the secretory and vacuolar transport pathways. In addition, trafficking of the essential SNARE KNOLLE from the TGN to the cell plate is impaired in dividing cells of *ap1m2* mutants (Park et al., 2013). More recently, TGN-localized AP1 γ-adaptins were found to mediate the targeting of membrane proteins with di-Leu motifs to the tonoplast (Wang et al., 2014). Intriguingly, Arabidopsis AP3 has been implicated in a TGN-bypass pathway that transfers cargo directly from Golgi cisternae to the vacuole and is facilitated by the HOPS-tethering complex (Feraru et al., 2010; Zwiewka et al., 2011; Feng et al., 2017). Perhaps with the exception of AP2, which operates in clathrin-mediated endocytosis at the plasma membrane (Krauss et al., 2006; Di Rubbo et al., 2013), a function in vacuolar transport appears to be the norm among Arabidopsis AP complexes. AP4 was recently found to localize to a TGN subdomain different from that of AP1 and for which mutants of four AP4 adaptins showed defects in the vacuolar sorting of the major storage protein 12S globulin (Fuji et al., 2016).

TGN AND THE CELL WALL: A PLANT-SPECIFIC CONNECTION

The Golgi apparatus and the TGN fulfill a highly dynamic and distinguishing function in plant cells: to sort and assemble plasma membrane cell wall biosynthetic enzymes, structural proteins, and the cross-linking glycans, pectin, and hemicellulose (Cosgrove, 2005; for review, see Worden et al., 2012; Kim and Brandizzi, 2016; van de Meene et al., 2017). Although extensive studies have led to the identification of the key enzymes involved in the biosynthesis of hemicellulose and pectin (for review, see Atmodjo et al., 2013; Pauly and Keegstra, 2016), comparatively little is known about their transport, deposition, and integration into the cell wall. Polysaccharides originate from distinct locations. Cellulose and callose are synthesized at the plasma membrane, while the Golgi apparatus is the synthesis site of noncellulosic cell wall polysaccharides, hemicellulose, and pectin, which are then transported through the secretory pathway to the apoplast (Driouich et al., 2012; Worden et al., 2012; Kim and Brandizzi, 2016). Our current knowledge of polysaccharide transport in the endomembrane system is derived mainly from immunohistochemical electron microscopy studies (Lynch and Staehelin, 1992; Zhang and Staehelin, 1992).

Golgi and TGN Involvement in the Biosynthesis of Xyloglucans and Pectins

The use of antibodies that recognize a number of xyloglucan (XyG) polymer epitopes identified trans-Golgi cisternae as the exclusive site of synthesis of the XyG backbone in a study conducted in suspension-cultured sycamore (*Acer pseudoplatanus*) cells. Fucosylated XyG side chains were detected in the trans-cisternae and the TGN, forming the hypothesis of an ordered mechanism of backbone biosynthesis and subsequent substitution in Golgi subcompartments (Zhang and Staehelin, 1992). The TGN involvement in XyG biosynthesis was highlighted further in studies with Arabidopsis roots, which showed labeling of TGN by a fucosylated XyG antibody (Kang et al., 2011). Earlier observations in tobacco BY-2 cells reported a sequence of events during XyG biosynthesis in cis- and medial Golgi cisternae (Chevalier et al., 2010), suggesting differences between species.

The Golgi apparatus also is the site of pectin biosynthesis. Pectins are synthesized and secreted in their methyl esterified form into the cell wall, where they are deesterified by pectin methyl esterases (Caffall and Mohnen, 2009). Studies in sycamore suspension cells showed that the synthesis of the nonesterified Rhamnogalacturonan I (RGI)/Homogalacturonan backbone and the methylesterification of GalUA residues take place in the cis-medial Golgi with subsequent completion in the medial cisternae. More complex pectin oligosaccharides, such as RGI-containing arabinose side chains, are detected only in the TGN (Zhang and Staehelin, 1992). However, the labeling of pectin epitopes differs among cell types of the root tip, suggesting that Golgi function may be altered/reorganized during cell differentiation (Lynch and Staehelin, 1992).

Several enzymes involved in both pectin and XyG biosynthesis have been identified and characterized. Contrasting the pectin biosynthesis assembly line hypothesis is the observation that several glycosyl transferases involved in the biosynthesis of pectin are present in multiprotein complexes at the Golgi. Currently, two pectin biosynthesis models have been proposed: the classical model, which predicts the consecutive addition of sugar residues to the growing polysaccharide; and a recently developed model, in which a block transfer of pectin from one domain onto another domain occurs (Atmodjo et al., 2013). The isolation of TGN SVs that carry polysaccharide cargo will contribute substantially to a more comprehensive understanding of the transport and assembly of cell wall components.

Cellular Determinants of Cell Wall Component Transport

Post-Golgi routes deployed by the plant cell to transport Golgi/TGN-synthesized polysaccharides to the plasma membrane are not fully elucidated. A TGN-resident complex formed by ECHIDNA (ECH) and two members of the YIP family of RAB GTPase-interacting proteins has been implicated in the secretion of pectin and XyG. Mutant plants of YIP4A and YIP4B are defective in cell elongation and the secretion of XyG and RGI pectins, a defect also observed in *ech* mutants (Gendre et al., 2011, 2013). ECH also seems to be necessary for the proper TGN localization of the ADP-Ribosylation Factor1 (ARF1)-GTPase and the ARF-guanine-exchange factor BIG4. This pathway mediates secretion of the auxin carrier AUX1 from the TGN to the plasma membrane (PM) during hook development (Jonsson et al., 2017). In tobacco BY-2 cells, immunostaining of pectin showed that the Secretory Carrier Membrane Protein2 (SCAMP2) vesicles are involved in pectin transport (Toyooka et al., 2009). A potential interplay between the SCAMP2 and ECH machineries in pectin secretion has not been explored yet.

A pioneering study of plant intracellular vesicle isolation and proteomic analysis revealed that the syntaxin SYP61 defines a TGN compartment carrying cell wall-relevant cargo. Several CSCs were identified in the SYP61 proteome, and electron microscopy immunostaining evidenced the colocalization of CESA6 and SYP61 in TGN vesicles and in close proximity to the PM (Drakakaki et al., 2012). The exogenous administration of CESTRIN, a small molecule that reduces the motility of CSCs at the plasma membrane, increases the association of CESAs with SYP61 vesicles, further implicating the SYP61 compartment in CESA trafficking (Worden et al., 2015). Both ECH and YIP proteins are cargo of SYP61 vesicles, favoring the hypothesis that SYP61-mediated trafficking is involved in the transport of cell wall components. Furthermore, antibodies for fucosylated XyG label a RABA4b TGN compartment, and colocalization of RABA4b and SYP61 was observed, supporting the role of SYP61 in the trafficking of cell wall components (Kang et al., 2011).

Despite the essential roles of glycoproteins in cell wall remodeling, development, and responses to biotic stress, their secretory routes remain poorly characterized. In addition to conventional secretion via TGN, exemplified by SYP61 and SCAMP2 vesicles, evidence pointing to the existence of TGN-independent, unconventional protein secretion pathways is accumulating, which may be implicated in cell wall protein transport (for review, see De Marchis et al., 2013; Davis et al., 2016a; Robinson et al., 2016; van de Meene et al., 2017).

TGN AND THE CELL PLATE: A TIMELY CONNECTION

The TGN's key role in organizing and shipping cell wall material is never more obvious than during cytokinesis, in which an entirely new cell wall is built from inside the parent cell. Cytokinesis begins with the delivery of Golgi/TGN-derived vesicles to the plane of division, where they immediately start to fuse and tubulate. The vesicles continue to coalesce into a membrane network (the cell plate) following the tracks laid down by the radially expanding phragmoplast (Samuels et al., 1995; Seguí-Simarro et al., 2004; Smertenko et al., 2017). Deposition of polysaccharides leads to the maturation of the formed structure, which finally joins to the parental cell wall (Drakakaki, 2015).

Chemical inhibition of either endocytosis or secretion in dividing plant cells indicates that both pathways have a role during cell plate formation via the TGN. It is plausible that endocytosed proteins merge into the late secretory pathway and, thus, are delivered to the division plane instead of being recycled to the PM (Dhonukshe et al., 2006; Reichardt et al., 2007; Richter et al., 2014; Müller and Jürgens, 2016).

The TGN is intimately connected to the cell plate, as evidenced by the various proteins shared and shuttled between them, of which a few key components are mentioned below (Fig. 2). Excellent reviews describe in detail the cytoskeletal and membrane dynamics during cytokinesis (McMichael and Bednarek, 2013; Boruc and Van Damme, 2015; Müller and Jürgens, 2016).

A key event in cell plate formation is vesicle fusion mediated by SNARE complexes (El Kasmi et al., 2013), with the complex formed by the Q-SNARE KNOLLE and the R-SNAREs Vesicle-Associated Membrane Protein721 (VAMP721) or VAMP722 playing a preponderant role (Lauber et al., 1997; Zhang et al., 2011). Additional proteins in this complex include the SEC1/Munc18 protein KEULLE, SNAP33, and NPSN11 (Assaad et al., 2001; Heese et al., 2001; Zheng et al., 2002). Interestingly, of the SNAREs involved in cell plate formation, only KNOLLE is specific to the process.

RABA2 and RABA3 preferentially localize to the leading edge of the cell plate, suggesting a function in the delivery and incorporation of new membrane material to the cell plate (Chow et al., 2008). Because overlapping localizations and complementary functions are common among RABAs, a complete roadmap for the multiple pathways and processes in which each is involved is still being drawn. RABA2a and RABA1e vesicles display a different spatiotemporal pattern during cytokinesis, which is exaggerated by the cytokinesis inhibitor Endosidin7 (ES7; Davis et al., 2016b). TGN/EE-resident RABA1d accumulates at early cell plate stages during cytokinesis, and its association with PM proteins suggests a role in the recycling of material from the PM to the growing plate (Berson et al., 2014). Given the fact that the RABA clade is highly elaborated in plants (26 of the 57 total RAB GTPases identified thus far; Woollard and Moore, 2008), it will be interesting to see how/if they are functionally connected to meet the myriad trafficking demands in a plant cell, dividing or otherwise. In addition to RABAs, RABE1s also localize to the cell plate, where they interact with the Stomatal Cytokinesis-Defective (SCD) complex. Inhibition of RABE1 causes cytokinesis defects, emphasizing its role in trafficking to the cell plate (Speth et al., 2009; Ahn et al., 2013; Mayers et al., 2017).

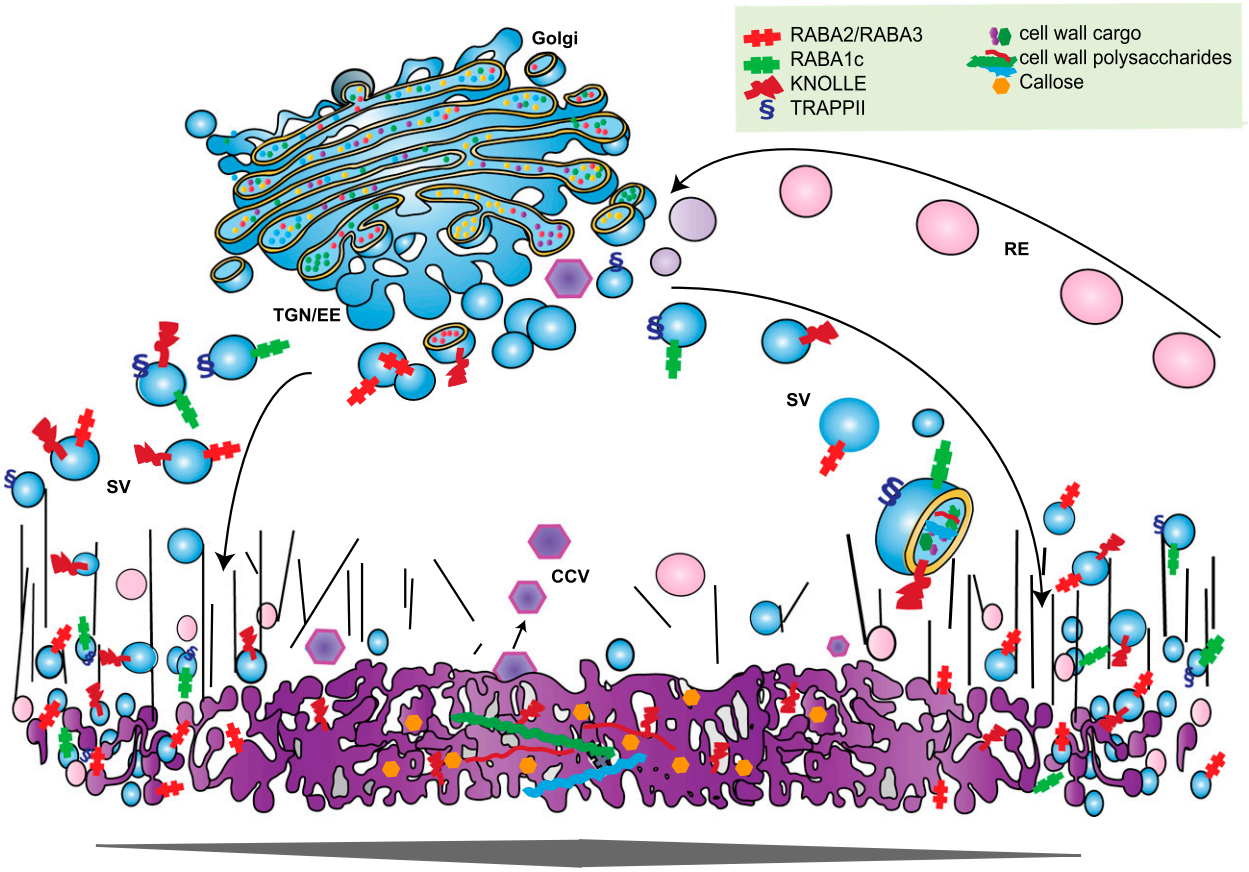

Figure 2. Illustration of TGN-cell plate trafficking. The TGN acts as a sorting hub for cell plate formation during cytokinesis. Representative components of the trafficking routes between the TGN and the cell plate are depicted. During early stages of cell plate formation, TGN compartments labeled by the GTPases RABA2/RABA3 and RABA1c relocate to the cell plate margins, where they are involved in vesicle targeting and the delivery of membrane to the expanding plate. The TRAPPII tethering complex is involved in cell plate biogenesis and expansion. The cytokinesis-specific SNARE protein, KNOLLE, which is found throughout the entire cell plate, mediates vesicle fusion. Cell plate maturation occurs radially from the interior directed outward toward the parental cell wall and involves the deposition of cell wall polysaccharides and the removal of excess membrane through clathrin-mediated recycling (purple hexagons). RE, Recycling endosome.

TRAPP tethering complexes are known to act as guanine exchange factors (GEFs) and, thus, activate RAB GTPases (Jones et al., 2000; Wang et al., 2000; Pinar et al., 2015). Colocalization at the TGN and functional studies suggest that TRAPPII acts as a GEF for RABA1c, facilitating RABA1c-mediated trafficking of material from the TGN to the cell plate (Qi et al., 2011). Mutants of the TRAPPII subunit, AtTRS130, exhibit severe cytokinesis defects and irregular aggregations of RABA1c around cell plate-like structures (Jaber et al., 2010; Qi et al., 2011). The expression of constitutively active RABA1c partially rescues *attrs130* (Qi et al., 2011), supporting the role of AtTRS130 upstream of RABA1c. During cytokinesis, subunits of the exocyst-tethering complex interact with TRAPP subunits, suggesting synergistic activities of the two complexes (Rybak et al., 2014; for review, see Vukašinović and Žárský, 2016).

In addition to RAB GTPases and their regulators, other protein classes with vesicle formation/budding functions at the TGN participate in cell plate formation. For example, Clathrin Light Chain, Dynamin-Related Proteins, Epsin-like adaptors, and the adaptin-like T-PLATE all have been identified at the cell plate, providing evidence for clathrin-mediated endocytosis in the removal and/or recycling of excess membranes from the cell plate (Fujimoto et al., 2008; Konopka and Bednarek, 2008; Van Damme et al., 2011; Song et al., 2012; McMichael and Bednarek, 2013). Additionally, SCD1 and SCD2 act as a complex to mediate post-Golgi trafficking to the plasma membrane and the cell plate. Multiple lines of evidence point to the interaction between the SCD complex, the exocyst, and RABE1 GTPases in the trafficking of material to the cell plate (Mayers et al., 2017).

The aforementioned AP1, and specifically the μ-subunit (AP1M2), is found in the TGN and is essential for the trafficking of KNOLLE to the cell plate. In an *ap1m2* mutant background, KNOLLE is mislocalized around

the division plane and cell wall stubs are present, indicating a role of AP1M2 in targeting KNOLLE to the cell plate (Park et al., 2013; Teh et al., 2013).

Exciting discoveries in the nature and composition of cytokinesis vesicles are awaiting, which will form a better picture of membrane and polysaccharide delivery for the buildup of such an essential and dynamic structure.

OUTSTANDING QUESTIONS

- What determines the different subpopulations of TGN?
- How many different TGN subpopulations participate in TGN to PM trafficking and what is their specific cargo? Do environmental cues (e.g. stresses) re-program their cargo composition and trafficking rates?
- How are GA-TGN and GI-TGN functionally connected? Which functions are specific to each compartment?
- Which are the distinct molecular features of TGN subpopulations that traffic material to the cell plate? What is the polysaccharide cargo of TGN?

TGN AS AN EE: TWO DIRECTIONS BUT HOW MANY LANES?

The plant TGN is unique in that it acts not only in the secretory but also in the endocytic pathway as an EE (Tanchak et al., 1988; Dettmer et al., 2006; Viotti et al., 2010). This distinct, additional function of plant TGN has been associated with the absence of the tubulated endosomes dedicated to recycling, normally found in animal cells (Paez Valencia et al., 2016). The function of TGN as an EE has been demonstrated by live imaging and electron microscopy studies (Dettmer et al., 2006; Lam et al., 2007; Viotti et al., 2010). Immunogold electron microscopy showed an accumulation of the PM-localized brassinosteroid receptor BRI1 to BFA bodies, not prevented by the protein synthesis inhibitor cycloheximide, lending evidence to the exclusively endocytic origin of the material accumulated in the BFA compartment (Viotti et al., 2010).

Recycling of PM proteins through the TGN/EE has proven crucial for the polar distribution of plasma membrane proteins, including auxin carriers like PIN1 (Geldner et al., 2003; Kleine-Vehn et al., 2008, 2011; Luschnig and Vert, 2014). Endosomal recycling in plants largely depends on the activity of small GTPases of the ARF family and their associated GTPase-activating proteins and GEFs (Casanova, 2007; Kleine-Vehn et al., 2008; Paez Valencia et al., 2016). Twelve ARF genes are present in the genome of Arabidopsis (Robinson et al., 2007). The best-characterized ARF1 localizes to endocytic organelles and is implicated in the establishment of apical-basal polarity in epidermal cells (Xu and Scheres, 2005).

Among Arabidopsis ARF-GEFs, GNOM has been arguably the most studied in its function of restricting PM protein localization to basal domains (Geldner et al., 2003). BFA treatments inhibit GNOM, causing the accumulation of the internalized auxin effluxer PIN1 in aggregating GNOM-positive intracellular compartments (Geldner et al., 2003). However, superresolution/electron microscopy studies showed its exclusive localization to Golgi cisternae, thereby challenging its function solely in protein recycling (Naramoto et al., 2014). In support, GNOM was recently implicated in the ER-to-Golgi transport of PIN1 (Doyle et al., 2015). BEN1 is another, BFA-insensitive ARF-GEF that localizes to early endocytic compartments distinct from GNOM-positive endosomes and whose mutants display cell polarity defects (Tanaka et al., 2009). Finally, a role for the BIG subfamily in nonbasal trafficking of plasma membrane proteins was recently supported by pharmacological evidence (Li et al., 2017). Such functions place BIGs distinct from GNOM in the scheme of factors regulating the polarity of PM proteins. Interestingly, and in contrast with GNOM, BIGs do not seem to affect recycling but only protein secretion (Richter et al., 2014). Such functional divergence could lie at the core of the observed stage-dependent, mutually exclusive involvement of GNOM and BIGs in the regulation of the secretion of AUX1 influx carrier to the plasma membrane from the TGN during hook development (Jonsson et al., 2017).

Several lines of evidence support a model for the maturation of TGN/EE into late endosomes or multivesicular bodies (LE/MVB; Scheuring et al., 2011; Singh et al., 2014). Endocytosed plasma membrane proteins that are not recycled back are transferred from EE (TGN) to LE/MVB, where they are internalized into the intraluminal vesicles of the LE. Fusion of the LE with the lysosome/vacuole releases the vesicle cargoes, leading to their degradation. Scheuring et al. (2011) showed that the formation of intraluminal vesicles takes place already at the TGN/EE, while Singh et al. (2014) suggested that endosomal maturation in Arabidopsis originates in a subdomain of the TGN/EE that recruits Rab5-like ARA7 and subsequently transitions into an MVB. The topics of plant EE and LE are covered extensively by other reviews in this issue of *Plant Physiology*.

EXPERIMENTAL TOOLS

The plant TGN comprises an extremely dynamic and diverse vesicle population, which raises many questions for most of which we do not have an answer; meanwhile, technological advances are helping us on the road. Improved protocols for the immunoisolation of vesicles based on specific, vesicle membrane markers have been successfully established, an example of which is the characterization of the SYP61 compartment (Drakakaki et al., 2012; Groen et al., 2014; Heard et al., 2015). Organelle proteomics is allowing the identification of vesicle protein cargoes, and extending glycomic analysis to isolated vesicles will help us to better characterize the secretory routes of cell wall polysaccharides (Obel et al., 2009; Pattathil et al., 2010; Drakakaki et al., 2012; Parsons et al., 2013; Heard et al., 2015; Kračun et al., 2017; Wood et al., 2017). Chemical genomics is enabling the characterization of vesicle-trafficking pathways, recently evidenced by the use of the small molecules ES7 and ES16 to discern the contributions of two RAB GTPases to cell plate formation and to

demonstrate the specificity of a trafficking pathway involved in cell polarity, respectively (Davis et al., 2016b; Li et al., 2017). Spatiotemporal image correlation spectroscopy has proven useful to characterize the dynamics of vesicle trafficking to the cell plate (Hebert et al., 2005; van Oostende-Triplet et al., 2017). Finally, lipid profiling, metabolic click labeling, and the use of oligosaccharide-based probes for high-resolution real-time imaging of glycans have recently added to the list of promising avenues to dissect the role of TGN in cargo transport (Anderson et al., 2012; Pattathil et al., 2012; Mravec et al., 2014; Wattelet-Boyer et al., 2016). Such a panoply of tools promises new exciting discoveries about the multiple functions of the plant TGN.

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