Membrane traffic and fusion at post-Golgi compartments

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Several thousand proteins are delivered to their sites of action and turnover by membrane trafficking. Cargo proteins include vacuolar proteases, storage proteins, membrane-associated receptors and their soluble (secreted) peptide ligands, cell wall-modifying enzymes, nutrient and hormone transporters, ion channels, and PAMP receptors involved in pathogen defense. Thus, cellular homeostasis, cell–cell communication in development, and physiological responses to changes in the environment all depend on membrane traffic. In this review, we will summarize recent advances on post-Golgi membrane traffic covering compartments, trafficking pathways, and molecular players involved.

DIVERSITY OF POST-GOLGI COMPARTMENTS

Major ultrastructurally defined endomembrane compartments in post-Golgi trafficking are the trans-Golgi network (TGN), the multivesicular body (MVB)/prevacuolar compartment (PVC), and two types of vacuole, the lytic vacuole (LV) and the protein storage vacuole (PSV). Additional compartments such as the recycling endosome (RE) have been postulated or inferred from experimental studies or marker localization data but have not been identified ultrastructurally in plants (Figure 1). The TGN appears to be formed from the trans-most cisterna of the Golgi stack but can also move away (Viotti et al., 2010; Kang et al., 2011). The TGN is a major sorting station for exocytic cargo proteins except that some storage proteins are sorted at the ER or cis-Golgi (Hara-Nishimura et al., 1998; Park et al., 2004). Importantly, the TGN also functions as an early endosome (EE) in plants, as revealed by time-course experiments with the lipophilic endocytic tracer FM4-64 (Dettmer et al., 2006). Thus, the TGN is at the intersection of the secretory and endocytic traffic. In addition, RAB-A class proteins related to the mammalian recycling Rab11 GTPase localize at a subpopulation of TGN (Chow et al., 2008; Kang et al., 2011). These observations suggest that distinct sorting functions are performed by the TGN, although there is no structural evidence for subdomains. TGN markers commonly used include the a1 subunit of the vacuolar H+ -ATPase (VHA) and the Qc-SNARE SYP61 (Bassham et al., 2000; Sanderfoot et al., 2001; Dettmer et al., 2006). The latter has been used to identify the TGN proteome by mass spectrometry (Drakakaki et al., 2011). The TGN appears to be formed from the trans-most cisterna of the Golgi stack (Zhang and Staehelin, 1992), possibly by matura-
tion. Its integrity seems to be maintained by anterograde traffic toward the plasma membrane (PM) and the vacuole as well as by retrograde traffic to the Golgi apparatus.

PREVACUOLAR COMPARTMENT/MULTIVESICULAR BODIES

Multivesicular bodies are ultrastructurally distinct, with intralu-
menal vesicles formed by local endosomal sorting complex required for transport (ESCRT)-mediated invaginations of the limiting membrane (Tse et al., 2004; Otegui and Spitzer, 2008; Stierhof and El Kasmi, 2010). MVBs act as a PVC and relay TGN-sorted cargo proteins toward (lytic) vacuoles, thus functionally corresponding to the late endosomes (LE) of animal cells (Tse et al., 2004). A similar PVC [possibly related to the dark intrinsic protein (DIP) organelle] is also observed in trafficking to the PSV (Jiang et al., 2000; Shen et al., 2011) and might actually be identical.

Abbreviations: AALP, Arabidopsis aeurain like protein; ABA, abscisic acid; CCV, clathrin-coated vesicles; CP11, cyclopropanolpredol isomerase 1; ER, endoplasmic reticu-
le; PAMP, pathogen-associated molecular pattern; PIP5K2, phosphatidylinositol-
4-phosphate 5-kinase 2; PME1, pectin methylesterase inhibitor protein 1; PIP3, phosphatidylinositol-3-phosphate; RMR, receptor homology region transmem-
brane domain ring H2 motif protein; RPA, ROOT AND POLLEN ARF–GAP; SNARE, soluble N-ethylmaleimide-sensitive factor attachment receptor; SYP, syn-
taxin of plants; TFL1, TERMINAL FLOWER 1; TRAPP, transport protein particle; VAMP, vesicle-associated membrane proteins.
Although the recent data strongly support a maturation model, Frontiers in Plant Science (Scheuring et al., 2011). This has been demonstrated, for example, their membrane-bound cargo into the vacuole for degradation fuse with the tonoplast, releasing the intralumenal vesicles, and to the PVC in lytic vacuolar traffic (Miao et al., 2008). By analogy with the non-plant systems in which LE fuse with the lysosome (reviewed in Luzio et al., 2010), it is generally accepted that MVBs fuse with the tonoplast, releasing the intralumenal vesicles, and their membrane-bound cargo into the vacuole for degradation (Scheuring et al., 2011). This has been demonstrated, for example, for the syntaxin KNOLLE, which is detected on the intralumenal compartments, the PVC and the vacuole, respectively. Recently, however, Uemura et al. (2010) demonstrated functional redundancy of the two syntaxins and also showed by double labeling that the two proteins largely colocalize on both endomembrane compartments. Additionally, MVBs are morphologically altered by treatment with wortmannin, an inhibitor of phosphatidylinositol-3 kinase (PI3K), which causes swelling and vacuolation of PVCs and is thus commonly used to identify PVCs (Tse et al., 2004; Wang et al., 2009). However, wortmannin has additional effects on endosomes and also impairs endocytosis from the PM (Lam et al., 2007).

Recently, Foresti et al. (2010) proposed that a late PVC/MVB exists as an intermediate compartment between the PVC and the central vacuole in the tobacco leaf epidermis, which was based on the localization of the recycling-defective vacuolar sorting receptor (VSR) VSR2. However, the PVC marker RHA1/RAB-F2a (see also below) was used to visualize this late PVC/MVB. It is thus important to employ additional unique subcellular markers to verify the presumed existence of a novel late PVC (see also Bottanelli et al., 2011b).

RECYCLING ENDOSONES

Recycling endosomes have not been identified morphologically in plants. However, they were first functionally demonstrated as the site of action of the brefeldin A (BFA)-sensitive ADP ribosylation factor (ARF)–guanine nucleotide exchange factor (GEF), GNOM, which is required for the recycling of the auxin-efflux carrier PIN-FORMED1 (PIN1) to the basal PM in the root vasculature (Geldner et al., 2003). In contrast, GNOM function is not required for the recycling to the PM of AUXIN-RESISTANT1 (AUX1), PIN2, and PM-located H⁺-ATPase (Kleine-Vehn et al., 2006), which suggests the existence of multiple functionally distinct REs. Although the partial colocalization of GNOM with FM4-64 would be compatible with the notion that REs might be part of the TGN (Geldner et al., 2003), the two compartments seem to differ in BFA sensitivity (Geldner et al., 2009). Moreover, there is no direct ultrastructural evidence supporting a subdomain organization of the TGN that could be unambiguously related to distinct trafficking roles. Interestingly, ARA7/RAB-F2b-positive endosomes are morphologically abnormal in gnom mutant cells, resembling wortmannin-treated MVBs (Geldner et al., 2003). However, this effect might be indirect since GNOM does not localize at the PVCs/MVBs. Moreover, delivery of the brassinosteroid receptor BRI and the boric acid/borate exporter BOR1 from the PM to the PVCs/MVBs appears to target these proteins to the LV rather than recycling them back to the PM (Viotti et al., 2010). Thus, it is unlikely that the PVCs/MVBs serve as REs. Recently, RAB-A1e...
Apart from the vacuoles themselves, there are additional compartments (PACs), and DIP-positive organelles that lie on the plasma membrane (PM). These organelles are not only located at the PM and a PSV-like organelle but also colocalize with the δ-TIP subunit of the AP-3 complex which was more recently shown to be involved in vacuolar biogenesis (see below for details). Although the PSV-like organelle remains to be characterized morphologically and functionally, its existence may imply the occurrence of hitherto unappreciated vacuolar functional diversity in differentiated cell types.

Commonly used markers include aleurain, sporamin, and γ-TIP for the LV/CV and lectin, globulin, albumin, and α-TIP for the PSV. Apart from the vacuoles themselves, there are additional compartments such as dense vesicles (DVs), precursor-accumulating compartments (PAGs), and DIP-positive organelles that lie on the PSV trafficking pathways.

**CELL PLATE**

Plant cells generate a transient membranous compartment named cell plate in the plane of cell division during cytokinesis. Formation of the cell plate occurs during cytokinesis and progresses toward the periphery until the margin of the cell plate fuses with the parental PM. The cell plate is mainly built by homotypic fusion of Golgi/TGN-derived vesicles whose delivery to the plane of cell division is guided by the dynamic cytoskeletal array of phragmoplast microtubules. By contrast, endocytosis seems to participate in the recruitment of the cortical division zone. A commonly used marker for the plane of cell division and the forming cell plate is the cytokinesis-specific syntaxin/Qa-SNARE KNOLLE/SYP111.

**POST-GOLGI TRAFFICKING PATHWAYS**

**LATE SECRETORY PATHWAY(s) TO THE PLASMA MEMBRANE**

Traffic of soluble proteins from the ER to the PM and out of the cell occurs by default, the only requirement being an N-terminal signal peptide for protein translocation across the ER membrane, as shown for several soluble enzymes as well as GFP. Conversely, a key regulator of Arabidopsis stem-cell homeostasis, the peptide ligand CLAVATA3 (CLV3), which is normally secreted from the cell, was diverted to the vacuole when fused to a C-terminal vacuolar sorting signal. Thus, the absence of a sorting signal for vacuolar trafficking is required for secretion of soluble proteins, supporting the notion that secretion is a default pathway.

Secretory trafficking of membrane proteins is less well characterized. Membrane proteins with a single transmembrane domain appear to reach their destination along the secretory pathway according to the length of their hydrophobic region: proteins with a shorter membrane span are held back in the Golgi stack whereas those with a longer membrane span are trafficked to the PM. The situation might be different for other membrane proteins such as those with multiple membrane spans or those with a hydrophobic tail anchor such as SNARE proteins that are inserted into the ER membrane by the GET machinery. For example, the rice secretory carrier membrane protein 1 (SCAMP1) has four transmembrane domains of which two domains appear to mediate export from the Golgi stack and another one appears to mediate traffic from the TGN to the PM.

Concanamycin A (ConC) inhibits the activity of the TGN/EE-residing VHA. As a consequence, TGN and MVB are incorporated into the Golgi apparatus, and the Golgi stacks are morphologically altered as well. Consequently, ConCA blocks downstream pathways of the TGN/EE (Dettmer et al., 2006; Reichardt et al., 2007; reviewed in Robinson et al., 2008). Interestingly, ConC inhibits the secretion of secGFP at the TGN/EE (Viotti et al., 2010), but other markers are not affected. Thus, one or more pathway(s) might be involved in the secretion of soluble proteins. Additional functional studies are required to resolve this issue.

**TRAFFICKING TO THE CELL DIVISION PLANE AS A SPECIALIZED SECRETORY PATHWAY**

Phragmoplast-assisted cell-plate formation is a unique mode of cytokinesis that evolved in the plant lineage only. Golgi/TGN-derived membrane vesicles that deliver the necessary material for building the PM and the cell wall are targeted to the plane of cell division. The available evidence suggests that both secretory and endocytic traffic contribute to cell-plate formation (Dhonukshe et al., 2006; Reichardt et al., 2007, 2011). Interestingly, cell-plate formation is critically dependent on secretory traffic delivering de novo synthesized KNOLLE syntaxin whereas endocytic traffic appears to be a consequence of preventing recycling of internalized membrane proteins to the PM. Many proteins that are detected at the PM during interphase accumulate at the plane of division during cytokinesis (Steinmann et al., 1999; Zuo et al., 2000). However, only cycling PM proteins arrive at the division plane by endocytosis.
whereas non-cycling PM proteins such as SYP132 have to be newly synthesized and delivered by secretion to accumulate at the forming cell plate (Reichardt et al., 2011). This observation may also indicate that protein trafficking to the cell plate relies on a default pathway. How KNOLLE syntaxin reaches the plane of cell division has been analyzed in transgenic plants expressing chimeric syntaxins in which protein domains have been swapped between KNOLLE and MVB-localized PEP12/SYP21 (Touihri et al., 2011). KNOLLE syntaxin with its tail anchor replaced by that of the pre-vacuolar syntaxin PEP12 still reaches the cell plate and rescues a knolle mutant whereas an N-terminal region from PEP12 targets the chimeric protein to the MVBPVC (Touihri et al., 2011). This result supports the notion of trafficking to the plane of cell division being a default pathway.

**ENDOCYTOSIS AND RECYCLING TO THE PLASMA MEMBRANE VS. TARGETING TO THE VACUOLE FOR DEGRADATION**

Upon internalization from the PM, endocytosed proteins face two options: They may be recycled to the PM or they may be passed on to the vacuole for degradation. In Arabidopsis, many PM proteins including auxin-efflux carriers PIN1 and PIN2, brassinosteroid receptor BRI1 and boron transporter BOR1 undergo constitutive endocytosis and recycling (Steinmann et al., 1999; Geldner et al., 2003, 2007; Geldner and Jürgens, 2006; Takano et al., 2010). There are only a few exceptions known such as the Qa-SNARE SYP132, which does not constitutively cycle and rather stays at the cell plate where PIN interacts with dynamin-related protein 1A (DRP1A; see below; Mravec et al., 2011), although clathrin often does not clearly colocalize with DRP1A at the cell plate (Ito et al., 2011). Thus, the molecular machinery of protein retrieval from the cell plate appears to be similar to that of endocytosis. Whereas PIN1 is endocytosed from the cell plate and then retargeted to the PM, the cytokinesis-specific syntaxin KNOLLE/SYP111 is endocytosed and then delivered to the LV for degradation (Reichardt et al., 2007). Hence there must be a selective sorting mechanism, possibly at the TGN or cell plate (see below).

Clathrin-mediated endocytosis in mammalian cells also involves the AP-2 complex, with its μ-adaptin subunit selecting cargo with a tyrosine-based sorting motif for internalization from the PM (reviewed in Boehm and Bonifacino, 2001). Tyrphostin A23 is a competitive inhibitor of the interaction of the sorting sequence Yxxφ (where Y is a tyrosine, x is any amino acid, and φ is a bulky hydrophobic residue) of cargo proteins with the medium (μ2) subunit of mammalian AP-2 complex, and this has been used to explore clathrin-dependent trafficking pathways (Bannyaury et al., 2003). In plants, tyrphostin A23, but not its structural analog tyrphostin A51, inhibits endocytosis of FM4-64, and the artificially expressed human transferrin receptor (Ortiz-Zapater et al., 2006; Dhonukshe et al., 2007). Although tyrphostin A23 appears to have non-specific deleterious effects in plant cells (see below), the inhibitory effect of tyrphostin A23 might result from the existence of a plant equivalent to μ2 adaptin, which has not been identified. There is also clathrin-independent endocytosis which, however, has not been well analyzed in plants. So far, a distinct route of endocytosis has been demonstrated by ultrastructural tracing of charged nanogold in the presence of ikarugamycin, which inhibits clathrin-dependent endocytosis (Moscatelli et al., 2007; Onelli et al., 2008). It will be important to study the underlying mechanism of this presumed novel endocytic route at the molecular level.

If not recycled, PM proteins are delivered, via PVCs/MVBs, to the LV for degradation (Kleine-Vehn et al., 2008; Viotti et al., 2010). It is not at all clear where the two routes of recycling and degradation diverge among the post-Golgi endosomal compartments in plants. All endocytosed PM proteins are delivered to the TGN/EE. If the MVBs indeed mature from some subdomain of TGNs and the REs are also derived from TGNs, the sorting would likely occur at the TGNs (see above). Apart from the difficulty of ultrastructurally identifying REs, there are conflicting (or incomplete) data regarding the recycling vs. degradation. For example, the sorting nexin 1 (SNX1)-labeled PVC/MVB has been proposed to be the site of sorting (Jaillais et al., 2006). However, PM proteins to be recycled have not been detected at the PVC/MVB (Viotti et al., 2010). Instead, the recycling pathway might be affected indirectly by interfering with vacuolar trafficking.

Ubiquitination is likely an endocytic signal for PM proteins to be targeted to the vacuole for degradation (Abas et al., 2006; Kleine-Vehn et al., 2008). After having been trafficked to the endosomes, ubiquitinated proteins seem to be recognized by ESCRTs, which in turn promote MVB formation (Spitzer et al., 2006; Otegui and Spitzer, 2008). For example, PIN1, PIN2, and AUX1 proteins are known cargo proteins of the ESCRT machinery (Spitzer et al., 2008). As an example for ligand-dependent endocytosis, the immunity-related pattern recognition receptor FLS2 is degraded in response to ubiquitination and BAK1-mediates phosphorylation triggered by the bacterial elicitor flagellin 22 (Lu et al., 2011). Similarly, endocytosis of IRON-REGULATED

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**ENDOCYTOSIS AND RECYCLING TO THE PLASMA MEMBRANE VS. TARGETING TO THE VACUOLE FOR DEGRADATION**

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Clathrin-mediated endocytosis in plants has been demonstrated for PIN proteins and the endocytic tracer FM4-64, using both overexpression of the dominant-negative hub fragment of the clathrin heavy chain and T-DNA insertional clathrin heavy chain mutants (Dhonukshe et al., 2007; Robert et al., 2010; Kitakura et al., 2011). Wortmannin has also been widely used to interfere with endocytosis (Emans et al., 2002; Reichardt et al., 2007; Ebine et al., 2011), in addition to its known disruptive effects on vacuolar trafficking, although this drug has rather ill-defined effects on endosomes (see above). Wortmannin was recently shown to cause aggregation of clathrin at the PM, which might explain the inhibitory effect of wortmannin on endocytosis (Ito et al., 2011).

Clathrin is also involved in the retrieval of PIN protein from the cell plate where PIN interacts with dynamin-related protein 1A (DRP1A; see below; Mravec et al., 2011), although clathrin often does not clearly colocalize with DRP1A at the cell plate (Ito et al., 2011). Thus, the molecular machinery of protein retrieval from the PM appears to have non-specific deleterious effects in plant cells (see above). Apart from the difficulty of ultrastructurally identifying REs, there are conflicting (or incomplete) data regarding the recycling vs. degradation. For example, the sorting nexin 1 (SNX1)-labeled PVC/MVB has been proposed to be the site of sorting (Jaillais et al., 2006). However, PM proteins to be recycled have not been detected at the PVC/MVB (Viotti et al., 2010). Instead, the recycling pathway might be affected indirectly by interfering with vacuolar trafficking.

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TRANSPORTER 1 (IRT1) and traffic of BOR1 from the PM to the LV depend on their ubiquitination (Barberon et al., 2011; Kasai et al., 2011).

**VACUOLAR CARGO TRAFFICKING PATHWAY(s)**

Newly synthesized soluble cargo proteins destined to the vacuoles need an N- or a C-terminal vacuolar sorting sequence (known as NTPP or CTPP), as supported by the vacuolar trafficking of NTPP-tagged ER-translocated secGFP (Di Sansebastiano et al., 1998). Generally, LV- and PSV-directed soluble cargo proteins have NTPP and CTPP, respectively, as sorting sequences that are thought to bind to corresponding VSRs for targeted delivery. VSR1/ELP (one of seven homologs), for example, recognizes the N-terminal sorting sequence, NPIR, of AALP or sporamin at the TGN/EE for sorting, and delivery to the MVB/PVC (Sanderfoot et al., 1998; Ahmed et al., 2000). However, this notion was questioned recently by the observation that transiently expressed ER-anchored pea VSR caused retention of soluble vacuolar cargo molecules in the ER (Niemes et al., 2011), suggesting that sorting to the vacuole may occur at an earlier step. More direct evidence is needed to identify the endomembrane compartment(s) at which VSRs interact with their vacuolar cargo proteins normally.

The VSR1/ELP interacts with the μ1 medium subunit of the mammalian AP-1 complex and with *Arabidopsis* μ1A-adaptin in vitro through a tyrosine residue-based sorting sequence, YMPL (Sanderfoot et al., 1998; Ahmed et al., 2000), implying that clathrin-coated vesicles (CCVs) are likely involved in vacuolar trafficking. However, this idea was challenged by the recent observation that transient overexpression of the truncated clathrin heavy chain, the so-called clathrin hub, does not interfere with vacuolar trafficking, which was consistent with the alternative MVB maturation model (Scheuring et al., 2011). However, it is not known how efficiently the clathrin hub interferes with CCV formation (see below), although endocytosis of FM4-64, PIN1, and PIN2 proteins is clearly inhibited (Dhonukshe et al., 2007; Scheuring et al., 2011). Moreover, the MVB maturation model does not explain why a mutation of the adaptor protein (AP) complex-recognition sequence, YMPL, of pea VSR causes its mistargeting in tobacco protoplasts (daSilva et al., 2006) and why homodimerization-defective VSR1 is less detected in a CCV-enriched fraction in *Arabidopsis* leaf than is pea VSR (Kirsch et al., 1994; Kim et al., 2010). *Arabidopsis* VSR2 and a lily ortholog, LIVSR, have been localized polarly or asymmetrically, i.e., on one side of the cell (Steinmann et al., 1999; Swarup et al., 2004; Takano et al., 2005, 2010). These include several members of the PIN family of auxin-efflux carriers as well as other PM proteins such as BOR1 and its paralog BOR4 (Miwa et al., 2007), the boron importer NIP5;1 (Takano et al., 2010), exporter PIS1/PDR9/ABCG37 of the plant hormone precursor indole-3-butyric acid (Langowski et al., 2010), the Caspian strip membrane domain proteins CASPs in the endodermis (Roppolo et al., 2011), and the ABCG-type transporter DSO/AtWBC11 in the epidermis (Panikashvili et al., 2007). In addition, the GPI-anchored COBRA protein is present only on the lateral surfaces of root vascular cells (Schindelman et al., 2001). How the polar localization comes about has not been well studied in most cases. For PIN1, however, it was demonstrated that the

DELIVERED TO THE VACUOLES VIA MEMBRANE FUSION OF THE PVCs/MVBs WITH THE VACUOLE (Scheuring et al., 2011), VSR was presumed to be recycled from the PVCs/MVBs to the TGN/EE by the retromer complex (Sanderfoot et al., 1998; daSilva et al., 2006; Oliviusson et al., 2006; Jaillais et al., 2007). However, this long-held belief has recently been questioned by the controversial localization of the retromer complex to the TGN, rather than the MV, in *Arabidopsis* and tobacco (Jaillais et al., 2006, 2007, 2008; Niemes et al., 2010; Pourcher et al., 2010). The localization of the retromer complex to the TGN would be consistent with the maturation model for the origin of the MVB (see above).

Fusion of the PVCs/MVBs with the vacuole may require QaSNARE SYF2 proteins and the homotypic fusion and protein sorting/class C-VPS protein (HOPS/C-VPS) complex comprising the *Arabidopsis* VPS16-homolog VCL1, VPS11, and VPS33 (Rojo et al., 2001, 2003; Shirakawa et al., 2010). However, the latter two proteins have yet to be functionally studied.

Different trafficking pathways to the PSV have been shown in diverse species including pumpkin, bean, and *Arabidopsis* (Frierio et al., 1998; Harashinimura et al., 1998; Hinzu et al., 1999; Park et al., 2004, 2005). RMRs are suggested to be PSV sorting receptors in *Arabidopsis*, tobacco, and rice (Jiang et al., 2000; Park et al., 2005, 2007; Hinzu et al., 2007). RMRs were studied in *Arabidopsis* and rice. RMR1 and RMR2 have been localized at the Golgi, a PVC-like organelle and the PSV (or protein bodies); these proteins interact with the C-terminal vacuolar sorting sequences of storage proteins in vitro (Park et al., 2005, 2007; Hinzu et al., 2007). Unlike VSRs in lytic vacuolar traffic, RMRs appear not to be recycled and instead are bound to the aggregates of soluble cargo proteins (Park et al., 2007). More recent mutant studies in *Arabidopsis* have challenged the role of RMRs in PSV trafficking and identified VSR1, VSR3, and VSR4 as the major sorting receptors that function redundantly in the targeting of soluble cargo proteins to the PSV and the LV/CV (Shimada et al., 2003; Zouhar et al., 2010). This result suggests that VSRs presumably fulfill multiple functions and that vacuolar biogenesis of PSV and LV/CV might be closely linked, especially in early embryogenesis.

**ASYMMETRIC LOCALIZATION OF PLASMA-MEMBRANE PROTEINS**

Most PM proteins are located in the PM all around the cell rather than being confined to a specific surface area (Geldner and Jürgens, 2006; Geldner et al., 2007). However, several PM proteins localize polarly or asymmetrically, i.e., on one side of the cell (Steinmann et al., 1999; Swarup et al., 2004; Takano et al., 2005, 2010). These include several members of the PIN family of auxin-efflux carriers as well as other PM proteins such as BOR1 and its paralog BOR4 (Miwa et al., 2007), the boron importer NIP5;1 (Takano et al., 2010), exporter PIS1/PDR9/ABCG37 of the plant hormone precursor indole-3-butyric acid (Langowski et al., 2010), the Caspian strip membrane domain proteins CASPs in the endodermis (Roppolo et al., 2011), and the ABCG-type transporter DSO/AtWBC11 in the epidermis (Panikashvili et al., 2007). In addition, the GPI-anchored COBRA protein is present only on the lateral surfaces of root vascular cells (Schindelman et al., 2001). How the polar localization comes about has not been well studied in most cases. For PIN1, however, it was demonstrated that the
initial accumulation in the PM is non-polar, which might reflect non-polar secretory trafficking, whereas endocytosis and targeted recycling bring about the polar localization of PIN1 (Dhonukshe et al., 2008). PIN1 is actively localized at the basal PM in the root vasculature by the ARF–GEF GNOM and PP2A phosphatases that counteract the PINOID kinase (Steinhann et al., 1999; Michniewicz et al., 2007). In contrast, PIN2 localizes at the PM apically and basally in the epidermis and cortex, respectively, and only the basal localization seems to be dependent on GNOM function (Geldner et al., 2003). In general, apical targeting of PIN proteins requires the PINOID kinase and its homologs WAG1 and WAG2, which phosphorylate their PIN substrates (Dhonukshe et al., 2010). Additionally, the sterol composition mediated by the ER-residing CP11 affects PIN2 redistribution after cytokinesis (Men et al., 2008). PIN3, which is required for phototropism, locates polarly at the PM of epidermis, cortex, endodermis, and vasculature, but apolarly in the columella (Friml et al., 2002). Upon shading, PIN3 relocates polarly toward the inner membrane of the endodermis, which depends on the function of GNOM and PINOID, and thus triggers apical hook development (Ding et al., 2011). Whereas the polar localization of some PIN transporter proteins reflects the (changeable) direction of auxin flow, the polar localization of other PM proteins might rather reflect the intrinsic polarity of the cell in which they are expressed. This might apply to DSO in the outer PM of the epidermis or BOR1 in the inner PM of various root cells including the epidermis, endodermis, and columella. BOR1 accumulation, but not its polarity, responds to changes in the external supply of boron. BOR1 cycles between the PM and endosomes when the external concentration of boron is low; however, BOR1 is fast endocytosed and delivered to the ER when the root is exposed to a high concentration of boron (Takano et al., 2005, 2010). Tyrosine residues appear to be important in BOR1 turnover (Takano et al., 2010), although their specific role is not clear.

**MOLECULAR PLAYERS OF POST-GOLGI TRAFFIC**

**VESICLE FORMATION BY ARF GTPases AND THEIR REGULATORS, ARF–GEFs, AND ARF–GAPs**

Small GTPases of the ARF family recruit coat proteins by undergoing GTP/GDP exchange cycles that are tightly controlled by specific regulatory proteins, ARF–GEFs, and ARF–GAPs. The *Arabidopsis* genome encodes approx. one dozen ARF GTPases; the precise number is unknown because divergent ARFs cannot easily be distinguished from functionally distinct ARFs (ARF-LIKE proteins). Of the three eukaryotic ARF classes, only ARF1 isoforms are present in plants, which, on the other hand, also have plant-specific ARF classes such as ARFA and ARFB (and possibly additional ARF classes; Jürgens and Geldner, 2002). ARF1 predominantly accumulates at the TGN/EE and the Golgi stacks and thus likely recruits both COPI and AP complex/clathrin coat proteins (Pimpel et al., 2000; Matheson et al., 2007; Sterhof and El Kasmı, 2010). Barley isoforms of ARF1 named ARFA1b/1c function in carlose deposition and preinvaginating basal defense and have been localized to MVBs (Böhlenius et al., 2010). However, this localization has been disputed (Robinson et al., 2011). Plant-specific ARF6 was detected at the PM and proposed to be the plant equivalent of mammalian ARF6, although no functional assays have been performed (Matheson et al., 2008). Moreover, there is no ortholog of the mammalian ARF6 exchange factor EFA6 in *Arabidopsis*.

The *Arabidopsis* genome encodes eight ARF–GEFs that are all 150–220 kDa in size and can be grouped into two clades related to human GBF1 and BIG, respectively (Anders and Jürgens, 2008). Importantly, BFA can be used to conditionally inactivate specific ARF–GEFs and thus determine the trafficking pathways these ARF–GEFs regulate. Sensitivity or resistance to BFA critically depends on specific amino acids in the catalytic SEC7 domain of ARF–GEFs, which forms the basis for engineering fully functional BFA-sensitive or BFA-resistant variants of ARF–GEFs (Geldner et al., 2003; Richter et al., 2007). BFA-sensitive GNOM regulates endosomal recycling of PIN1 and PIN3 proteins (Geldner et al., 2003; Ding et al., 2011), but only partially the recycling of PIN2 and PM-localized H^+-ATPase (Geldner et al., 2003), which suggests the existence of multiple recycling pathways. A similar conclusion could be drawn from the observation that the small compound endosidin 1 has differential effects on endocytic trafficking of several proteins tested (Robert et al., 2008). Additionally, GNOM functionally complements its closest homolog GNOM-LIKE 1 (GNL1), which is BFA-insensitive and functions in COPI complex recruitment at the Golgi stacks in retrograde traffic to the ER (Richter et al., 2007). Recently, GNOM was proposed to act in the internalization of FM4-64 at the PM (Naramoto et al., 2010). The third GBF1-related ARF–GEF, GNOM-LIKE 2 (GNL2) is required for pollen germination (lia et al., 2009), GNL2 appears to be functionally related to GNOM, being able to mediate polar recycling of PIN1 when ectopically expressed in the seedling root (Richter et al., 2011). Interestingly, GNOM and GNL2 promote polar growth of root hairs and pollen tubes, respectively (Richter et al., 2011). The BIG clade comprises five members. Not much is known about BIG1 to BIG4. The catalytic SEC7 domain of BIG3 (originally designated BIG2) was demonstrated to catalyze the nucleotide exchange on ARF1 in vitro in a BFA-insensitive manner (Nielsen et al., 2006). BIG5 (also known as MIN7 or BEN1) was shown to play a role in immunity, being degraded in response to its interaction with the HopM1 effector of *Pseudomonas* (Nomura et al., 2006). Additionally, BIG5 might act in the trafficking of PIN1, PIN2, and PM–ATPase from the TGN/EE to the RE (Tanaka et al., 2009).

The *Arabidopsis* genome encodes 15 ARF–GAPs that are grouped into four different classes (Jürgens and Geldner, 2002). Class 1 ARF–GAP VASCULAR NETWORK DEFECTIVE 3 (VAN3), also known as SCARFACE (SFC) and ARF–GAP domain protein 3 (AGD3), locates at the TGN (Koizumi et al., 2005; Sieburth et al., 2006). Recently, VAN3 was proposed to be a putative ARF–GAP counteracting GNOM at the PM by regulating endocytosis of PIN1 (Naramoto et al., 2010), NEVERSHELDED (NEV)/AGD5, an ortholog of yeast Ace2, functions in the trafficking of cargo molecules for floral organ abscission at the TGN/EE and RAB-A1-positive endosomes (Liljegren et al., 2009). RPA and AGD1 were shown to act in root hair growth (Song et al., 2006b; Yoo et al., 2008). The rice ARF–GAP OsAGAP is involved in vesicle traffic in the auxin-influx pathway (Zhuang et al., 2006). However, the ARF-substrate specificity of ARF–GAPs has been barely analyzed. For example, ARF–GAPS AGD5, AGD7, and RPA were shown to activate ARF1 in vitro (Song et al., 2006b; Min et al., 2007;
Stefano et al., 2010). In addition, AGD5 was shown to interact also with ARFB 
*in vitro* (Stefano et al., 2010). Interestingly, AGD7 interacts 
with ARF1 
*in vivo*, and overexpression of AGD7 inhibits γCOP 
recruitment to the Golgi membrane and also disrupts anterograde 
ER-Golgi traffic (Min et al., 2007).

**MEMBRANE VESICLE COAT PROTEINS**

Unlike mammals, *Arabidopsis* lacks the equivalent of caveolin coat 
protein. Furthermore,斯顿in and Golgi-localizing γ-car homology, 
ARF-binding protein (GGA) are not found in *Arabidopsis* 
(Boehm and Bonifacino, 2001). Thus, clathrin presumably plays 
a major role in plant post-Golgi traffic by binding to AP complexes. 
Non-coated secretory vesicles (SV) have been observed at the 
Golgi/TGN by electron tomography and proposed to deliver 
memory secretory cargo proteins to the PM (Staehelin et al., 1990; 
Kang et al., 2011). However, the functional significance of the 
non-coated vesicles has not been demonstrated.

The *Arabidopsis* genome encodes three and two homologs of 
clathrin light chain and clathrin heavy chain, respectively, which 
have been detected at the TGN, the cell plate, and the PM (Otegui 
et al., 2001; Dhonukshe et al., 2007; Mravec et al., 2011). Recently, 
the clathrin light chain was also shown to be associated with 
ARA6/RAB-F1-positive MVBs, but not with RHA1/RAB-F2a-
positive MVBs (Itou et al., 2011). To date, however, there is no report 
on the participation of clathrin plaques in membrane invagination 
at the MVBs in plants, although a thick layer of ESCRTs complexes 
had been observed at the limiting surface of PVCs/MVBs (Tse 
et al., 2006; Stierhof and El Kasmi, 2010). Thus, further analysis 
is needed to define the role of clathrin at ARA6/RAB-F1-positive 
MVBs.

Up to now, functional and pharmacological analyses have 
demonstrated the involvement of clathrin in endocytosis in 
*Arabidopsis* and tobacco (Dhonukshe et al., 2007; Zhao et al., 
2010; Kitakura et al., 2011). Tyrphostin A23 is broadly used to 
explore clathrin-dependent trafficking pathways (Banbury et al., 
2003; Ortiz-Zapater et al., 2006; Dhonukshe et al., 2007). However, 
Tyrphostin A23 appears to have non-specific deleterious effects 
in *Arabidopsis* and tobacco cells (I. Reichardt and G. Jürgens, 
unpublished data; also reviewed in Robinson et al., 2008). Hence, 
proper controls are absolutely necessary to distinguish specific 
from non-specific interference when Tyrphostin A23 is used to 
study membrane traffic.

The clathrin hub has been used to interfere with clathrin-
mediated trafficking pathways in mammals and plants (Liu et al., 
1995; Dhonukshe et al., 2007). This fragment comprises the C-
terminal third of the clathrin heavy chain and is supposed to 
compete with the endogenous clathrin heavy chain in interacting 
with clathrin light chains (Liu et al., 1995). Fortunately, the find-
ing of clathrin-dependency in endocytosis that had been revealed 
by the combinatorial approaches of the clathrin hub overex-
pression and tyrphostin A23 was consistent with the results of 
a functional study of *clathrin heavy chain* mutants (Dhonukshe 
et al., 2007; Robert et al., 2010; Kitakura et al., 2011). Based on 
both clathrin hub overexpression and ultrastructural analysis of 
PVC/MVB, the vacuolar trafficking pathway was proposed to be 
clathrin-independent (Scheuring et al., 2011). In our knowledge, 
however, it is not fully explained how the clathrin hub interferes 
with CCV formation at the molecular level in plants. For example, 
do all three clathrin light chain proteins have the same affinities for 
the clathrin hub? Thus, an in-depth functional study of clathrin is 
needed to elucidate fully the role of clathrin in plant membrane 
traffic.

Heterotetrameric AP complexes recognize a tyrosine- 
or dileucine-based sorting motif of cargo molecules, which in turn 
recruit cytosolic clathrin to the membrane for CCV formation. 
Although the sequence similarity of adaptins with their mam-
malian counterparts reveals four different types of AP complexes 
and five homologs of the μ subunit (named as μA-μD instead of 
μ1-μ4) in *Arabidopsis* (Boehm and Bonifacino, 2001), they have 
been hardly studied in plants. In addition, the existence of an 
additional AP complex (AP-5) locating at the LE has been recently 
demonstrated in mammalian cells; their homologs (μ5, B5, and c) 
were found in *Arabidopsis* and *Physcomitrella patens* by sequence 
similarity, even though their corresponding sigma subunit (σ5) 
was not found yet (Hirst et al., 2011).

The AP-3 complex consisting of β3/μD/σ3 seems to be 
involved in vacuolar biogenesis (Ferrar et al., 2010; Zwiewka et al., 
2011). Interestingly, elimination of the AP-3 complex appears to 
have no obvious phenotypic effect. However, the knockout alleles 
of AP-3 subunits β and δ suppress the zigzag (*zig*) phenotype of 
plants lacking the vacuolar trafficking Qb-SNARE VTI11, and zig 
suppressor 4 (*zip4*) was identified as a loss-of-function allele of 
μD adaptin (Niihama et al., 2009). μA was proposed to be the 
putative medium subunit of the AP-1 complex as inferred from 
the localization at the trans-Golgi in *Arabidopsis* and from the 
*in vitro* interaction with the tyrosine sorting sequence of VSR-PS1 
or TGN38 (Hapfel et al., 2004). However, there is no functional 
in *vivo* evidence supporting this notion. The ENTH-domain con-
taining monomeric adaptor, Epsin1 is functionally involved in 
vacuolar trafficking, but not in the secretory pathway (Song et al., 
2006a). Epsin R2 interacts *in vitro* with the AP-3 complex and 
VTI12, giving a hint at its involvement in PSV traffic (Lee et al., 
2007). The ANTH-domain-bearing monomeric adaptor AP180 
interacts with AtSpC-adaptin, one of putative large subunits of AP-2 
(Barth and Holstein, 2004).

**VESICLE BUDDING BY DYNAMIN-RELATED GTPases**

Dynamin-related proteins (DRPs) are GTPases that constrict or 
pinch off membranes and thus function in vesicle budding from 
diverse endosome compartments such as the PM, cell plate, and 
Golgi/TGN and also mediate fission of mitochondria and 
plastids (reviewed in Praefcke and McMahon, 2004; reviewed in 
Pucadyl and Schmid, 2009). DRP2B/ADL6 is involved in the 
vacuolar trafficking pathway (Jin et al., 2001; Lam et al., 2002). 
Moreover, DRP2B/ADL6 and DRP1A/ADL1 participate in CCV 
formation at the PM and cell plate (Fujimoto et al., 2010; Mravec 
et al., 2011). DRP2A and DRP2B are functionally redundant, local-
ize to the tip of root hairs where endocytosis occurs and play an 
esential role in gametophyte development (Taylor, 2011). Rice 
BRITTLE CULM 3/OsDRP2B mediates vesicle trafficking involved 
in cellulose biosynthesis (Li et al., 2010).

**VESICLE TETHERING BY RAB GTPTases AND TETHERING FACTORS**

Tethering of transport vesicles to their target membrane requires 
RAB GTPTases and their effector proteins whereas the subsequent 
fusion of the membranes is mediated by the SNARE fusion
machinery and its regulators. The *Arabidopsis* genome encodes 57 RAB GTPases representing eight clades A–H (Rutherford and Moore, 2002).

*Arabidopsis* RAB-E1d, which is related to mammalian Rab8 and yeast Ypt2, locates at the Golgi, regulates the secretory pathway, but not the vacuolar pathway, in the tobacco leaf epidermis, and interacts with PM-residing PIP5K2 (Camacho et al., 2009; Bottanelli et al., 2011a).

RAB-A2 and RAB-A3 localize at the VHA-a1-positive TGN and also at the growing margin of the cell plate during cytokinesis (Chow et al., 2008). In contrast, tobacco NtRAB11b labels Golgi stacks in the apical clear zone of growing pollen tubes; GDP-locked NtRAB11b inhibits traffic of exocytic and recycling vesicles to the pollen tube tip (de Graaf et al., 2005). RAB-A4b affecting both root hair and pollen tube growths preferentially labels the TGN and cell-wall materials-containing SV near the PM in growing tips (Preuss et al., 2004, 2006; Szumianski and Nielsen, 2009; Kang et al., 2011). These findings suggest a role for RAB-A class proteins, which are related to mammalian recycling Rab11 and yeast Ypt3, in exocytosis and recycling pathways. This idea might be also supported by the observation that null mutations eliminating sub-units of TRAPPII, which is a putative GEF for RAB-A1c, inhibit the secretory pathway, but not vacuolar traffic (Qi et al., 2011).

There are three RAB-F class proteins in *Arabidopsis*. Whereas RH1/RAB-F2a and ARA7/RAB-F2b colocalize at the PVCs/MVBs (Lee et al., 2004; Reichardt et al., 2007), plant-specific ARA6/RAB-F1 locates in differential populations of the endosomes, although their localizations overlap to some extent (Ueda et al., 2001, 2004). Additionally, ARA6/RAB-F1 is more resistant to BFA than is ARA7/RAB-F2b (Ueda et al., 2004). While the GDP-locked mutant of RAB-F2 proteins inhibits vesicular targeting of AALP in *Arabidopsis* transient assays, the homologous mutation of plant-specific ARA6/RAB-F1 does not (Ueda et al., 2001; Sohn et al., 2003), suggesting that only RAB-F2 proteins act in vacuolar traffic. However, overexpression of the nucleotide-free ARA6/RAB-F1 was recently shown to cause mis-targeting of vacuolar soluble cargo proteins to the apoplasm in the tobacco epidermis (Bottanelli et al., 2011a). Similarly, a putative ARA6/RAB-F1 ortholog, m-Rabmac in *Mesembryanthemum*, was also proposed to be involved in vacuolar targeting at the PVCs/MVBs (Bolte et al., 2004). However, the loss-of-function mutant of ARA6/RAB-F1 did not disturb substantially the vacuolar transport of sporamin; moreover, whereas RAB-F2 proteins are genetically linked to the vacuolar Qa-SNARE VAM3/SYP22/SGR, ARA6/RAB-F1 is not (Ebine et al., 2011). In fact, the mutant phenotype of VAM3/SYP22/SGR was almost completely suppressed by the loss-of-function mutation of ARA6/RAB-F1 (Ebine et al., 2011), indicating the counteracting role of ARA6/RAB-F1 in vacuolar trafficking mediated by VAM3/SYP22/SGR. Therefore, ARA6/RAB-F1 is unlikely involved in vacuolar traffic in *Arabidopsis*, in contrast to RAB-F2. Instead, ARA6/RAB-F1 was shown to modulate PEN1/SYP121–VAMP727-driven vesicle fusion at the PM, which was elicited by environmental stimuli such as salinity (Ebine et al., 2011). Thus, there are likely multiple types of MVBs with distinct functions, although it is entirely unclear how they might originate. These three RAB-F class proteins are activated by the same RAB-GEF, VPS9a, *in vitro* (Goh et al., 2007). The *in vivo* situation might be more complex since the vps9a mutant phenotype is suppressed by the overexpression of the GTP-locked form of ARA7/RAB-F2b, but not of ARA6/RAB-F1 (Goh et al., 2007; Ebine et al., 2011). In the tobacco epidermis, however, overexpression of VPS9a titrated out the negative effect of the nucleotide-free ARA6/RAB-F1, but not of RHA1/RAB-F2a (Bottanelli et al., 2011b). Thus, further analysis is required to understand precisely the biological functions of these RAB-F GTPases and their regulator, VPS9a.

RAB-H related to mammalian Rab6 was demonstrated to rescue the yeast ypt6 mutant, revealing its potential role in the retrograde trafficking from endosomes to the Golgi stacks (Bednarek et al., 1994; Johansen et al., 2009), but this was not clearly addressed.

Rice Rab7 belonging to the RAB-G subclass localizes at the tonoplast in *Arabidopsis* transient assays, consistent with its proposed involvement in vacuolar fusion (Nahm et al., 2003). By analogy, the overexpression of the nucleotide-free *Arabidopsis* Rab7 inhibits vacuolar targeting in tobacco epidermis (Bottanelli et al., 2011a). Rice prenylated Rab acceptor, OsPRA1 was shown to affect the fusion of PVCs/MVBs with the vacuole by interacting with both VAM3/SYP22/SGR and OsRAB7 (Heo et al., 2010).

**MEMBRANE FUSION BY SNARE COMPLEXES AND REGULATORY SM PROTEINS**

Membrane-anchored SNARE proteins form complexes that mediate membrane fusion, e.g., between a transport vesicle and its target membrane. Based on the analysis of yeast and mammalian SNARE complexes, each SNARE complex comprises a helical bundles of four SNARE domains (R, Qa, Qb, and Qc) that are contributed by one R-SNARE protein on the vesicle and two or three Q-SNARE (Qa, Qbc or Qa, Qb, and Qc) proteins on the target membrane (Fasshauer et al., 1998). The *Arabidopsis* genome encodes 54 SNARE proteins that grouped into 18 Qa-, 11 Qb-, 8 Qc-, and 14 R-SNAREs (Uemura et al., 2004). To date, however, only a few SNARE complexes have been characterized. SNARE complexes comprising SYP4/TLG2 (Qa = syntaxin), VT11 (Qb), SYP61/OSM1 (Qc), and an unknown VAMP (R-SNARE) protein mediate the fusion of PVC/MVB-derived vesicles at the TGN (Sanderfoot et al., 2001; Uemura et al., 2004). The SYF2 syntaxin family includes two members, PEP12/SYP21 and VAM3/SYP22/SGR, that differ in subcellular location, PVC/MVB vs. vacuole, but nonetheless are functionally redundant in vacuolar trafficking (Foresti et al., 2006; Tyrrell et al., 2007; Shirakawa et al., 2010; Uemura et al., 2010). However, RAB-F2 GTPases are genetically linked to VAM3/SYP22/SGR, but not to PEP12/SYP21 (Ebine et al., 2011). Furthermore, the SNARE complex comprising VAM3/SYP22/SGR (Qa), ZIG/VT11 (Qb), SYP51 (Qc), and VAMP27 (R-SNARE) protein is involved in vacuolar traffic, seed maturation, vacuole biogenesis, and also in shoot gravitropism (Sanderfoot et al., 1999; Yan0 et al., 2003). ZIG/VT11 can substitute for VT112, which is related to PSV trafficking, but not vice versa (Sannmartin et al., 2007).

Syntaxins (Qa-SNARE proteins) of the SYF1 family are preferentially located at the PM except for KNOLLE/SYP111, which is specifically targeted to the plane of cell division (Lauber et al., 1997; Uemura et al., 2004; Enami et al., 2009; Reichardt et al., 2011).
Interestingly, the closest KNOLLE homolog, SYP112, behaves like KNOLLE when expressed from the KNOLLE promoter, although SYP112 seems to have no function of its own (Müller et al., 2003). Other SYP1 family members such as SYP124, SYP125, and SYP131 are exclusively expressed in pollen and SYP123 is preferentially expressed in root hair cells (Enami et al., 2009; Silva et al., 2010). Overexpression of cytosolic fragments lacking the hydrophobic tail anchor of the PM-localized syntaxins PEN1/SYP121 and SYP122 and Qc-SNARE SYP71, which localizes at both the PM and the ER, were shown to suppress secretion of secGFP (Geelen et al., 2002; Tyrrell et al., 2007; Suwastika et al., 2008), but not of the chimeric protein secGFP-PMEI1 (De Caroli et al., 2011). Thus these findings suggest that there might be differentially regulated fusion mechanisms at the PM. It should be noted that the dominant-negative effect of the cytosolic fragment of PEN1/SYP121 is caused by titrating out SNARE interaction partners such as SNAP33, which possibly also form complexes with other SYP1 syntaxins (see below). PM-resident PEN1/SYP121 (Qa) confers non-host susceptibility or rather features of specific and distinct compartments. This might also be important for the distinguishing between models for the origin of specific compartments, e.g., MVB maturation. It is also obvious that we need additional specific, both soluble and membrane-bound, cargo markers for each traffic destination for live imaging of trafficking pathways. All this should be combined with the genetic tools available in Arabidopsis, which have not been exploited fully and systematically to analyze regulatory mechanisms in membrane traffic. Furthermore, the crucial role of membrane lipids in post-Golgi traffic as well as raft-mediated endocytosis (Men et al., 2008; Kale et al., 2010; Markham et al., 2011) needs to be addressed in more detail.

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