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Chapter

Endomembrane Trafficking in Plants

Birsen Cevher-Keskin

Abstract

The functional organization of eukaryotic cells requires the exchange of proteins, lipids, and polysaccharides between membrane compartments through transport intermediates. Small GTPases largely control membrane traffic, which is essential for the survival of all eukaryotes. Transport from one compartment of this pathway to another is mediated by vesicular carriers, which are formed by the controlled assembly of coat protein complexes (COPs) on donor organelles. The activation of small GTPases is essential for vesicle formation from a donor membrane. In eukaryotic cells, small GTP-binding proteins comprise the largest family of signaling proteins. The ADP-ribosylation factor 1 (ARF1) and secretion-associated RAS superfamily 1 (SAR1) GTP-binding proteins are involved in the formation and budding of vesicles throughout plant endomembrane systems. ARF1 has been shown to play a critical role in coat protein complex I (COPI)-mediated retrograde trafficking in eukaryotic systems, whereas SAR1 GTPases are involved in intracellular coat protein complex II (COPII)-mediated protein trafficking from the endoplasmic reticulum (ER) to the Golgi apparatus. The dysfunction of the endomembrane system can affect signal transduction, plant development, and defense. This chapter offers a summary of membrane trafficking system with an emphasis on the role of GTPases especially ARF1, SAR1, and RAB, their regulatory proteins, and interaction with endomembrane compartments. The vacuolar and endocytic trafficking are presented to enhance our understanding of plant development and immunity in plants.

Keywords: GTPases, ARF1 (ADP-ribosylation factor 1), SAR1 (secretion-associated RAS superfamily 1), COPI (coat protein complex I), COPII (coat protein complex II), membrane traffic, clathrin

1. Introduction

Endomembrane trafficking plays a crucial role for maintaining fundamental cellular functions (signal transduction, cellular homeostasis, etc.) and in response to environmental stimuli. The membrane trafficking pathways start from the endoplasmic reticulum (ER) then go through the Golgi apparatus to different destinations including vacuoles/lysosomes, endosomes, and the plasma membrane (PM) [1].

In plant cells the membrane trafficking system comprises three major trafficking pathways: the biosynthetic secretory pathway, the endocytic pathway, and the vacuolar transport pathway. (i) *The biosynthetic secretory pathway* transports newly synthesized proteins from the endoplasmic reticulum to the plasma membrane

and/or the extracellular space. (ii) *The endocytic pathway* functions in the recycling of PM-localized and extracellular factors between the PM and the endosomal compartments. (iii) *The vacuolar transport pathway* drives the transportation of newly synthesized protein to the vacuole (**Figure 1**) [3].

Each trafficking pathway is mediated by the following steps: (i) budding of the transport vesicle from the donor membrane, which is mediated by ARF/SAR1 GTPase (and coat proteins in many cases); (ii) transport and targeting of the transport vesicle; (iii) tethering of the vesicle by tethering proteins under the regulation of RAB GTPase and fusion of the transport vesicle to the target membrane mediated by soluble N-ethylmaleimide-sensitive-factor attachment protein receptors (SNARE); and (iv) recycling of the transport machinery components to the donor membrane (**Figure 2**).

In eukaryotic cells, small GTP-binding proteins involve the largest family of signaling proteins. The activation of small GTP-binding proteins (GTPases) is essential for vesicle formation from a donor membrane. Four main subfamilies have been identified in plants: (i) ADP-ribosylation factor (*ARF*)/secretion-associated RAS superfamily (*SAR*), (ii) *RAB*, (iii) Rho-like proteins in plants (*ROP*), and (iv) *RAN* [5–7]. Over the evolution of eukaryotic organisms, the conservation of GTPases explains their significance in cellular signaling processes [7–9]. Small GTPases serve as molecular switches that transduce signals by exchanging between the GTP- and GDP-bound conditions. Guanine nucleotide exchange factors (GEFs), GDP dissociation inhibitors (GDIs), and GTPase-activating proteins are regulators of small GTP-binding proteins.

GEFs activate small GTPases, which in turn interact with specific effectors to stimulate downstream pathways. GAPs trigger the intrinsic GTPase activity, thereby accelerating the inactivation of the GTPases' regulatory activity. GEFs convert the GDP-bound inactive form of the GTPases to the GTP-bound active form by stimulating the dissociation of GDP from the GDP-bound form. In the "active" state, the GTP-bound GTPases interact with various downstream effector proteins that execute diverse cellular functions. GTPases are inactivated through either the intrinsic capability of the GTPase to hydrolyze GTP to GDP + Pi or an interaction with another protein group, the GTPase-activating proteins (GAPs). These proteins

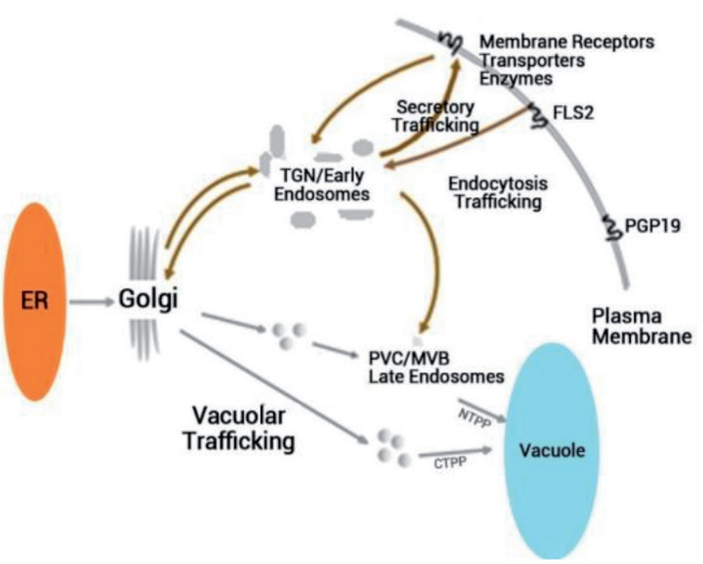


Figure 1.
The membrane trafficking pathways are grouped into three major categories: (i) the biosynthetic secretory pathway, (ii) the endocytic pathway, and (iii) the vacuolar transport pathway (modified from Inada and Ueda [2]).

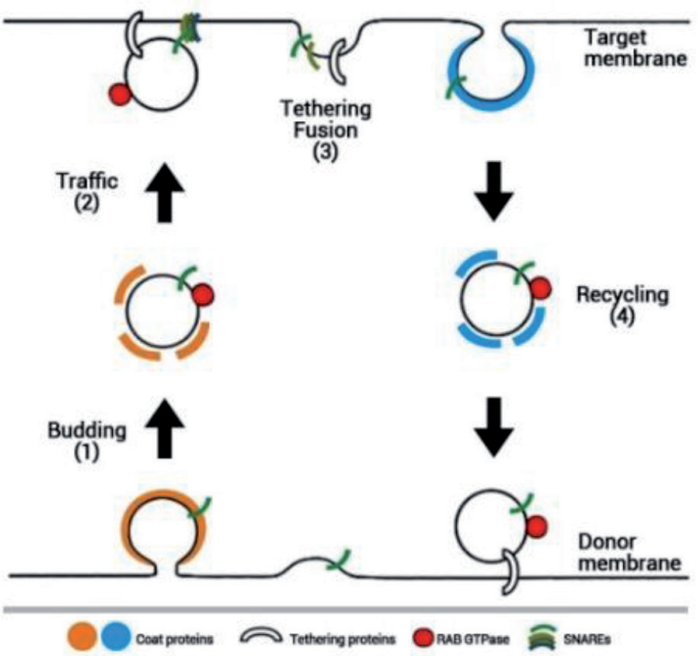


Figure 2.
The general machinery of membrane trafficking. Each trafficking pathway is mediated by the following steps: (i) budding of the transport vesicle from the donor membrane, which is mediated by ARF/SAR1 GTPase (and coat proteins in many cases); (ii) transport and targeting of the transport vesicle; (iii) tethering of the vesicle by tethering proteins under the regulation of RAB GTPase and fusion of the transport vesicle to the target membrane mediated by SNARE proteins; and (iv) recycling of the transport machinery components to the donor membrane [2, 4].

catalyze the hydrolytic activity of GTPases, which then return to the inactive state GDP-bound state [6]. The improvement of fluorescent protein-labeled GTPases and cargo molecules has enhanced the assignment of subcellular locations for these proteins within the endomembrane system.

The traffic between organelles is bi-directional. (i) Starting at the ER and leading toward the destination organelles (the forward trafficking) is called anterograde transport, and (ii) the reverse pathway is called retrograde transport.

2. Membrane trafficking pathways

2.1 The biosynthetic secretory pathway

2.1.1 Anterograde transport (forward trafficking)

2.1.1.1 ER-to-Golgi protein transport

The conventional trafficking pathway starts at the ER; protein synthesis and modification occurs and undergoes further modification [10]. Proteins leave the ER via COPII carriers to reach the Golgi. ER and Golgi compartments are closely associated with each other to ease the movement of cargo between them [11]. This ER-to-Golgi transport is termed "anterograde transport" and is mediated by COPII proteins, which are highly conserved in eukaryotes [12]. From the ER, synthesized proteins are exported to the cis-Golgi and are transported via Golgi stacks where protein modifications occur. Modified proteins are sorted into the extracellular space or storage and lytic organelles from the Golgi. In plants, proteins can also be sorted from the Golgi into the chloroplast [13].

The accumulation of secretory cargo, deformation of the membrane, and formation of transport vesicles are mediated by COPII. In mammalian cells and in most of the plant cell types, the ER and Golgi are in close proximity, and the COPII cycles on and off the ER with a fast turnover rate [14, 15]. COPII coat proteins are mostly distributed in the cytosol and concentrate at ERES that appear in association with motile Golgi stacks in plant cells. These proteins also accumulate in punctate structures that are not associated with the Golgi (**Figure 2B**).

The recruitment of COPII coat proteins involves SAR1 GTPase and its GDP/GTP exchange factor, SEC12 [16, 17]. The *Arabidopsis* genome encodes five genes for SAR1, seven genes SEC23, three genes for SEC24, two genes SEC13, and two SEC31 isoforms [18].

The assembly of COPII occurs at distinct sites on ribosome-free transitional ER (tER) or ER exit sites (ERESs) [19]. The cytosolic GTPase SAR1 is activated by the ER membrane-associated GEF SEC12, and then SAR1 associates with the ER lipid bilayer membrane, and after the COPII coat composed of the SEC23-24 and SEC13-31 heterodimer complexes is recruited [20–22]. The cargo recruitment complex involving SEC23-24 and SAR1 sorts transport and ER resident proteins [23, 24]. The COPII coat includes four proteins, assembled as an internal receptor/cargo-binding dimer of SEC23 and SEC24 and an outer cage dimer of SEC31 and SEC13. SEC16 is important for ER protein export by recognizing the COPII assembly region at the ERES [25]. The cargo selection is achieved by the SEC23/SEC24-SAR1 complex (pre-budding complex) [26]. This complex recruits SEC13-SEC31, which offer the outer layer of the coat and manage membrane deformation to constitute COPII vesicles. The SEC16 and SED4 are the other additional proteins for the COPII assembly. SEC16 comprises COPII coat component domains and has an important role as a scaffold for coat assembly [27]. SEC16 is a key organizer of ERESs in yeast and mammalian cells [28, 29]. The two encoded from *Arabidopsis* SEC16 genes resemble the human small isoform, and it was shown that they are important for ER export and tER organization in HeLa cells [29].

COPII is also involved in the physical deformation of the ER membrane that drives the COPII carrier formation [30]. SAR1-mediated GTP hydrolysis leads to COPII carrier un-coating and follows the exposure of the carrier membrane to fusion with the Golgi membrane [31].

In the GTP-bound conformation, SAR1 protein binds directly to the lipid bilayer which it does by an N-terminal amphipathic alpha-helix [32]. In the GDP-bound conformation, SAR1 binds membranes with lower affinity [25, 31].

The SED4 is responsible for the rate of ER-to-Golgi transport as an integral membrane protein at the ER membrane [32]. The deletion of SED4 causes to reduce the transportation rate of ER-to-Golgi in *S. cerevisiae* wild-type cells [33]. The SED4 and SEC12 have close homology with the cytoplasmic domain, but no GEF activity has been reported in *S. cerevisiae* [34].

It has been reported that SAR1 reduces the mechanical rigidity of the lipid bilayer membrane to which it binds in yeast [35]. Because of the ability of SAR1, it was suggested that membrane-bound SAR1-GTP decreases the energetic cost for the other COPII coat proteins (Sec13, Sec31, etc.) to generate curvature [35].

In *Arabidopsis*, three SAR1 homologs have been identified (AtSARA1a, AtSARA1b, and AtSARA1c). AtSARA1A and AtSARA1B have a 93% amino acid sequence identity [36]. The AtSARA1a expression level correlated with the secretion activity level from ER membranes. The AtSARA1a mRNA upregulation has been reported to cause the blockage of ER transport to the cis-Golgi compartment [37]. The COPII protein-encoding genes are ubiquitously expressed except SAR1 (At1g09180) and a SEC31 (At1g18830) isoform by microarray analyses [18]. Tissue

specificity was observed for the SEC31 isoform At1g18830, while all other genes appear to be ubiquitously expressed in all tissues and developmental stages [18].

SAR1 accumulation was observed to concentrate predominantly in crude ER fractions of *Pisum sativum* L. seedlings [38]. The COPII protein coat recruitment by SAR1p has been intensively studied [39]. In human development and disease, the SEC24 and SAR1 isoforms have specificity for the trafficking of selective cargo [40, 41]. In plant cells, specific amino acid sequences in the primary proteins affect the selective export of membrane cargo [42]. Diacidic sequence induces the accumulation of SEC24A to ERESs. The interaction occurs between the K channel KAT1, which contains the specific amino acid sequence in the cytosolic tail, and SEC24A [43, 44].

Different export signals in SEC24 proteins might lead to selective accumulation of cargo in COPII carriers in mammalian and plant cells. It was suggested that more efficient intracellular trafficking is likely achieved by cargo specialization of COPII isoforms in multicellular organisms [45]. **Figure 3** shows the basic diagram of the retrograde and anterograde transport in plant cells [47].

The COPII machinery has significant importance for ER-to-Golgi transport in the early secretory pathway in plants [48]. The retention of secretory cargo molecules or membrane proteins that cycle between the ER and Golgi apparatus leads to blockage of the ER export [14, 43, 48]. COPII machinery is involved in biotic and abiotic stress responses in plants. It has been shown that functional SEC24A is essential for systemic turnip mosaic virus movement by interaction in a signal specific manner with the N-terminal domain 6-kDa viral protein 6 K [49]. In high-temperature conditions, overexpression of SEC31A has been reported in the IRE1 mutant which leads to improvement of the male sterility phenotype in *Arabidopsis* [50].

2.1.2 Retrograde transport (reverse trafficking)

2.1.2.1 Retrograde transport and COPI

Of the 12 ARF isoforms, ARF1 is targeted to the Golgi and post-Golgi structures in plant cells. *Arabidopsis* ARF1 has been shown to be involved in different trafficking pathways including ER-Golgi traffic, vacuolar trafficking, and endocytosis and/or recycling [51, 52]. Arfs are divided into three classes and express six isoforms, namely, Arf1 to Arf 6 (with Arf2 being absent in human) in the mammalian system.

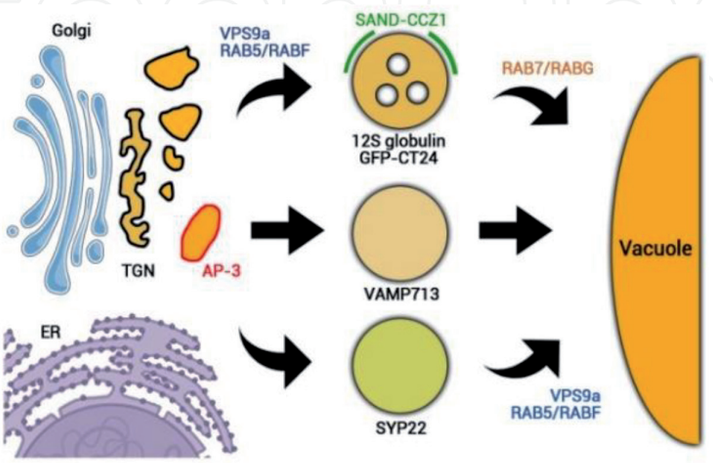


Figure 3.
Model of membrane trafficking to the vacuole in plant cells. The vacuolar trafficking pathway involves three trafficking routes in Arabidopsis *(i) depending on the sequential action of RAB5 and RAB7, (ii) AP-3-dependent but RAB5- and RAB7- independent pathway, and (iii) RAB5-dependent and AP-3-independent route (modified from Ebine et al. [46]).*

ARF1 manages ER-to-Golgi transport and Golgi-derived transport to the plasma membrane, depending on the COPI vesicle coat protein components [53, 54]. A large number of ARF in plants suggest the possibility for highly regulated vesicle trafficking [53]. Similar to other small GTPases, ARF GTPases cycle between an active state, when associated with GTP (membrane-bound form), and an inactive state when bound to GDP (predominantly cytosolic form).

In its GDP form, ARF1 is present in the cytosol and is recruited to the surface of Golgi membranes by a GEF. A SEC7-type GEF stimulates the binding of GTP to ARF1. This progression can be inhibited by the fungal metabolite Brefeldin A (BFA) in mammalian cells [55]. In the same system, the GDP-bound form of ARF1 interacts with p24 cytosolic tails [56]. The cytosolic ARF1 activation initiates COPI biogenesis. The GTP-bound form of ARF1 interacts with coatomer, which can also interact directly with the p24 cytosolic tails. In this manner, the p24 cytosolic tail can interact both with ARF1 and coatomer [56]. The conformational change of ARF1 occurs by the GTP/GDP exchange that may cause its dissociation from p24 cytosolic tails [56].

COPI vesicles mediate different transport steps, including ER-to-Golgi intermediate compartment transport, Golgi transport, and/or intra-Golgi transport (anterograde transport and/or retrograde transport) [57, 58]. Two types of COPI-coated vesicles form containing anterograde or retrograde cargo (KDEL receptor), and low amounts of Golgi enzymes have been reported to exist at the Golgi apparatus level [59]. COPI proteins are involved in transport along the endocytic pathway [60]. During the selective transport of vesicles, the coat proteins must distinguish between cargo and resident proteins of the donor organelle. *Arabidopsis* has single genes for γ-COP and δ-COP and multiple genes for the other COPI subunits [61]. COPI coatomer forms a coat around vesicles budding from the Golgi. Two different sizes of COPI (COPIa and COPIb) vesicles have been identified by multiparameter electron tomography analysis in *Arabidopsis* [62]. COPIa coats are retrograde transport vesicles, and COPIb vesicles are restricted to medial- and trans-cisternae and are involved for retrograde transport within the Golgi stack. The multiple copies of COPI in plants suggest the presence of different classes of COPI vesicles. The protein complex COPI coatomer is composed of seven subunits (α, β, β', γ, δ, ε, and ζ-COP). COPI represents approximately 0.2% of soluble cytosolic protein indicating their roles as unassembled precursors of COPI vesicles [63].

In intracellular transport, cargo transmembrane protein sorting at each step depends on the specific interaction of certain signals in their cytoplasmic tails with the correct coat proteins [64]. In yeast and mammalian cells, the cytosolic dilysine motif is essential for the ER localization of type I membrane proteins [65]. The two lysine residues must be in the −3, −4 (KKXX) or − 3, −5 (KXKXX) positions relative to the carboxy (C) terminus [65]. For ER localization, the lysine residue at the −3 position is the most critical residue [66]. In mammals, lysine residue mutations within the KKXX motif lead to the expression of reporter proteins at the cell surface [65]. In contrast, the same mutation leads to vacuolar transfer in yeast [67]. The p24 proteins have been suggested to function in Golgi-to-ER retrograde transport, as they contain cargo receptors on their luminal side and coatomer and/or ARF1 receptors on their cytoplasmic side in mammalian cells [68] COPI is necessary for recycling p24 proteins to the ER from the Golgi apparatus [69].

In general p24 proteins are only found in the ER. The binding of p24 proteins to COPI is mediated by dilysine motifs at the −3 and − 4 positions of p24 [69]. Up to 11 different p24 family members proteins have been identified in *Arabidopsis*. The p24 proteins appear to bind COPI with higher affinity than COPII. In the cytosolic tail of the *Arabidopsis* p24 (Atp24), the dilysine motif is important both for binding of coatomer subunits and ARF1 [70].

ARF1 has been shown to localize to Golgi and endosomes and regulate cell proliferation, cell elongation, and fertility, whereas ARF6 is associated with plasma membrane and important for actin remodeling and receptor endocytosis in plant cells [54]. The ARF6 overexpression was shown in breast cancer cells and also involved ERK signaling during invasion. On the other hand, the use of ARF1 protein as a prognostic marker for gastric cancer has been reported [71].

Low expression level of ARF1 (Q71L) mutant in tobacco mesophyll protoplasts has been reported to lead to wtp24 accumulation in the Golgi apparatus [69]. These studies verify the COPI-recycling mechanism can efficiently function in plants. COPI-binding dilysine motif-deficient p24 mutants are transported to the PVC and vacuole [69]. It was observed that p25 may function as an anchor for the p24 proteins in retrograde transport [69].

2.1.2.2 Intra-Golgi transport

Two different models for intra-Golgi transport were suggested: (i) vesicular transport and (ii) cisternal progression/maturation.

Between two different models, the direction of COPI vesicles is a critical distinguishing factor. (i) The *vesicular transport model* assumes that anterograde cargo is transported between static cisternae by coordinated budding and fusion reactions of anterograde-directed COPI vesicles [72]. Retrograde-directed COPI vesicles antagonize the continuous loss of material at the trans-Golgi. Therefore, two different COPI vesicles are involved for this model, one mediating anterograde transport and the other mediating retrograde transport. (ii) In the *cisternal progression/maturation model*, Golgi cisternae are stable compartments. In anterograde COPII vesicles, secretory cargoes are transported from one cisterna to the next, which finally disassemble at the trans-Golgi. Anterograde cargo would not leave the lumen, and resident Golgi proteins are maintained in the cisternae [72].

The COPI vesicles contain Golgi enzymes at a concentration that is up to 10 times higher than that found in the cisternae in animal cells [73]. The cisternal progression/maturation model does not clarify the presence of anterograde cargo within COPI vesicles or different anterograde cargo transportation rates in animal cells [74].

The "cisternal progression/maturation" model is the most widely accepted model for distinct and essential trafficking tasks in the Golgi. The stack of Golgi cisternae involves the historical record of progression from entry at the cis-face to exit at the trans-face [75]. The cargo molecules stay within a given cisternae as it passes, across a regular of seven locations within the Golgi stack on its way to the *trans*-face, and exit from the Golgi by transport carriers. In the cisternal progression, the newly arrived cargo in the Golgi exited with exponential kinetics rather than exhibiting a discrete lag or transit time [76]. Conserved oligomeric Golgi (COG) complex proteins accelerate the tethering of the vesicles to the target cisternae [77]. Resident Golgi proteins are assumed to recycle from older to younger cisternae. In retrograde COPI vesicles, transmembrane Golgi proteins may recycle. Peripheral Golgi proteins may recycle by dissociating from a given cisternae and then bind and combine to a younger cisternae.

2.2 Vacuolar trafficking

Plants have a complex vacuolar transport system different from that of mammalian systems by assigning evolutionarily conserved machinery to unique trafficking pathways. These pathways provide a fundamental basis for plant development at the cellular and higher-ordered levels [78]. Plants have evolved unique and complex vacuolar trafficking pathways compared with non-plant systems (**Figure 3**) [46].

The diverse functions of plant vacuoles are fulfilled through tight regulation of trafficking to and from the vacuoles, which involves evolutionarily conserved machinery components including Rab GTPases [79]. However, the basic framework of the Rab GTPase action is well conserved in eukaryotic cells [80]. Recent comparative genomic studies suggest that each eukaryotic lineage has acquired a unique repertoire of Rab GTPases during evolution [81] Autophagy-related and Golgi-independent transport from the ER to the vacuole is another example of such trafficking pathway [82]. This pathway also involves an exocyst subcomplex, although Rab and SNARE molecules associated with this pathway have not been identified thus far.

2.2.1 RAB GTPases

RAB GTPases constitute the largest family of small GTPases; 57 members are encoded in the *Arabidopsis* genome [83]. Based on their similarity to animal RAB GTPases, RAB GTPases are grouped into eight clades, i.e., RAB1/RABD, RAB2/RABB, RAB5/RABF, RAB6/RABH, RAB7/ RABG, RAB8/RABE, RAB11/RABA, and RAB18/RABC in angiosperms [84]. Plants also harbor a unique set of Rab GTPases partly characterized by diversification of the RAB5 group acting in endosomal/vacuolar trafficking pathways [85]. RAB7 is also proposed to regulate vacuolar traffic in plants [86]. In animal cells, a sequential action of RAB5 and RAB7 mediated by the effector complex HOPS [18] and a guanine nucleotide exchange factor for RAB7 consisting of SAND1/Mon1 and CCZ1 is responsible for the maturation from early to late endosomal compartments (**Figure 4**) [86].

Future studies on the molecular mechanisms of these plant-specific vacuolar trafficking pathways will reveal how plants have used unique vacuolar trafficking routes and how plants have developed their unique vacuolar trafficking pathways during evolution. The tethering of transport vesicles to the target membranes is mediated by the interaction between RAB GTPases and specific sets of tethering factors, many of which have been shown to be RAB effectors, which bind to specific RABs at the GTP-bound active state in yeast and animal systems [80]. After the tethering of transport vesicles by the tethering factors, soluble N-ethylmaleimide-sensitive-factor attachment protein receptors lead to the membrane fusion [80]. Tethering factors comprise long coiled-coil proteins and protein complexes called

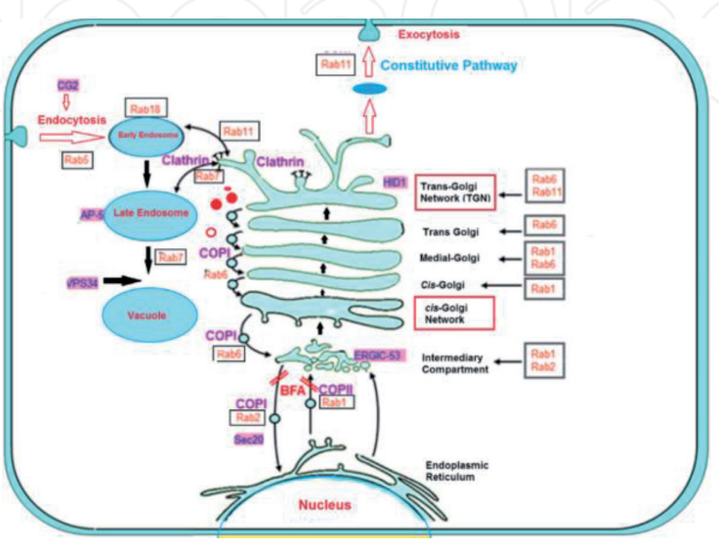


Figure 4.
RAB and the other proteins in intracellular trafficking (modified from Malaria Parasite Metabolic Pathways [47]).

tethering complexes. Each tethering step is mediated by a specific tethering complexes such as COG (functioning in retrograde trafficking within the Golgi), HOPS-CORVET (tethering with the lysosome/vacuole), and exocyst (functioning in the last step of the secretory pathway). In plants, homologous genes encoding these tethering complex proteins are also found, whereas some fibrous coiled-coil proteins are not conserved [84].

2.3 The endocytic pathway

Endocytosis in plant cells has an essential role for basic cellular functions and communication with the environment. Through the formation of closed membrane vesicles (60–120 nm), the uptake of extracellular molecules or the internalization of plasma membrane lipids and proteins is achieved [37]. During the life cycle of the plant, endosomes have vital importance for different processes including lateral organ differentiation, hormone signal transduction, root hair formation, embryo patterning, and plant immunity [36, 87–92]. Transportation of various cargo molecules involved in a broad range of physiological processes from the plasma membrane into the cytoplasm is achieved by this pathway. **Figure 5** shows the general organization of the endosomal trafficking system in plants [36].

As in animal cells, endocytosis in plant cells is mediated by (i) *clathrin-mediated* (CME) and (ii) *clathrin-independent pathways* (CIE) [93].

2.3.1 Clathrin-mediated pathway

In plants, the major endocytic mechanism depends on the coat protein clathrin. This pathway starts at the plasma membrane by clathrin-coated vesicle formation. CME is important for different physiological processes involving cell signaling, cell adhesion, nutrient uptake, developmental regulation, etc. The pathway starts by clathrin-coated vesicle formation at the plasma membrane; in the cytosolic parts of different transmembrane cargo molecules, the clathrin coat binds to specific binding sites. The recruitment of the pioneer proteins to the plasma membrane is ensured by the cargo molecules and enhanced by the initiation of an endocytic pathway. Clathrin involved in a variety of other processes such as the salt stress response, the defense response, cryptogein-induced signaling, and cytokinesis [94–96].

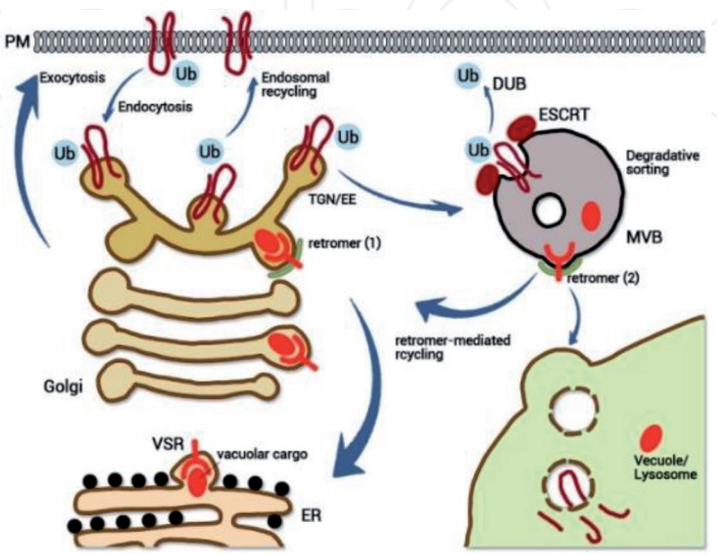


Figure 5.
The general organization of the endosomal trafficking system in plants. Current models of retromer localization and function place the retromer recycling complex in the TGN, in the MVB, or both [36].

Many viruses act as endocytic cargoes for the entry into the cell [97]. A large number of "coat-associated clathrin adaptor proteins" and "scaffold proteins" serve as cargo adaptors by interaction with specific cargoes. Short linear sequence motifs or covalent modifications such as phosphorylation or ubiquitylation in cargo proteins are important for cargo adaptor interactions [98]. Most cargo adaptors also interact directly with lipids and with other coat proteins. These complex interactions cause the initiation of clathrin coat assembly and its further expansion [99]. Binding of the clathrin coat proteins to the cytosolic sites of different transmembrane cargo molecules is essential for the cargo recruitment to the region of the plasma membrane that will form the vesicle.

Because of the difficulty of visualizing and manipulating, studies on cargo and lipids are very difficult [100]. The most widely studied one is the maintenance of polar localization of auxin transporters, namely, the PIN proteins. Polar localization of PIN proteins involves three steps: (i) nonpolar secretion, (ii) clathrin-dependent endocytosis, and (iii) polar recycling [91]. Dynamic regulation of PIN polarity provided with this mechanism is important in response to environmental and developmental stimuli [101, 102]. Mutations in Rab5 or clathrin cause endocytosis disruption and auxin-related developmental defects [91]. Endocytosis works as a negative feedback of the signaling process. After internalization, flagellin-sensitive 2 (FLS2) is targeted for degradation by ubiquitination which then terminates the signal transduction process [103, 104]. The polarly localized *Arabidopsis* boron transporter 1(BOR1), the tomato ethylene-inducing xylanse receptor (LeEIX2), and the iron transporter 1 (IRT1) are the other plasma membrane cargoes in plant cells [92, 105]. For accurate development and growth regulation, the equilibrium of cargo localization in the endomembrane system and the dynamic trafficking machinery is essential during the plant life cycle.

2.3.2 Clathrin-independent pathway

Several endocytic pathways that do not use clathrin-coated vesicles are involved in a CI pathway that was mediated by caveolae. Some of these pathways are constitutive, whereas others are activated by specific signals or by pathogens [106]. Furthermore, their mechanisms and kinetics of endocytic vesicle formation, associated molecular machinery, and cargo direction are different. Some members of the ARF and Rho subfamilies of small GTPases have been suggested to have key roles in regulating different pathways of CI endocytosis [107]. CI pathways are grouped in terms of those that use a "dynamin-mediated scission mechanism" (dynamin-dependent) and those that require other processes (dynamin-independent). A second characteristic is a contribution of small GTPases in several CI pathways [108].

2.4 The endomembrane system in plant development and plant defense

The dysfunction of the endomembrane system can affect plant development and signal transduction [109, 110]. The interaction between the actin cytoskeleton and the endomembrane system involves various aspects of plant cell function and development [111–113].

The actin cytoskeleton is involved for the dynamic feature of the ER [114]. Microtubules have been reported to also influence the mobility of the ER, but to a lesser degree or at a much slower rate [115]. ARF1 plays an essential role in normal cell growth, plant development, and cell polarity and is ubiquitously expressed in all organs of *Arabidopsis* [116, 117]. In de-etiolated pea shoots, ARF1 was concentrated mainly in the crude Golgi fractions [38]. Antisense RNA studies show that ARF also affects cell expansion and cell size in *Arabidopsis* [118]. BFA-visualized

exocytic trafficking defective1 (BEX1) has been reported to require for recycling of PIN transporters and auxin-mediated development in *Arabidopsis* [52]. BEX1 encodes ARF1A1C which localizes to the TGN/EE and Golgi apparatus. For normal venation patterning, polar auxin transport by PIN1 is required [118, 119]. Vascular network defective 4 (VAN4) is required for cellular growth and venation development [120]. VAN4 encodes a putative TRS120 subunit of the TRAPPII complex protein that functions as a Rab-GEF and/or tethering factor [121]. VAN4 is involved in polar localization and the recycling of PIN proteins. VAN3/SFC, ARF-GAP, and VAN7/GNOM ARF-GEF have been reported to regulate venation pattern by regulating the activity of the ARF GTPase [122].

Another relation with endomembrane trafficking and plant development was revealed by the continuous vascular ring mutants (COV1). Parker et al. have reported that the COV1 mutant is involved in ectopic differentiation of vascular *Arabidopsis* cells [123]. Afterward, COV1 has been reported as a TGN-localized membrane protein that is required for Golgi morphology and vacuolar protein trafficking and for the development of myrosin cells in leaves [124].

The ubiquitin-proteasome system (UPS) is important for the cytosolic and nuclear protein degradation, whereas certain proteins are degraded by autophagic degradation. De-ubiquitylating enzymes (DUBs) are essential for endosomal trafficking by affecting the fate of endocytosed cargo [125]. Endosomal sorting complexes required for transport (ESCRT) components are crucial for plant growth and development. Mutations of ESCRT or ESCRT-associated proteins in plants lead to ubiquitin accumulation, embryonic and seedling lethality, and misregulation of different signaling pathways, which can be associated with endosomal sorting defects in *Arabidopsis* [10, 126]. ESCRT mutations in *Arabidopsis* cause it to die at different developmental stages [127]. Under optimal growth conditions, autophagy seems to be unessential for plant life cycle. But a lack of autophagy can be the reason of the carcinogenesis and neurodegenerative diseases in the mammalian system [128].

Plants protect themselves with the help of small RNA-dependent immune system in response to biotic stress [129]. sRNAs are short regulatory RNAs (20–30 nucleotides) that silence genes with complementary sequences [130]. Against pathogens, several groups of plant sRNAs have important roles in plant defense. Plants send sRNAs in extracellular vesicles (exosomes) to the pathogen to silence virulence genes [130–132]. Host *Arabidopsis* cells have been shown to secrete exosome-like extracellular vesicles to deliver sRNAs into fungal pathogen *Botrytis cinerea*. These sRNA-containing vesicles accumulate at the infection sites of plant and are occupied up by the fungal cells. Transferred host sRNAs cause silencing of virulence-related genes critical for pathogenicity. Plant extracellular vesicles, mainly exosomes, have been reported to play a crucial role in cross-kingdom sRNA trafficking between *Arabidopsis* and the fungal pathogen *B. cinerea* [129].

3. Conclusions

The functional organization of eukaryotic cells requires the exchange of proteins, lipids, and polysaccharides between membrane compartments through transport intermediates. Transport from one compartment of this pathway to another is mediated by vesicular carriers, which are formed by the controlled assembly of coat protein complexes (COPs) on donor organelles. The plant endomembrane system is mostly conserved among eukaryotes but shows complex features. The structural organization of the endomembrane system is important for correct membrane trafficking and plant physiology. The trans-Golgi network (TGN) is a unique subcellular structure, which is a sorting center that integrates upstream cargoes

from secretory vesicles, the plasma membrane, and other organelles. The TGN functions as an early endosome compartment, adding to the complexity of sorting mechanisms in plant cells. Protein sorting at the ER-Golgi interface is important for the protein defects. However, the specificity and quantity of cargo sorting control mechanisms between endosome compartments are not completely clarified. More comprehensive studies on endomembrane trafficking will be necessary for the illumination of development, disease responses, hormone signaling (ABA and auxin), and plant immune system via sRNAs in exosomes in plant cells.

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Conflict of interest

The author declares no conflict of interest.

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