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Review article

Synergism of vesicle trafficking and cytoskeleton during regulation of plant growth and development: A mechanistic outlook

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ABSTRACT

The cytoskeleton is a fundamental component found in all eukaryotic organisms, serving as a critical factor in various essential cyto-biological mechanisms, particularly in the locomotion and morphological transformations of plant cells. The cytoskeleton is comprised of three main components: microtubules (MT), microfilaments (MF), and intermediate filaments (IF). The cytoskeleton plays a crucial role in the process of cell wall formation and remodeling throughout the growth and development of cells. It is a highly organized and regulated network composed of filamentous components. In the basic processes of intracellular transport, such as mitosis, cytokinesis, and cell polarity, the plant cytoskeleton plays a crucial role according to recent studies. The major flaws in the organization of the cytoskeletal framework are at the root of the aberrant organogenesis currently observed in plant mutants. The regulation of protein compartmentalization and abundance within cells is predominantly governed by the process of vesicle/membrane transport, which plays a crucial role in several signaling cascades.The regulation of membrane transport in eukaryotic cells is governed by a diverse array of proteins. Recent developments in genomics have provided new tools to study the evolutionary relationships between membrane proteins in different plant species. It is known that members of the GTPases, COP, SNAREs, Rabs, tethering factors, and PIN families play essential roles in vesicle transport between plant, animal, and microbial species. This Review presents the latest research on the plant cytoskeleton, focusing on recent developments related to the cytoskeleton and summarizing the role of various proteins

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in vesicle transport. In addition, the report predicts future research direction of plant cytoskeleton and vesicle trafficking, potential research priorities, and provides researchers with specific pointers to further investigate the significant link between cytoskeleton and vesicle trafficking.

1. Introduction

Membrane trafficking in eukaryotes maintains the endomembrane system and transports proteins to their sites of action in the cell. The endoplasmic reticulum (ER) transports newly produced proteins to appropriate subcellular compartments [1,2]. Transport vesicles transport cellular organelles such as the Golgi apparatus, vacuoles, ER, endosomes and lysosomes (Fig. 1). Vesicle transport involves a number of stages, that including tethering, budding, fusion, transport, and docking. The coat protein complexes I and II (COPI and COPII) are necessary for bidirectional membrane trafficking between the ER and the Golgi [3,4]. The initial interaction between the target membrane and the vesicles is facilitated by the tethering factors or complexes [5,6]. Many different types of vesicles move throughout the cell carrying different types of cargo used for transport across different membranes. The secretory pathway, characterized by the transportation of recently synthesized proteins into the plasma membrane (PM), and the extracellular space-bound pathway, originating from the endoplasmic reticulum (ER), are two significant mechanisms involved in the transport of membranes. The subsequent route is referred to as the endocytic pathway, which facilitates the recycling of proteins located on the outer surface of the plasma membrane (PM) and conveys internalized cargo towards the vacuole by means of endosomes [7]. Both processes involve the vesicles budding from the donor membrane, sequential transport, anchoring, and fusing of the vesicles towards the target membrane [8,9].

1.1. Vesicle trafficking

Most of the knowledge about vesicle transport in plants focuses on the model plant *Arabidopsis thaliana*. Like the animal and fungal systems, plants also rely heavily on vesicle-facilitated transport. Plants have been found to contain the crucial components, including the coat proteins, Rab, GTPases, and SNAREs. The plant secretory system has certain distinct differences from the yeast secretory system, such as the absence of the ER-Golgi intermediate compartment (ERGIC), the minimal mobility of the Golgi stacks, and the early

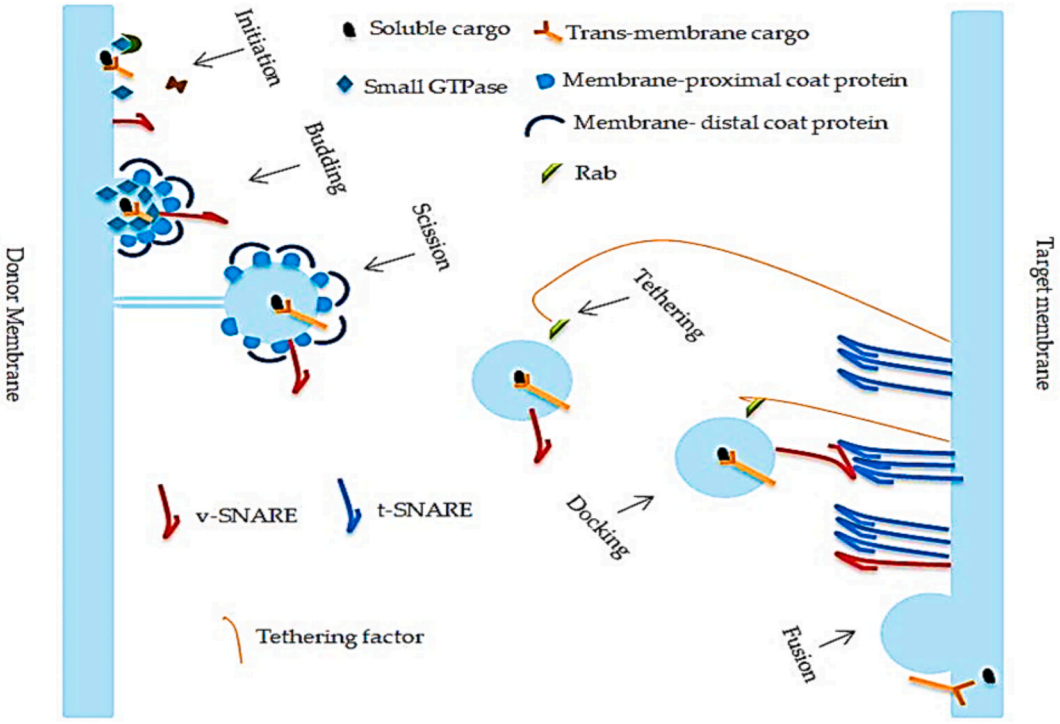

Fig. 1. [11]. Generalized mechanism of vesicle trafficking. The initiation of vesicle trafficking starts with the formation of the vesicle at the donor membrane. After that, the prosses of budding, scission, uncoating, tethering, docking, at last, the fusion. All steps of vesicle trafficking mediated via the help of specific members of large protein families, Rab GTPases as well as tethers, the designed vesicles transported after that tethered towards the target membrane. Finally, the completion of membrane fusion among the transport vesicles as well as the target membranes accomplished via the SNARE proteins.

endosome activity of the trans-Golgi (TGN) [10]. The secretory pathways often involve the presence of membrane-bound compartments that are interconnected through the use of vesicles, facilitating the transportation of molecules across these compartments. Membrane trafficking is crucial for eukaryotes because it makes compartmentalization, food absorption, and communication between cells and make the environment possible. Transporters, receptors, secreted enzymes, and peptide ligands that travel to extracellular space are only a few examples of the secretory traffic that newly generated proteins use to reach the plasma membrane (PM) from the endoplasmic reticulum (ER). Plant cells, like other multicellular eukaryotes, possess a multitude of proteins. The process of trafficking plays a vital role in facilitating the transport of proteins, lipids, and polysaccharides across various membrane-bound organelles. Endoplasmic reticulum (ER), plasma membrane, Golgi apparatus, and trans-Golgi network (TGN) are among the organelles that are bound by a single membrane layer [11]. The concept of "membrane trafficking" pertains to a cellular mechanism that establishes interconnections among various organelles through the use of vesicular and tubular membranous transport carriers. A variety of consecutive methodologies are employed in the process of membrane trafficking, commencing with the generation of cargo on the donor membrane through vesicles and tubules, subsequently leading to membrane fusion. These are made up of a particular set of regulatory machinery, such as coat protein complexes (CPSs), which helped with cargo selection, and dynamin-related GTPases (DRPs), which help with donor membrane tabulation and scission. These take part in the formation of tubular or vesicular carriers [10, 12].

1.2. Steps in vesicle trafficking

The fundamental processes that are necessary for all eukaryotic cells are brought about by the membrane trafficking system. This comprises the endoplasmic reticulum (ER), endosomes, and Golgi apparatus. Additionally, it comprises proteins that facilitate the transportation of cargo within vesicles between different cellular compartments and the plasma membrane. In particular, coat proteins (COPI, COPII), Sar1 or Arf (small GTPases), and adaptin complexes are involved in the membrane trafficking strategy of proteins [13]. Membrane trafficking employs diverse methodologies to facilitate the transportation of cargo, such as the utilization of transport vesicles that are bound by membranes. The transportation of proteins, macromolecules, and pathogens across membranes within distinct organelles is a common occurrence in intracellular processes. This system is very tightly controlled, ensuring that the proper cargo is delivered to the right location. Membrane trafficking involves three basic steps: Vesicle budding, tethering, and fusion (Fig. 1) [14,15].

1.3. Vesicle budding

The primary stage of vesicular trafficking often entails the participation of coat protein complexes. There are three distinct types of coated vesicles, namely COPI, COPII, and clathrin coated vesicles. The COPI and COPII are known as COP-coated vesicles (COP, coat proteins) or non-clathrin coated vesicles, function to carry cargo onward with a secretory pathway toward Golgi apparatus by budding from the ER. The third type of coated vesicles is clathrin-coated vesicles that involved in to the uptake of extracellular molecules from the plasma membrane [14,16]. The COPI contains F–COP and B–COP; subunits combine to form a coatomer. The F–COP comprises of four proteins (b-COP, g-COP, d-COP, and z-COP), and COP–B contains three proteins a-COP, b0-COP, and e-COP) [15].The COPII vesicles probable fuse directly with the Golgi in plants and yeast, which is situated near to ERES. Though, in the mammalian cells, COPII vesicles transport from ER toward Golgi similarly comprises a series of membranes, recognized as vesicular tubular clusters (VTCs) or the ER-Golgi intermediate compartment (ERGIC) [16]. The COPII coat comprises almost five proteins, namely Sar1, Sec23, Sec24, Sec13, and Sec31, that arranged successively. These organized utilizing an inner receptor or cargo-binding dimer of SEC23 and SEC24, besides that of an outer cage dimer of SEC13 and SEC31. The coated assembly started via stimulation of the small GTPase Sar1, the member of the Ras superfamily. The member of Ras superfamily, GTPase, by the activation of this coat assembly started [11,15]. The process of trafficking vesicles and tubules within the early secretory route and its representation also demonstrates the participation of many compartments in the transportation of proteins between the endoplasmic reticulum (ER) and the Golgi apparatus. Vesicles are able to travel towards the acceptor compartment with the assistance of cytoskeletal diffusion and track mechanisms. The enhancement of efficiency and accuracy in SNARE-mediated membrane fusion processes is achieved by the implementation of tethering mechanisms [15,17].

1.4. The tethering and fusion

The process of tethering involves the initial capture of the transport vesicle at a specific distance from the target membrane. Through this mechanism, the two membranes are brought into close proximity to one other. The enhancement of efficiency and accuracy in SNARE-mediated membrane fusion processes is achieved through the utilization of tethering mechanisms [7,15]. The tethering term is describing the early interface among the vesicle and target membrane, and tethers are proteins or protein complexes. In determining the specificity of vesicle targeting, together with small GTPases and Rabs, the tethers show a key role [18,19]. Membrane fusion is a process of significant importance, facilitated by the SNARE complex. This complex consists of distinct subtypes of SNARE proteins, namely t-SNARE proteins located on the target membrane, and v-SNARE proteins located on the vesicle membrane [19,20].

1.5. Role of tethers and SNAREs in vesicle transport

The tethering factor facilitates the first interaction between the transport vesicle and the target membrane, serving to connect the transport vesicle to the target membrane. Additionally, it plays a role in determining the potential for fusion between the vesicle and the target membrane [21]. Tethering factors interact with the corresponding transport vesicles to regulate membrane fusion, and these factors have a certain degree of conservation in plants, animals, and fungi. Extensive research has been conducted on yeast and mammals, while investigations on plants, particularly *Arabidopsis thaliana*, are very nascent [22]. The currently identified long-coil tethering factors include the localization of the Golgi apparatus and endosomes. The Golgin protein family about (20 members) located on the Golgi apparatus mainly includes Golgin-45, Golgin-97, Golgin-245, GM130, p115, GMAP-210, Goglin-84, TMF, GCC88 etc. Regulated by GTPases of the Rab and Arf1 families, it acts during the tethering process between the membrane on the Golgi apparatus and among the membrane and the cytoskeleton. Golgins attached to small GTPases includes Arf/Ar1 proteins, on the Golgi complex exterior via C-terminal GRIP/GRAB domains (Fig. 2) mainly positioned on endosomes are the EEA1, Rabaptin-5 and Rabiptin-4 proteins [6,23]. There are 9 types of multi-subunit complexes, these includes CORVET (class C core vacuole/endosome tethering), HOPS (homotypic fusion and protein sorting), GARP (Golgi-associated retrograde protein), VFT (Vps 53, it's a vacuolar protein sorting), TRAPPI (Transport protein particle), Ds11((Depends on SLY1-20), TRAPPII, TRAPPIII, COG (conserved oligomeric Golgi), and exocyst. The multi-subunit complexes (MTCs) can be categorised into two distinct groups: the spiral complexes, also known as CATCHR complexes, and the class C vacuolar protein sorting receptor (Vps) complexes. The Ds11, COG, and GARP proteins are members of the CATCHR protein family. Despite having low sequence homology, these three proteins share a conserved helix bundle structure. The HOPS and CORVET belongs to class C vacuolar protein sorting receptors, which regulates the process of trans-Golgi to endosome/lysosome tethering [6]. The HOPS and CORVET complexes facilitate distinct vacuolar trafficking pathways in plants through the coordination of various SNARE proteins and RAB GTPase. These complexes are specifically involved in the highly specialized endosomal and vacuolar transport pathways [24].

It has previously reported that in Arabidopsis about three different transport pathways function in vacuolar transport, the first one includes RAB5 as well as RAB7, while second needs RAB5 only, and the third pathway accountable for the transportation of SYP22 which resembles with CORVET, hence its proved that SYP22 needs CORVET function used for vacuolar localization [25]. Tethering complexes have the ability to interact with SNARE proteins, hence influencing the assembly process of SNARE complexes. Moreover, multi-subunit tethering complexes (MTCs) that undergo gradual construction demonstrate the capability to recruit and engage with SNARE proteins across several organelles via distinct subunits. The base has the potential to engage with t-SNARE concurrently on both the endoplasmic reticulum and Golgi apparatus, hence augmenting the stability of the assembly of the t-SNARE subcomplex. MTC plays a very important role in the process of recruiting SNARE subunits. The formation of t-SNARE sub complexes is an intermediate step in the formation of t-SNARE complexes. Recent research has demonstrated that Cog4 subunits play an active role in the process of assembling paired SNARE complexes on the Golgi apparatus, so effectively preventing the occurrence of incorrect assembly. The exocyst subunits sec6 and sec9 interacts to prevent the formation of the Sec-Sso1 t-SNARE complex before exocyst recruits to Sec1. The MTCs can also inhibit non-fused SNARE assembly or premature assembly of fused SNARE on biofilms [26]. Tethering factors serve a

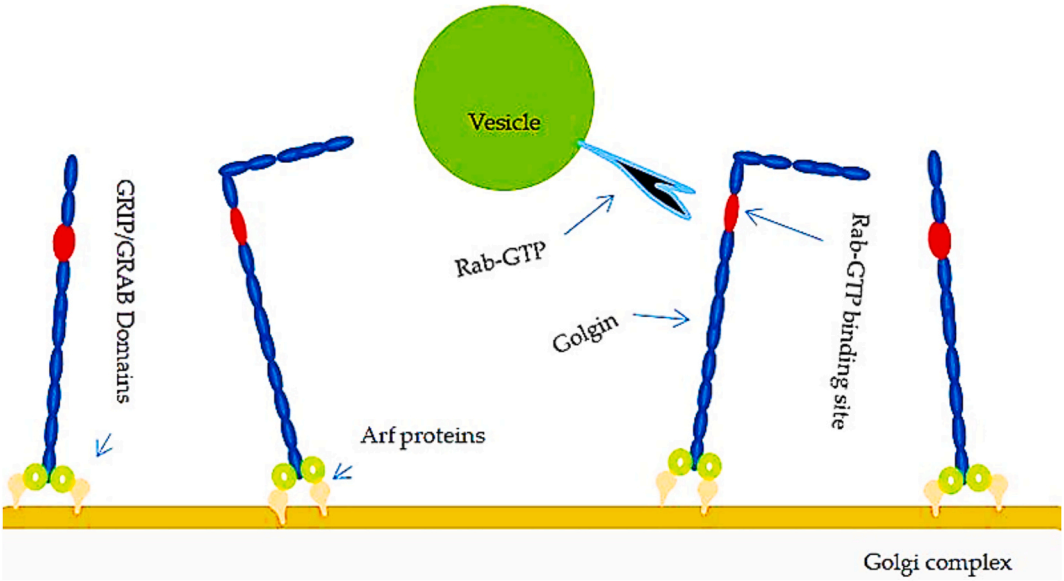

Fig. 2. [39,40]. The Rab-GTPase carrying via the captured Golgins vesicles. Golgins these are attached to small GTPases includes Arf/Ar1 proteins, on the Golgi complex exterior via C-terminal GRIP/GRAB domains. While the several binding locations within golgin, because of this there is opportunity via a succession of binding and unbinding actions. The vesicle contains suitable Rabs which may entered as well as reserved inside the golgin meshwork and after that transported towards right Golgi cisternae.

crucial function in facilitating the interaction between upstream SNARE proteins, hence aiding in the regulation of intracellular trafficking. Multi-subunit tethering complexes (MTCs) are responsible for regulating the attachment and fusion of the SNARE complex. The plant exhibits a notable association with TGN-mediated trafficking, which involves the participation of the TRAPP family and the Golgi-associated retrograde protein complex (GARP) [27]. In mammals and yeast, the TRAPPS gathers into properly well-described multi-subunit complexes and in mammals for retrograde trafficking as of endosomes toward Golgi required TGN-localized tetrameric GRAP [28].

The process of vesicle capturing is facilitated by tethering factors, which are characterized by their significant size and association with SNAREs. Tethering occurs at the initial contact between the donor and recipient membranes, representing a highly selective stage in trafficking. Additionally, tethering factors play a crucial role in facilitating vesicle docking and fusion. SNAREs are a class of integral membrane proteins that play a crucial role in facilitating the fusion of vesicles with their target membranes.SNAREs characterized as v-SNAREs arranged on the vesicle, and t-SNAREs arranged the target membrane. Once a vesicle comes near toward target, then v-SNARE on vesicle interacts by three t-SNAREs on the target membrane, making a hetero-tetrameric *trans*-SNARE complex that drives membrane fusion. SNARE proteins described as the intracellular membrane fusion that comprises conserved groups of membrane proteins. SNAREs are the soluble attachment protein receptor (SNARE); these are the important modules of trafficking machinery (Fig. 3) [21, 27]. The SNARE proteins can be classified into two distinct categories, namely R-SNAREs and Q-SNAREs. This classification is based on the specific amino acid present in the O-layer inside the helical SNARE domain. Furthermore, the distribution of R-SNAREs and Q-SNAREs is determined by their sequence similarity [22]. The RAB GTPase in eukaryotic cells function as a molecular switch in membrane trafficking via cycling among active GTP-bound and inactive GDP-bound conditions. The key role of the active RAB GTPase provokes various downstream responses, this contains the transport vesicles tethering towards the objective membrane, movement of organelles, as well as maturation of organelles [29]. SNARE plays a role in cell pathogen defense, homeostasis, and morphogenesis. The SNAREs, by physical interactions with K^+ channels, coordinate solute uptake. The best example of this is SYP121 and to assure their entrance at the plasma membrane [30].

The RAB GTPase in eukaryotic cells function as a molecular switch in membrane trafficking via cycling among active GTP-bound and inactive GDP-bound conditions. The active RAB GTPase plays a crucial role in eliciting several downstream responses, including the anchoring of transport vesicles to the target membrane, organelle motility, and organelle maturation [29]. SNAREs boost the regulation of biological processes, complexity, and fidelity, which facilitated via SNAREs [31]. The trafficking processes inside the endomembrane system of *Arabidopsis* involve the participation of several SNAREs. These SNAREs aid in various secretory and vacuolar trafficking phases. Notably, Arabidopsis utilizes a greater number of SNAREs compared to mammalian or unicellular systems, thereby enabling more efficient facilitation of these trafficking processes [32]. The process of SNARE complex building and membrane fusion in

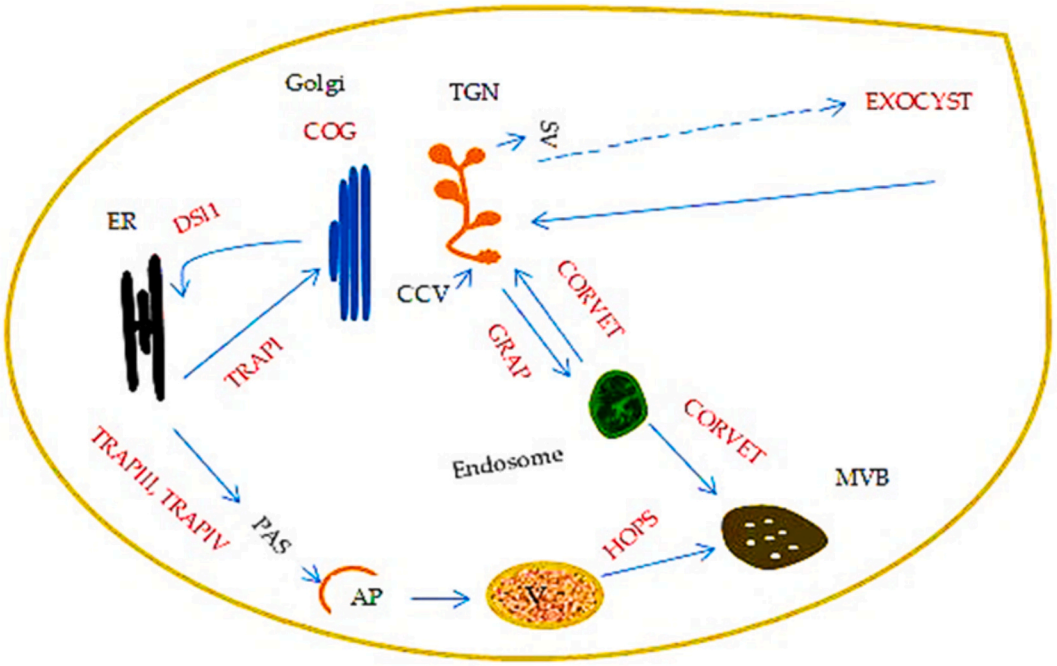

Fig. 3. [41,42]. The trafficking of multi-subunit tethering complexes in yeast. The above figure indicates that the ER to Golgi traffic mediated via the TRAPPl complex, while COG mediates intra-Golgi traffic and the TRAPPll leave from the Golgi. The TRAPPll as well as EXOCYST complex from trans -Golgi mediates secretion towards the plasma membrane. The HOPS complex mediates the tethering of vesicles intended for the PVC and the vacuole. The GARP, as well as the CORVET complexes, mediates the trafficking among the endosome,trans-Golgi, PVC, and MVB, while the DSL1 complex mediates the retrograde trafficking from Golgi towards the ER. The TRAPPlll, as well as TRAPPIV, play its role in autophagy or vacuolar targeting.

yeast involves the interaction of GTPases with tethering factors [33,34].

The transport protein particle (TRAPPI), complex mediates endoplasmic reticulum (ER) to Golgi traffic, while from intra-Golgi conserved oligomeric Golgi complex (COG), from the Golgi TRAPPII exit as well as from the trans-Golgi in yeast. The secretion toward plasma membrane is arbitrated via the TRAPPll as well as EXOCYST complexes (Fig. 3) [35]. The Golgi-associated retrograde protein (GARP) and class C core vacuole/endosome tethered (CORVET) complexes play a crucial role in facilitating the trafficking of endosomes between the trans-Golgi network and the multivesicular body (MVB). The homotypic fusion, protein sorting (HOPS) and TRAPPlll/lV complexes, these play a role in tethering of vesicle or autophagosomes destined for the vacuole [36,37]. The retrograde movement from the Golgi apparatus to the endoplasmic reticulum is enhanced by the Slyl (DSL1) complex [38]. The presence of TRAPl, TRAPPlll, TRAPPIV as well as CORVET still to be established in plants, while there is no evidence of TRAPPll role in plant endocytosis (Fig. 4). This part of review focuses mainly on tethering and SNAERs interaction during vesicle trafficking.

1.6. Cytoskeleton importance in vesicle transport

Recent studies are making sure that plant cytoskeleton plays a key function in the fundamental methods of intracellular trafficking, such as mitosis, cytokinesis, and cell polarity. The particular involvement of the cortical cytoskeleton in plant cell wall construction and morphogenesis has been investigated. Furthermore, it should be noted that plants possess distinctive features, like the advancement of pollen tubes through female reproductive tissue, the control of water loss through the actions of stomatal guard cells, and the presence of structures such as trichomes and root hairs. These characteristics are also influenced by the cytoskeleton [44]. The studies have shown that the cytoskeleton functions dynamically in modulating the plant's response to variations around the environment; against other organisms. The plant cytoskeleton has a significant role in cellular processes, identified as significant to morphogenesis, organogenesis, and development of the cell. All the objectives investigated using techniques referred to as a single-cell model. Presently, extant research indicates the presence of aberrant organogenesis in plant mutants, which can be attributed to inherent deficiencies in the organization of the cytoskeleton. The presence of microtubules and actin filaments in plant cells and organs contributes to the process of cellular imaging. Utilizing of current tools has further enhanced comprehension of this phenomenon.

The cytoskeleton plays a crucial role in maintaining the cellular structure of plant cells, as well as supporting intracellular signaling processes [45,46]. The specific role of the cytoskeleton depends on the manner in which the microtubules and microfilaments are organized and dispersed. It also depends on the modification of proteins that are directly associated with complete polymers and

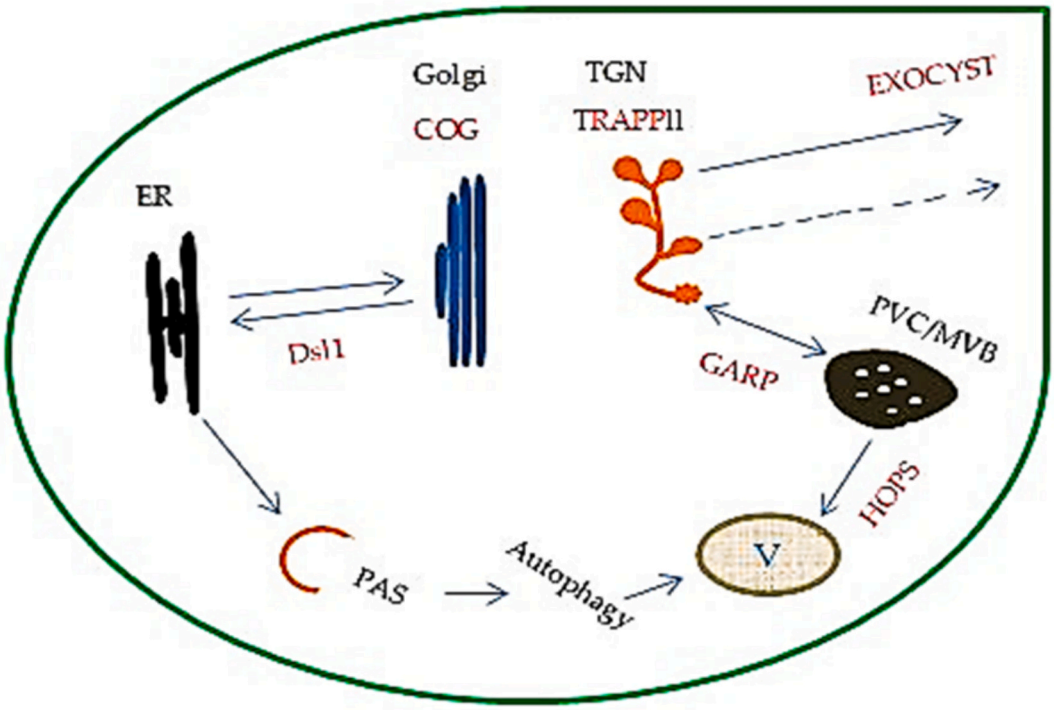

Fig. 4. [34,43]. Multi-subunit tethering complexes in plants. The ER to Golgi traffic mediated via the TRAPPl complex, while COG mediates intra-Golgi traffic and the TRAPPll leave from the Golgi. The TRAPPll as well as EXOCYST complex from trans-Golgi mediates secretion towards the plasma membrane. The HOPS complex mediates the tethering of vesicles intended for the PVC and the vacuole. The GARP, as well as the CORVET complexes, mediates the trafficking among the endosome,trans-Golgi, PVC, and MVB, while the DSL1 complex mediates the retrograde trafficking from Golgi towards the ER. Note The presence of TRAPl, TRAPPlll, TRAPPIV as well as CORVET still to be established in plants, while there is no evidence of TRAPPll role in plant endocytosis.

monomer subunits [47]. Actin filaments, also known as F-actins, and microtubules, referred to as MTs, are fundamental components of the cytoskeleton within eukaryotic cells. Both of these factors play a crucial part in the process of cell morphogenesis in tip-growing cells, as well as being relevant in diffuse-growing cell types. Moreover, they are also engaged in essential cellular processes, including cell division, directional cell expansion, organelle flexibility, and signal transduction [48,49]. The actin cytoskeleton involves in a cellular association such as vesicle trafficking, an association of actin networks, and cell wall assembly are combined and response on one another. The cortical microtubules (MTs) have a role in determining directionality and facilitating the advancement of plant cells. This is primarily achieved by guiding the positioning of newly formed cellulose microfibrils during cell wall production [50]. To discuss the role of microtubules, actin in plants with a correlation of vesicle trafficking makes the understanding clear.

1.7. Actin

The actin filaments function in intracellular trafficking in numerous eukaryotic cells, cytoskeletal elements, e.g., actin filaments, microtubules, function intracellular trafficking [50,51]. The reformation of actin filaments is assisted by small GTPases, such as the ADA ribosylation factor (Arf). Additionally, the group of endocytic vesicles requires Rho for docking purposes [52,53]. In addition, both directly and indirectly, the interplay of many actin-binding proteins plays a crucial role in the process of endocytosis [54]. Such as binding protein F-actin called Abp1, which relates to dynamin by SH3 domain, and dynamin2 relates right with cortactin. The cortactin in the plasma membrane act as an actin binding protein [55,56]. In the same way, actin plays a role in trafficking, function in the molecular scaffolding, making potency to collapse membranes, easing vesicles via cytoplasm. The current studies highlight association among the trafficking receptors that influences cell migration and actin dynamics [56,57]. The precise manner in which the actin-based cytoskeleton governs cellular physiological processes is a significant issue in the area that has yet to be fully elucidated.

Existing studies highlight the association between receptor trafficking, cell migration, actin dynamics, and actin filament function in pollen tube and root tip growth [56,58]. Actin filaments, especially apical filaments, are extremely active and vital for pollen tube growth. It has been shown that FIM5 enhances actin filaments, especially in the apical and control groups, toward the determination of polarized pollen tube growth. The actin cytoskeleton is progressively known to be a key controller of pollen tube growth [59]. The actin cytoskeleton is believed to play a crucial role in the process of root gravitropism. The phenomenon of gravitropism plays a crucial part in determining the directional growth of plants by responding to the gravitational forces. This process involves the disruption of amyloplast sedimentation and the facilitation of polar auxin transit through the regulation of PIN protein trafficking. Additionally, the ARP3/DIS1 protein plays a significant role in the gravitropic response of plant roots [60]. The H2S, auxin, and actin firmly regulate the root system development because of the intertwined signaling network between them. The H2S plays a significant part in moderating auxin passage via the actin-dependent process, and this case a change in root development in Arabidopsis [61]. The transit of auxin in Arabidopsis is facilitated by a potential allelochemical called narciclasine, which disrupts the intracellular trafficking of AUX1 and PIN proteins by interfering with the actin cytoskeletal network [62]. The arrangement of cargo proteins begins from Golgi toward vacuole, for that the actin filament dynamics and the appropriate functioning of adaptor complexes are needed (Table 1). The AP3M is the medium (μ) subunit of the AP3 complex, a significant role for the cargo sorting. This is because of the actin-binding activity of AP3M, which is mediated via AP3, and the stomatal closure of *Arabidopsis thaliana* is due to the proper function of AP3M in the regulation of F-actin dynamics [63]. The involvement of AtAIP-1 is crucial in the formation of a distinctive apical actin structure within the pollen tube. AtAIP-1 plays a critical role in the regulation of apical actin filament dynamics, functioning in conjunction with ADF [64].

Ethylene plays a great role, such as an upstream indicator of cGMP, besides mutually, these indicators stimulate pollen

Table 1
Examples of proteins involved in the plant's vesicle trafficking.

Proteins	Plant	Trafficking	Function	Reference
AP-2	*Arabidopsis thaliana*	trans-Golgi & endosome	Play a role in plant endocytic pathways, as well as floral organ development and plant reproduction.	[83]
EPSIN 1	*Arabidopsis thaliana*	TGN	Contribute to vacuolar trafficking and PM-derived immune responses.	[84]
MTV1 & NEV/AGD5	*Arabidopsis thaliana*	TGN &PVC	In plants, MTV1 and NEV/AGD5 are important effectors of CCV-mediated trafficking of vacuolar proteins from the TGN to the PVC.	[85]
TOL2/6	*Arabidopsis thaliana*	PM & Cytosol	Acts as ESCRT-0 in order to attract ubiquitinated cargos to the ESCRT pathway.	[86]
RabA1c	*Arabidopsis thaliana*	trans-Golgi	Play a role in cytokinesis, polar secretion and PM protein circulation	[87]
RabA2a	*Arabidopsis*	TGN & PM	Play a part in cytokinesis; vesicle secretion controls vesicle trafficking from the TGN to the PM; and K^+ homeostasis regulation.	[88]
RabE1c	*Arabidopsis*	Golgi &PM	Trafficking to the PM from the Golgi; play a role in the degradation of peroxisomal protein receptor peroxin 7.	[88]
RabF1/ARA6	*Arabidopsis thaliana*	Endosome & PM	Play a role in Endosome-to-PM trafficking pathway; may be involved in recycling and degradation.	[89]
RabF2b/ARA7	*Arabidopsis thaliana*	PVC & Vacuole	Contribute to cytokinesis, endocytosis, as well as vesicle trafficking between the PVC and the vacuole.	[90]
RabH1b	*Arabidopsis*	Golgi &PM	In hypocotyl growth, it influences cell elongation and cellulose production through regulate the transfer of cellulose synthase proteins among the Golgi apparatus as well as the PM.	[91]

germination, tube growth via regulation of F-actin and crucial to vesicular transport and cytoplasmic flowing [65]. In *Arabidopsis thaliana* the immune response positions of actin-dependent trafficking transports membrane integrated FORMIN4, in response this will strength the local cytoskeleton dynamics. The FORMIN4 is multi-layered and spatial element, temporally well-defined sequence of cytoskeleton [66]. The uneven supply of auxin can be attributed to a decrease in the accumulation of auxin efflux transporters known as PIN-FORMED (specifically PIN1 and PIN3). However, it is important to note that the placement of actin microfilaments in rpi1 root cells has undergone significant alterations, while the cortical microtubules remain unaffected. Recent research has shown evidence that disruptions in cellulose synthesis in rpil might negatively impact polar auxin transport, potentially due to alterations in F-actin association. This finding is of significant importance as it pertains to vesicle trafficking. Hence, the impact on auxin provision, as well as signaling and the facilitation of plant development by auxin, are significant factors to consider [67]. Isphenol A (BPA), apparently risky for humans, animals as well as in plants. The BPA is a ubiquitous environmental pollutant that affects pollen tube Ca (2^{+}) flux in *P. meyeri*, resulting in troublesome AF association, subsequent to irregular actin-dependent vesicle trafficking. Furthermore, it disrupts the deposition of cell wall components, and these discoveries offer a fresh comprehension of the mechanism behind the toxicity of BPA in the formation of pollen tube tips [68].

1.8. Microtubules

Microtubules (MTs) are crucial for eukaryotic cells utilizing division, modification in shape, and transport of organelles. Microtubules (MTs) are regarded as conserved polar polymers that serve as the primary constituents of the eukaryotic cytoskeleton and play a crucial role in several cellular functions [69]. Microtubules (MTs) and microfilaments are the primary mediators of growth and development, particularly in plants. The cytoskeletal structures undergo dynamic remodeling as a result of many morphological, environmental, and developmental cues [70]. These reforms assist common cellular functions; this includes identity and differentiation. Plant hormones considered as a key for cytoskeletal association and role in various developmental besides environmental perspectives [71]. The creation of plant shapes, uniqueness of meristems, and growth responses are regulated by the growth hormone auxin. This hormone is primarily synthesized in the shoot apex and subsequently transported towards the base, establishing a concentration gradient [72].

The plasma membrane-bonded transporter proteins mediate the auxin distribution in tissues and also passage auxin into and out of the cells. The best example of this is MTs in addition to CLASP in regulating sorting nexin1 (SNX1) vesicle morphology and activities, that relatives MT role toward auxin growth response. The interaction of microtubule-associated protein (CLASP) with the sorting nexin1 (SNX1) results in a link to microtubules and auxin transport through the reprocessing auxin efflux carriers PIN-FORMED2 (PIN2) in *Arabidopsis thaliana* [31,73,74]. The microtubules (MTs) mostly function in cell plate creation through cytokinesis; these also function in the regulation of localized secretion, PM of cellulose synthase. The positioning of functional organelles, as well as their morphology and structure, is facilitated by the microtubules [75,76]. Microtubules (MTs) play a key function in endosome trafficking and in exocytosis, especially in the central region of tip growth [77].

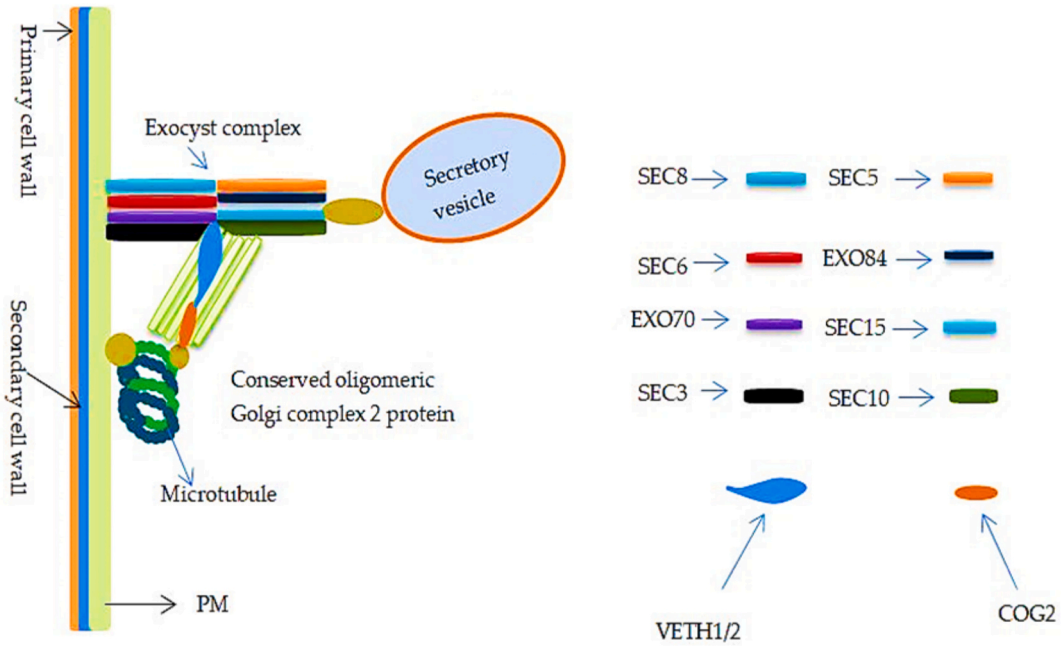

Fig. 5. [95,96]. The Cortical MTs describes the sites of SCW deposition of TEs. The interaction of COG2 and exocyst subunits forms a complex with VETH1/2 which is connected to cortical MTs. Therefore, the exocyst complex endorses secretory vesicle tethering at points of SCW deposition. Secondary cell wall (SCW), tracheary elements (TEs), oligomeric Golgi complex 2 protein (COG2).

Furthermore, microtubules (MTs) play a crucial role in facilitating the transportation of endosomes to vacuoles. A notable illustration of this phenomenon is observed when the disruption of MTs using nocodazole impedes the movement of endocytic vesicles towards vacuoles, as well as diverting endocytosed material towards the Golgi apparatus [78,79]. The satisfactory regulation of the exocytosis and endocytosis is curial for the pollen tube growth [80]. It investigated that, together with SYP21, the polymerization stage of microtubules is pretentious via different classes of drugs [81]. SYP21 was used as an indicator of prevacuolar compartments to illustrate the trafficking of prevacuolar compartments in the pollen tubes of *Nicotiana tabacum*. It has been verified that the transient alteration of pollen tubes by LAT52-YEP-SYP21 plays a crucial role in the distribution of prevacular compartments towards tubular vacuoles [82].

The recent investigation proved that the in *Arabidopsis thaliana* xylem subcellular localization of various exocyst subunits, and exocyst facilitated trafficking in TE development [92]. The modelling of secondary wall cellulose (SWC) and the thickening of tracheary elements (TEs) are significant factors in the process of shaping the places where secondary cell wall (SCW) deposition occurs in the context of microtubules (MTs) (Fig. 5) [93]. Through the MT contact the EXO70A1 subunit of the exocyst secretory vesicle tethering complex was concerned to be significant for TE progress [94].

1.9. Vesicle transport and the function of PIN proteins

The PIN gene family encodes a particular class of auxin-output transporter [97], Arabidopsis PIN1 was the first PIN gene to be identified, and since then, seven additional PIN genes, PIN2-PIN8, have been identified in the Arabidopsis genome [98]. To date, the PIN gene has been identified in 31 plant species, including brassica, glycine, leaf-cutting alfalfa, rice, poplar and maize [99–101]. The movement of auxins between and within cells in plants is facilitated by PIN proteins. Functional differences in PIN proteins depend on their different molecular structure and different subcellular localization [102].

All PIN proteins have a typical conserved hydrophilic loop (HL) structure with approximately 35 amino acids between the amino and carboxyl-terminal transmembrane domains (TD), potentially forming auxin transport channels. Depending on the size of the central HL, PIN proteins can generally be divided into two main subclasses, "long" and "short" PIN proteins. In Arabidopsis, PIN1-PIN4, PIN6 and PIN7 are long PIN proteins, and PIN5 and PIN8 are short PIN proteins. The long PIN protein is mainly located in the plasma membrane and acts as an auxin output vehicle that controls intracellular auxin output [103]. Some long PIN proteins have small "HLs", such as PIN6 in *Arabidopsis thaliana* localized to PM and endoplasmic reticulum [104], with five transmembrane domains, these long PIN proteins have unique intracellular HL between the amino and carboxyl terminals [105]. Short PIN proteins are located primarily in the endoplasmic reticulum and promote intracellular auxin homeostasis [106]. Based on the HL amino acid sequence, PIN proteins can be further split into seven subgroups because they have more conserved locations in the transmembrane region than HL [105].

Additionally, HL includes two variable domains (V1 and V2) as well as three conserved domains (C1–C3) [107]. The long PIN protein also has three conserved TPRXS sites that belong to the PINOID (PID) family kinase, D6PK (D6 protein kinase), and MAPK (mitogen-activated protein kinase). These sites contain T227/S1, T248/S2, and T286/S3 and this area, there are two more serine residues, designated S4 and S5 (Fig. 6). [106]. For PIN to be localized polarly, these phosphorylation sites are essential, two conserved cysteine residues on TD, specifically C39 and C560, influence the polar distribution of PIN2 in addition to the phosphorylation site [108]. In addition to the classification of "long" and "short" PIN proteins, "normal" and "non-normal" PIN proteins can be divided based on the highly conserved HC1-HC4 region in the central loop domain. PIN proteins with long central loops typically contain four highly similar conserved motifs, which are classified as canonical, and the rest are noncanonical [107].

In Arabidopsis, eight PIN proteins have different subcellular localization and play significant functions during auxin-regulated growth and development [110]. For example, plant auxin transport involved in PIN1 regulates organogenesis, flower bud formation, leaf morphology, vein formation, gravity response, and vascular development. PIN2 plays a role in controlling auxin tropic

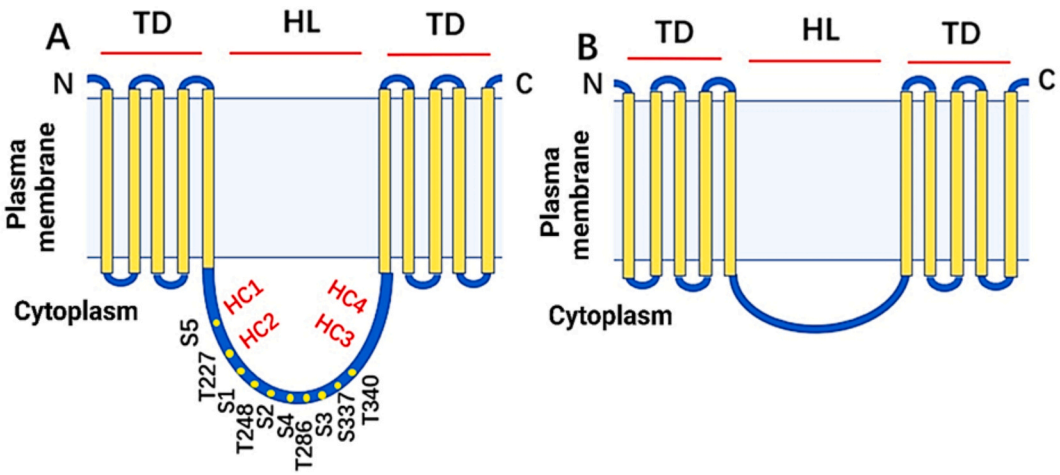

Fig. 6. [109]. Structures of long PIN proteins (PIN1–4, 6 and 7) (A) and short PIN proteins (PIN 5 and 8) (B).

transport and gravity and is mostly expressed in cortical and epidermal cells in the apical elongation area and during embryogenesis [111]. PIN3 is involved in early lateral root formation, root tip formation and maintenance, and gravitational and light responses [112]. In addition, PIN3 plays a role in the regulation of light protection and lateral root density induced by red and far-red light [113], similar to PIN3, PIN4 regulates photosensitivity and the growth of root tips [114]. In order to control the development of auxin gradients below the quiescent center, PIN4 is expressed in the meristem of adult roots [115]. By regulating the subcellular distribution of auxin, PIN5 located in the endoplasmic reticulum participates in a variety of auxin-related developmental processes, such as lateral root formation, cotyledon expansion, early embryogenesis, root and hypocotyl elongation [116]. PIN6 controls auxin transport and intracellular auxin homeostasis through dual localization of PM and endoplasmic reticulum. Additional research has revealed that the phosphorylation status controls the dual localization of PIN6 and PIN6 regulates the formation of lateral roots, the development and elongation of primary and lateral roots, root hair growth and apical dominance [117], and PIN6 also has a certain regulatory effect on plant pumping [104]. PIN7 is also associated with gravitational response, which negatively regulates radial growth in the root system [118]. PIN8 is an endoplasmic reticulum localization protein that regulates homeostasis of subcellular auxins and controls the development of pollen, male gametophytes, and sporophytes [119].

Additionally, advancements have been achieved in the functional examination of PIN proteins in the context of auxin transportation in plant species other than Arabidopsis. In the context of broken rice camelin, the PIN1 protein plays a crucial role in the facilitation of leaf development [120]. During maize embryogenesis, endosperm development, postembryonic feeding, and reproductive development, the ZmPIN1 protein is necessary for cell and tissue differentiation [121]. In tomatoes, SlPIN1 controls the buildup of auxin in the ovary and exfoliation zone to adversely restrict in vivo shedding [122]. The development of the fruit is unaffected by the joint silencing of SlPIN4 and SlPIN5, although the structure of the stem may change, resulting in a greater angle between the plant's base and the stem tip meristem [123]. In tobacco, NtPIN4 is induced by auxin, negatively regulating axillary bud growth [124].

In alfalfa, silencing MtPIN2/3/4 affects the formation of nodules, reducing the number of nodules [125]. Cotton PIN protein controls fiber growth, and *Arabidopsis thaliana* GhPIN1a, GhPIN6t, and GhPIN8 overexpression alters epidermal hair size and density [126]. The expression of OsPIN2 is commonly observed in the epidermal and cortical cells of rice roots, where it plays a crucial role in the regulation of both gravity response and root structure [127]. Overexpression of OsPIN2 leads to the absorption of aluminum ions by enhancing the vesicular transport capacity of the root tip [127]. In woody plants, overexpression of PtPIN9 in Populus brachyphyllum × Poplar promotes lateral root formation [128]. At the same time, overexpression of PtoPIN3a resulted in a shrunken leaf phenotype, indicating that this gene is involved in poplar leaf morphological construction [129]. Reduced MdPIN1b activity in apples causes Malling 9 root stock to become dwarfed [130]. In *Arabidopsis thaliana*, heterologous overexpression of MdPIN1 alters the root structure and promotes photosynthetic responses [131].

To facilitate the polar transit of auxins across cells, it is necessary for cells to not only collect auxins, but also to actively secrete auxins in a polarized manner. The localization of the auxin transporter PIN1 extends beyond the plasma membrane to include both recycled vesicles and endosomes [132], while auxin transport inhibitors do not affect auxin transport but rather inhibit the recovery cycle of PIN1 [133]. In vitro experiments have demonstrated active accumulation of auxin in plasma membrane-derived vesicles [134]. In vivo, the polar output of auxin can be accomplished through the formation of secretory vesicles formed by early endosomal production, capable of recirculation at the tip of the plasma membrane.

In addition, in order to enhance the transport polarity of auxin between cells, the cell may drive the output of auxin through exocytosis at one pole may be driven by the cell polarity based on the exocytosis of the vesicle cycle, and promote the input of auxin through endocytosis at the other pole of the cell, so as to enhance the transport polarity of auxin between cells. The influx of auxin is closely related to endocytosis that reverses the polarity of cells. Immunolocalization reveals that the actin filament microfilament backbone assembles into a longitudinal array that connects the apical and terminal ends of elongated cells, while auxin accumulates in vesicles near the plasma membrane [135]. Polar auxin transport is plant-specific and can lead to changes in auxin levels, thereby controlling organogenesis, development, and a series of physiological processes, such as vascular tissue differentiation, apical dominance, tropic growth, etc. Studies have shown that in Arabidopsis, the PAT process relies on output transporters (e.g., PIN family proteins) and input transporters (e.g., AUX1) [134]. PAT is precisely regulated by these two classes of transporters and mediated by the cellular transport system, regulating plant organogenesis, development, and root gravity. ARF (ADP-ribosylation factor)-GTPase is catalyzed by GEF to GTP-bound and binds to GDP under the action of GAP (GTPase-activating protein). Studies have shown that auxin output factors (such as PIN1) in *Arabidopsis thaliana* are regulated by the ARF-GEF factor GNOM, and GNOM-mediated vesicle transport contributes to auxin polar transport. ARF-GAP regulates auxin input factor AUX1 via vesicle transport system [136]. There is a vesicle transport-mediated feedback mechanism between ARF-GAP and GEF that regulates PAT by regulating auxin input and output, thereby controlling plant root development [137]. Both PIN1 and GNOM have been reported to be localized to endosomes, and GNOM mediates the sorting and transport of PIN1 from endosomes to the apex of the plasma membrane [138].

Overexpression of membrane steroid binding protein1 stimulated the root gravity response and the anti-gravity response of the hypocotyl in *Arabidopsis* seedlings, mainly due to enhanced redistribution of auxin in the curved part of the hypocotyl and root tip. MSBP1 overexpression inhibits the function of auxin polar transport inhibitor NPA, suggesting that MSBP1 promotes auxin polar transport. MSBP1 is localized in endosomes, and MSBP1 overexpression enhances vesicle trafficking. Seedlings overexpressing MSBP1 were insensitive to BFA treatment, and inhibition of MSBP1 expression led to a significant decrease in vesicle trafficking. Upregulation of MSBP1 expression does not affect the polar localization of PIN2, but stimulates PIN2 cycling and enhances the asymmetric redistribution of PIN2 under gravity. The findings of this study indicate that MSBP1 has the potential to augment the transport of PC2-containing vesicles, which are activated by gravity, hence promoting the redistribution of auxin. These results provide evidence for a potential connection between auxin and steroid-binding proteins [139]. Clathrin-mediated endocytosis is involved in the

internalization of PIN proteins localized by PM [140].

The internalization and transport of PIN proteins is regulated by developmental and environmental factors such as plant hormones, gravity, and light [141]. The application of synthetic auxin for a brief period has the capacity to inhibit the internalization of PIN protein in clathrin-mediated plasma membrane (PM) processes. As a result, this treatment leads to an augmentation in the abundance of PIN protein on the plasma membrane and subsequently enhances the output of auxin. Auxin is known to elicit the translocation of PIN1 protein from the basal to the lateral region of the plasma membrane (PM) in both the endothelial layer of the root and the middle column sheath cells [142]. Auxin also mediates the repositioning of PIN3 in the heavy response to terminate gravitational bending [143]. Prolonged auxin treatment leads to the degradation of PIN2 to the vacuole, mediated by the SCFTIR1/AFB (SKP-Cullin-F box [SCF], transport inhibitor resistant1/auxin signaling F-box [TIR1/AFB]) pathway. It has also been reported that auxins reduce the abundance of light-cured PIN2 on PM by inhibiting the transport of newly synthesized PIN2 to PM [144].

1.10. The correlation of vesicle trafficking and cytoskeleton

In plants, modern studies showed significant development in the considerate of the endomembrane system. There are various compartments of that system, several genes as well as proteins involved in membrane conversation. However, the major research studies demonstrate that the active interaction among membrane exchange protein controlled via the different ways in plants. The endomembrane trafficking, besides that movement of organelle in plants regulated via actin cytoskeleton, actually is a vigorous filamentous network that plays a key role in various cellular methods [145,146]. The vesicular trafficking routes are responsible for the transportation of components to various destinations. These ingredients originate from the endoplasmic reticulum. Despite the existence of connections between the endoplasmic reticulum and membrane compartments, other pathways are also utilized for the transportation of materials. Active organization in plant systems known as cortical endoplasmic reticulum; it associates the plasma membrane on the endoplasmic reticulum. The cortical endoplasmic reticulum in mammalian and fungal cells, play a role in transport of lipids and calcium inflow. The cortical endoplasmic reticulum are vital for endoplasmic reticulum and plasma membrane communication, the best example of this bridge is NET3C and VAP27.The NET3C is the class of actin-binding proteins and the VAP27 considered as connection site proteins in plant plasma membrane, endoplasmic reticulum of Scs2 yeast [147,148].

The current accessibility of consequently concluded genome sequences used for numerous eukaryotic organisms comprising *Arabidopsis thaliana* forms novel prospects toward address the part and purpose of these proteins on each well-defined step of vesicular trafficking. The discovery and characterization of diverse protein constituents play a crucial role in the identification of vesicular trafficking pathways (Table 2) [149,150]. The intracellular effort of membrane encircled material, is obligatory to the operational living cell, for that there is a determined method known as vesicular trafficking. The process of anterograde biosynthetic trafficking involves the encapsulation of biosynthetic cargo within a vesicle, which then proceeds to distribute from the endoplasmic reticulum to the Golgi apparatus, ultimately reaching the plasma membrane and vacuole. The process of vesicle formation through the inward

Table 2
Examples of different genes/proteins involved in plant vesicle trafficking and Cytoskeleton.

Gene/Proteins	Plant	Trafficking	Function	Reference
AtSEC22(*atsec22-4 mutant*)	Arabidopsis	ER & Golgi	Play important part in membrane trafficking and cytoskeleton dynamics during plant development	[170]
MAG2	Arabidopsis thaliana	ER & Golgi	Through its interaction with the ER-localized t-SNARE components SYP81/AtUfe1 and SEC20, it is involved in protein transport between the ER and the Golgi apparatus. The ER complex formed by MAG2 and the three MIP (MIP1, MIP2, MIP3) proteins is responsible for the effective transport of seed storage proteins.	[171]
SYP61/SYP121	Arabidopsis thaliana	Post-Golgi, PM	The SNARE complex is vital in the regulation of aquaporin transport through the plasma membrane.	[172]
cellotriose/CORK1	Arabidopsis thaliana	trans-Golgi	An early target in the phosphorylation pattern of proteins involved in cellulose synthesis and trans-Golgi transport.	[173]
ESCRT-III HvSNF7 & MVBs	Barley	ER & Golgi	To control seed storage protein buildup, which is becoming more important in health and nutrition issues	[174]
EXO70A1, Endosidin2 (ES2)	Arabidopsis		During normal root growth, the plant exocyst complex mediates constitutive dynamic trafficking of subsets of plasma membrane proteins.	[175]
ALA3 flippase	Arabidopsis	PM & trans-Golgi	Facilitating dynamic variations of subcellular trafficking rates that modulate the delivery of cargos, including PIN auxin efflux carriers, and lipids to the PM. These stages, in turn, allow for the modification of root development during plant adaptation to osmotic stress.	[175]
SEC15B	Arabidopsis thaliana	PM & Cytoplasm	Involved in cytokinesis and vesicle tethering to the PM.	[176]
EXO84B	Arabidopsis thaliana	ER, PM & Golgi	In the last phases of cytokinesis, it is required for cell plate maturation and cell plate to PM fusion; it influences CASP1 location in CSD and the secretion of several integral membrane proteins.	[177]
SEC6	Arabidopsis thaliana	trans-Golgi	SEC6 involved in the development of cell plates during pollen mitosis I, where it may have helped to anchor the vesicles prior to fusion.	[91]
TRS120, VAN4	Arabidopsis thaliana	Post-Golgi &TGN	Required for cell plate biogenesis during cytokinesis; PIN2 polarization; TGN exocytosis; and post-Golgi trafficking.	[178]

folding of the plasma membrane is known as endocytosis. During this process, the cargo is routed through several intermediary stages before ultimately reaching the vacuole for further processing or being transported back to the plasma membrane [11,151,152]. In plant endocytosis, significant findings indicated the presence of a lipophilic probe (FM). The FM functions in cell resistance, fluoresces luminously and solitary kinases that are capable of labeling the PM tracking endocytic internalization and movement of endocytosed vesicles [153,154]. The combined role of cytoskeleton, microtubules, as well as actin filaments, establishes to play a varied role in the growth and development of plants. The interaction of proteins with the microtubules and actin play possibly role in the cell wall assembly, these plant proteins include Kinesis, DREPP/MDP25, Formins, and Arp2/3 proteins [155]. The plant cell wall eases several events this includes cell growth, solute transport, protection, and intercellular communication [156].

Through guiding of cellulose synthase complex (CSC) microtubules direct the positioning of the cellulose microfibrils in the cell wall, the microtubules-associated proteins are components of the CSC, and this includes microtubule, CESA, as well as CSl1 [157,158]. Along with microtubules, the co-migration of the two proteins companion, the CC1 and CC2, directly interacted with microtubules and promoted in vitro microtubule polymerization [159,160]. The CESAs have detected in slight motile CESA compartments in accumulation to the Golgi apparatus and the plasma membrane, also recognized as MT-associated CESA compartments [161]. The recent studies proved that SmaCC/MASCs considered as a part of the TGN, which ease the transport of CESAs towards the plasma membrane [162]. The current understanding of polar vesicle trafficking within the trans-Golgi network is closely linked to the organization of vesicles originating from the Golgi apparatus [84]. The best example of this the PIN2 proteins in *Arabidopsis thaliana* apical plasma membrane root epithelial cells (vesicles enriched in sphingolipids) [163]. Actin filaments recognized to sustenance intracellular traffic of cytoplasmic organelles, vesicle trafficking, and cargo delivery [164].

The present studied proved that mutant act7 in *Arabidopsis* shows developmental phenotypes that are due to the faults in the transport of polar auxin, associating ACT7 which is a regulator of PIN1 and PIN2 expression [165]. The latest published work of cell wall releasing and expansion, among auxin signaling, and cell wall design. The cell wall synthesis machinery and stabilization of the microtubules, promoted via the microtubule-binding components of cellulose synthase complex (CSCs) [166], and the microtubule constancy which reprocessing of PIN2 directed by CLASP and SNX1 complexes [167]. The Kin7, separase complex stabilizes cortical MTs; it's important for the PIN2 polarization in the root cortex cells [168]. The auxin plays a key role in the transcription, transport, as well as the action of H + ATPase, K+ channels [169].

2. Future prospective and conclusion

In previous years, it seems that the knowledge of membrane trafficking has reached its exponential growth phase and moved into its stationary phase. The mechanism of vesicular trafficking, its generation, and regulation has been well studied, and there is nothing to discover, but the latest research and technology has proved that there is a lot to be discovered. The specific molecular mechanisms that regulate vesicle trafficking along the cytoskeleton in different types of plant cells. How the cytoskeleton and vesicle trafficking contribute to plant growth and development? particularly in response to environmental stresses such as drought or heat. The role of plant hormones in regulating vesicle trafficking and cytoskeletal dynamics. The potential for manipulating vesicle trafficking and cytoskeletal pathways to improve crop yields or enhance plant resistance to pests and diseases. Overall, there is a lot of exciting research being done in this area, and many opportunities for further exploration and discovery. The examination of the relationship between vesicle trafficking and the cytoskeleton in plants holds significant importance in the field of plant cell biology, since these two processes are fundamental in facilitating cell growth, development, and the ability to respond to environmental cues. The process of vesicle trafficking is accountable for the intracellular transportation of proteins, lipids, and various other substances, whilst the cytoskeleton serves the purpose of providing structural support and enabling mobility within the cell.

To further explore this field and enhance our understanding of these processes, researchers can employ various advanced technologies and techniques. Some of these include: (i) Advanced microscopy techniques: High-resolution imaging methods such as confocal microscopy, super-resolution microscopy (e.g., STED, PALM, STORM), and electron microscopy can provide detailed insights into the organization and dynamics of vesicle trafficking and the cytoskeleton in plant cells. (ii) Live-cell imaging: This technique allows researchers to monitor vesicle trafficking and cytoskeletal dynamics in real-time, providing a better understanding of the processes involved and their regulation. (iii) Genomic editing technologies: Techniques like CRISPR/Cas9 enable targeted manipulation of specific genes involved in vesicle trafficking and cytoskeleton organization. This can help researchers investigate the function of individual genes and their roles in these processes. (iv) Proteomics and Interactomics: Mass spectrometry-based proteomics and protein-protein interaction studies can help identify novel proteins involved in vesicle trafficking and cytoskeleton dynamics, as well as their functional interactions. (v) Computational modeling and bioinformatics: Integrating experimental data with computational models can help predict the behavior of vesicle trafficking and cytoskeleton systems under different conditions, enabling researchers to test hypotheses and design new experiments.

Through the utilization of these sophisticated technologies, scholars are able to get a more profound comprehension of the intricate dynamics between vesicle trafficking and the cytoskeleton within the context of plant biology. The acquisition of this knowledge has the potential to significantly contribute to the advancement of novel tactics aimed at enhancing plant growth, development, and stress tolerance. These findings hold promise for their practical applications in the fields of agriculture and biotechnology.

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CRediT authorship contribution statement

Muneer Ahmed Khoso: Writing – review & editing, Writing – original draft. **Hailong Zhang:** Formal analysis. **Mir Hassan Khoso:** Formal analysis. **Tika Ram Poude:** Formal analysis. **Sindho Wagan:** Validation, Formal analysis. **Tamar Papiashvili:** Formal analysis. **Sudipta Saha:** Visualization. **Abid Ali:** Formal analysis. **Ghulam Murtaza:** Visualization. **Hakim Manghwar:** Writing – review & editing. **Fen Liu:** Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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