



## The role of Rab GTPase in Plant development and stress

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### ABSTRACT

Small GTPase is a type of crucial regulator in eukaryotes. It acts as a molecular switch by binding with GTP and GDP in cytoplasm, affecting various cellular processes. Small GTPase were divided into five subfamilies based on sequence, structure and function: Ras, Rho, Rab, Arf/Sar and Ran, with Rab being the largest subfamily. Members of the Rab subfamily play an important role in regulating complex vesicle transport and microtubule system activity. Plant cells are composed of various membrane-bound organelles, and vesicle trafficking is fundamental to the existence of plants. At present, the function of some Rab members, such as RabA1a, RabD2b/c and RabF2, has been well characterized in plants. This review summarizes the role of Rab GTPase in regulating plant tip growth, morphogenesis, fruit ripening and stress response, and briefly describes the regulatory mechanisms involved. It provides a reference for further alleviating environmental stress, improving plant resistance and even improving fruit quality.

### 1. Introduction

Rab (Ras-like protein) is the largest subfamily of small GTPases. It can circulate between the GTP-bound active and GDP-bound inactive states in cytoplasm. These proteins are composed of approximately 200 amino acids (with 30–55% similarity) and have five conserved domains that can be divided into (1) guanine nucleotide-binding domains: G1, G3, G4 and G5; (2) effector binding domains: G2; and (3) membrane attachment domain: C-residues (Tripathy et al., 2021) (Fig. 1A) (Rutherford and Moore, 2002). In *Arabidopsis*, Rab GTPases are categorized into eight branches, namely RabD, RabB, RabF, RabH, RabG, RabE, RabA and RabC, which correspond to eight subfamilies in animals: Rab1, Rab2, Rab5, Rab6, Rab7, Rab8, Rab11 and Rab18. Among these, 26 Rabs belong to the AtRabA subclass, and the ARA6/RabF1 (Rab5) and RabA (Rab11) group possesses plant-specific features (Ebine et al., 2011). Studies have found that different Rab GTPases are localized to distinct organelles. In eukaryotes, Rab GTPases are specifically recruited to the cytosolic surface of intracellular membranes in a temporally controlled manner, and the C-terminal cysteine residues are

generally key for their association with membranes. Meanwhile, the mechanism of Rab GTPase-specific localization seems to be determined by the complex interaction of multiple factors, such as regulatory proteins, including guanine nucleotide exchange factor (GEF) and GTP enzyme activating protein (GAP) (Stenmark, 2009).

Rab GTPases function as molecular switches and are master regulators for intracellular vesicle trafficking. Plant cells are composed of many intracellular membrane structures, including Golgi apparatus, endoplasmic reticulum (ER), vacuole, trans-Golgi network/early endosome (TGN/EE) and multivesicular endosome (MVE). Vesicle transport is the fundamental system for protein, lipid and endogenous ion transport between organelles and plasma membranes. A single vesicle transport between donor and target organelle can be divided into four sequential processes: (1) vesicle formation starting from donor membrane, (2) vesicle motility, (3) vesicle binding with target membrane, and (4) vesicle tethering to acceptor membranes. Rab GTPase controls all aspects of intracellular vesicle trafficking by recruiting effector molecules in their active GTP-bound form (Fig. 2). One significant feature of Rab GTPase is the different intracellular localization patterns of the different members. For instance, AtRab5e (a member of AtRabA), located in the stroma and thylakoids (chloroplasts), participates in regulating the size, height and vesicle formation of plastid beads

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through interaction with its effectors (Karim et al., 2014). However, its homologous protein AtRab5c locates in the new compartment of young lateral roots (named geometric edges), regulating the cell geometry in the developing lateral organs by independently interfering with growth anisotropy and cytokinesis (Kirchhelle et al., 2016). Another characteristic of Rab GTPase is its redundancy. By changing the affinity of Rab GTPase for nucleotides, conservative activated mutants that bind to GTP and dominant-negative mutants that bind to GDP were formed to further explore the molecular function of Rab (Stenmark, 2009; Cai et al., 2015).

In fact, Rab GTPase typically interacts with specific regulators to fulfill its function. Rab effectors come in many forms and range from vesicle tethers to motors, kinases, phosphatases and various adaptor proteins (Sakurai et al., 2016). During vesicle transport, Rab GTPase is activated by GEFs and then inactivated by GAPs. This process is regulated by multiple factors. Firstly, GEFs can recognize specific residues in the switch regions and facilitate GDP release (Delprato et al., 2004). The high concentration of GTP (~1 mM) in the cytoplasm causes Rab to immediately bind to GTP once dissociated from GDP, resulting in the active form of GTPases. At present, some GEFs in plants have been identified and characterized, such as SAND/MON1-CCZ1 (Cui et al., 2014), Transport Protein Particle II (Kalde et al., 2019), monensin sensitivity 1 (MON1, Cui et al., 2014), calcium caffeine zinc sensitivity 1a (Pan et al., 2021) and VPS9a (Goh et al., 2007). However, compared with animals and yeast, most GEFs in plants are unidentified. Secondly, GDP dissociation inhibitors (GDIs) give an extra level of control of Rab GTPases. The GTPase activity of Rab is inherently low, and the effective hydrolysis of GTP requires the stimulation of GAP (Rittinger et al., 1997). Once GTP is hydrolyzed, the GDP-bound form of Rab will bind to GDIs, allowing it to dissociate from the membrane and return to the cytosol. Some RabGDIs have been reported to function in abiotic stress tolerance and (SchRabGDI1, OsGDI1, RabGDI $\alpha$ ) and fruit ripening (MiRab-GDI) processes (Liu et al., 2015). In addition, ubiquitination also can mediate Rab GTPase activation in animals. For example, the ubiquitin ligase-HACE1 can activate Rab11a by triggering ubiquitination of Rab11a-Lys145, thus promoting the recycle of the  $\beta$ 2-adrenergic receptor (Lachance et al., 2014). Furthermore, adenylylation and phosphocholination represent additional mechanisms for controlling Rab

activity. Research has shown that these process can modify the affinity of Rab:GDI, causing effective displacement of Rabs from GDI (Oesterlin et al., 2012). However, whether Rab GTPase in plants undergoes these modifications is worth further investigation.

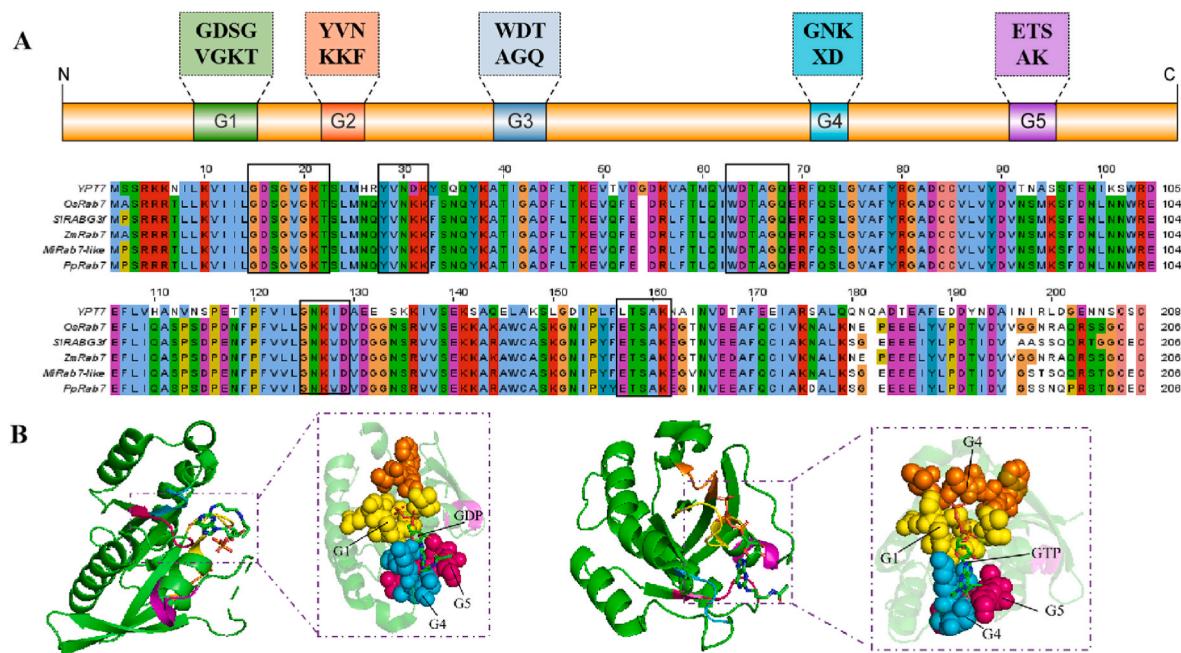
Compared with animals, higher plants appear to have followed a different evolutionary pathway from animal or fungal Rabs (Minamino and Ueda, 2019). Although our knowledge of Rab GTPase functions in plants is not as rich as in mammalian cells, significant progress has been made as demonstrated in the past two years. Studies using reverse genetic methods, mostly, but not entirely, by blocking the action of Rab GTPase, have revealed the central importance of Rab GTPase in plant life, whether in highly polarized cells, such as root hairs and pollen tubes, or in fruit ripening processes. Here, we provide a comprehensive overview of the role of Rab GTPase in plants.

## 2. Tip growth control

### 2.1. Pollen tube growth

Pollen tubes and root hairs exhibit characteristic polar cell expansion, commonly referred to as tip growth. During the reproductive process of flowering plants, pollen grains form a tube that grows through female tissue in a polarized manner, ultimately fertilizing the egg cells (Rounds and Bezanilla, 2013). This process is supported by the dynamic remodeling of the actin cytoskeleton and concentrated delivery of membrane, cell wall components and lipids (Cai et al., 2015; Li et al., 2021). Several reports have unveiled the important role of Rab GTPases in plant polarization and cellular morphogenesis (Table 1).

During plant tip growth, polarized delivery of secretory vesicles is the rate-limiting step, and depends on the fine regulation of molecular motor myosin XI and endomembrane properties (Vidali et al., 2010). Excitingly, studies have shown that Rab GTPase is an important factor connecting the plant endomembrane system and cytoskeleton (Orr et al., 2021). The RabE subfamily, the homolog of Sec4/Rab8, is involvement in anterograde transport to the plasma membrane from the Golgi, and is a general requirement for plant growth and cell division (Zheng et al., 2005). It localizes to sites of polarized secretion and co-localizes with



**Fig. 1.** Structure of Rab GTPase proteins. A: consensus amino acid sequences responsible for specific interaction with GDP/GTP and for GTPase activity. G1, G3, G4 and G5: guanine nucleotide-binding domains; G2: effector binding domains. B: spatial structure of Rab protein (from PDB database, Ypt); Left: the spatial structure of Rab combined with GDP; Right: the spatial structure of Rab combined with GTP.

myosin XI. Yeast two-hybrid assay uncovered a specific interaction between RabE and myosin XI, and the disrupt of this interaction results in a loss of polarized growth. This study provides a mechanistic link between RabE and polarized growth through an interaction with the molecular motor myosin XI (Orr et al., 2021).

Growing pollen tubes contain dynamic tubular vacuoles, and vacuolar biogenesis relies on vacuolar trafficking (Hicks et al., 2004). Hao et al. recently found that RabF/Rab5 can regulate the growth process of pollen tubes passing through the style by mediating vacuolar transport and affecting the homeostasis of the plasma membrane (Hao et al., 2023). In Arabidopsis, the genome encodes three RabF/Rab5 proteins, two canonical RHA1/RAB5F2a and ARA7/Rab5F2b, and a plant-unique ARA6/Rab5F1. Functional loss of canonical Rab5s compromises vacuolar trafficking of tonoplast proteins, vacuolar biogenesis and turgor regulation, and the functional loss of RHA1/RAB5F2a and ARA7-/Rab5F2b in Arabidopsis compromises endocytic and secretory trafficking at the plasma membrane (PM), causing the enhanced deposition of cellulose or polysaccharides, cytosolic acidification and failure of pollen tubes to grow through style and thus impairing male transmission (Hao et al., 2023). RabG3f/Rab7, which localize to prevacuolar compartments (PVCs) and tonoplast, also play an important role in pollen tube growth by mediating the fusion between PVC and vacuoles (Cui et al., 2014). In Arabidopsis, the MON1-CCZ1 complex is recruited to the PVCs by active ARA7/RabF/Rab5 protein and then serves as a GEF complex activating RabG3f/Rab7. Dominant-negative RabG3f/Rab7 mutations show that its function is crucial for maintaining the tapeta programmed cell death, thereby ensuring the successful germination of pollen and the subsequent growth of pollen tubes (Brillada et al., 2018).

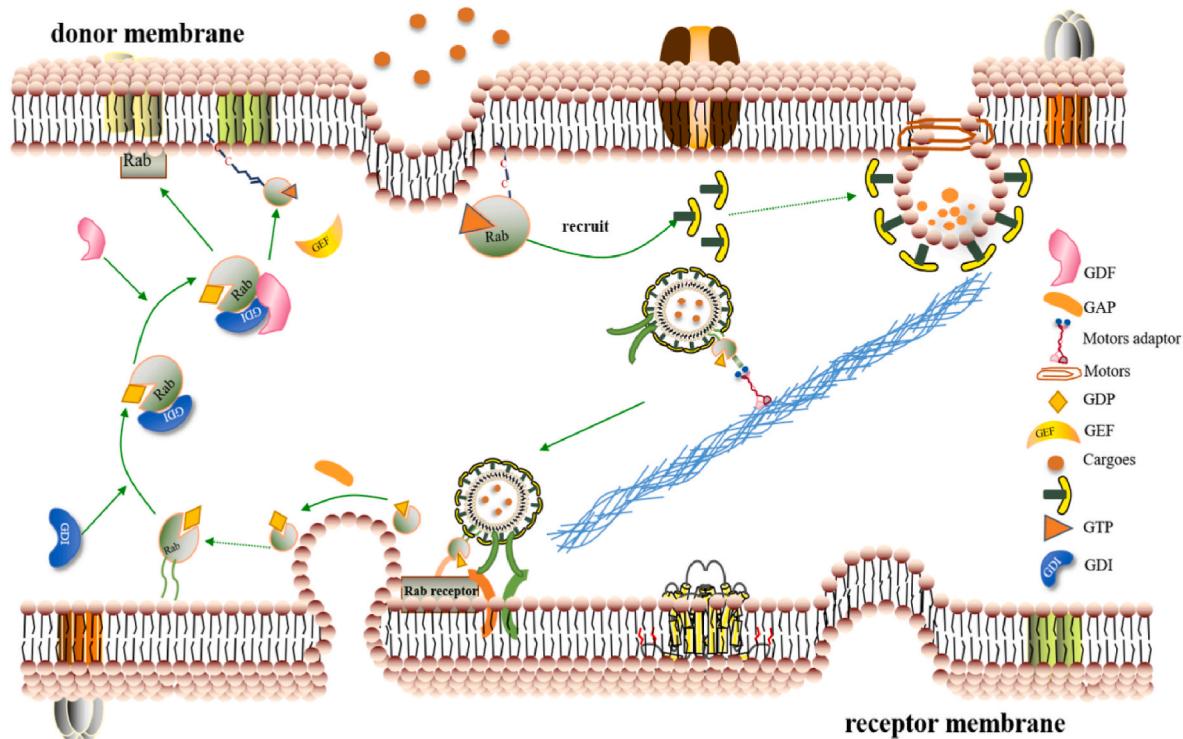
In addition, there are also some Rab GTPases that play important roles in pollen growth and for which the transport pathways they regulate is unknown. For example, RabA4d from Arabidopsis is the only member of RabA4 subfamily to be expressed in pollen. It interacts with PI4K $\beta$ 1 to maintain the direction and rate of pollen tube growth

(Antignani et al., 2015). Loss of RabA4d function resulted in the formation of bulges in pollen tubes with a reduced rate of growth, displaying altered deposition and/or modification of pectin (Szumlanski and Nielsen, 2009), and adenosine triphosphate 3 (ALA3), the effector of RabA4d, can regulate the specific distribution of RabA4d in pollen tubes by establishing potential phospholipid signaling through the formation of phosphatidylserine. The loss of ALA3 function leads to the mislocalization of RabA4d at the top of pollen tubes, resulting in a substantial increase in pollen tube width (Zhou et al., 2020). In Arabidopsis, the RabD subfamily has four members, AtRabD1, AtRabD2a, AtRabD2b and AtRabD2c. Among them, AtRabD2b and AtRabD2c are highly expressed in pollen, and their RNA accumulation levels are negatively correlated with the process of starch synthesis (Wang et al., 2012). *Arabidopsis* double-mutant plants displayed a short siliques and have many non-fertilized ovaries phenotypes because of the collapsed pollen, shorter pollen tubes and swollen tips. However, it has not been confirmed whether AtRabD2b and AtRabD2c located in Golgi play a role in vesicular transport between the endoplasmic reticulum to the Golgi (Peng et al., 2011).

## 2.2. Root hair growth

Root hairs are formed by root epidermal cells. Their development is divided into four stages: cell fate specification, initiation, tip growth and maturation (Gilroy and Jones, 2000). These processes involve a balance between the directed delivery of proteins and cell wall building blocks from post-Golgi compartments to the cell apex, as well as the loosening of local cell walls and the retrieval of surplus membranes (Chin et al., 2021).

The function of Rab in root hair growth has been confirmed (Table 1). AtRabA4b shares the similarity sequence with MtRab11G and Pra3, specifically located at the tips of growing root hair cells and disappearing in mature root hair cells. Tip-localized RabA4b compartments



**Fig. 2.** Schematic representation of Rab-dependent trafficking pathways. Active GTP-bound Rab can recruit a sorting adaptor to sort a receptor into a budding vesicle, then active Rab GTPases can mediate vesicle transport along actin filaments or microtubules (collectively referred to as cytoskeletal tracts) by interaction with motors; Rab GTPases can mediate vesicle tethering by interact with tethering factors. After membrane fusion/exocytosis, GAP catalyzes the hydrolysis of GTP to GDP, and guanine nucleotide exchange factor (GEF) converse the GDP-bound Rab into the GTP-bound form.

**Table 1**

Rab GTPase and its effectors involved in regulating various plant life activities.

	Rab GTPases	Location	Effector	Function	Species	References
Pollen tube tip growth	RabA4d	pollen tubes tips	PI4K $\beta$ 1、ALA3	Changing the components of cell wall deposition	Arabidopsis	Szumlanski and Nielsen (2009); Zhou et al. (2020)
	AtRabD1	pollen tubes tips		Positively regulates autophagosome biogenesis	Arabidopsis	Wang et al. (2012); Peng et al., 2011
	AtRabD2a	pollen tubes tips		Positively regulates autophagosome biogenesis	Arabidopsis	Wang et al. (2012); Peng et al., 2011
	AtRabD2b	Golgi		Affects starch synthesis	Arabidopsis	Wang et al. (2012); Peng et al., 2011
	AtRabD2c	Golgi		Affects starch synthesis	Arabidopsis	Wang et al. (2012); Peng et al., 2011
	PpRabE14 ARA6/RabF1	sites of polarized secretion punctate organelles	pMyoXI、AtMyoXI-K VPS9a、PLANT-UNIQUE RAB5 EFFECTOR 2 (PUP2)	Support plant growth and development Maintain the endocytosis and secretion transport of the plasma membrane		Hao et al. (2023)
	ARA7/RabF2b	punctate organelles	VPS9a、CORVET、HOPS	Critical for proton homeostasis that influences the dynamic organization of actin MFs and membrane homeostasis at the PM.		Hao et al. (2023)
Root hair tip growth	RabG3f/Rab7	prevacuolar compartments (PVCs) and tonoplas vesicles appearing from TGN and this Rab GTPase	MON1-CCZ1、CORVET、HOPS	Mediate the fusion between PVC and vacuoles		Brillada et al. (2018)
	RabA4b	Root Hairs	PI4K $\beta$ 1、PI4K $\beta$ 2ALA3	Regulate the transport of polarized membranes in root hair cells	<i>Phaseolus vulgaris</i>	Kang et al. (2011)
	RabA2			Required for the rhizobial-activated signal transduction pathways	<i>Phaseolus vulgaris</i>	Blanco et al. (2009)
Shape of plant organs	NbRabE1	young tissues containing actively dividing cells and in stomata guard cells		Function in stomata guard cell division	<i>Nicotiana benthamiana</i>	Ahn et al. (2013)
	RabA5c	membrane vesicles lying immediately beneath the plasma membrane at cell edges		Meets a requirement to specify this cellular spatial domain during organogenesis	Arabidopsis	Kirchhelle et al. (2016)
	RabC1	young stomata	SEIPIN2、SEIPIN3	Required to regulate lipid droplet dynamics and lipid metabolism	Arabidopsis	Ge et al. (2022)
	RabE1d	Golgi apparatus and plasma membrane of mesophyll cells	PIP5K2	Play a fundamental role in the secretion of extracellular matrix molecules	Arabidopsis	Speth et al. (2009)
	RabH1b	Golgi		Maintain Golgi morphology and modulating the trafficking of cellulose synthase complexes from endosomal compartments to plasma membrane	Arabidopsis	McFarlane et al. (2014)
Biotic stress respond	PvRabA2	root nodule		Function in the biogenesis of the peribacteroid membrane		Cheon et al. (1993)
	Rab11f	in the nodules of <i>Medicago sativa</i>		Function in the biogenesis of the peribacteroid membrane	<i>Medicago sativa</i>	Schiene et al. (2004)
	RabG3b	stomatal	NETWORKED	Involved in FLS2 triggered guard cell actin reorganization	Arabidopsis	Hawkins et al. (2023)
	PagRabE1b			Positively regulates autophagosome biogenesis	Poplar	Liu et al. (2021)
	OsRabA/OsRab11	widely expressed in plants	OsGAP1、OsGDI3 和 OsOPR8	Regulate vesicular transport from the TGN to the PM or vacuole	<i>Oryza sativa</i>	Li et al. (2011); Hong et al. (2013)
	RabA4c	plasma membrane	PMR4 (callose synthase)	Regulate the biosynthesis of the callose and enhances the deposition of callose	Arabidopsis	Ellinger et al. (2014)
Abiotic stress respond	AtRabG3e	induced during programmed cell death in leaves		Increase tolerance to salt and osmotic stresses	Arabidopsis	Mazel et al. (2004)
	ARA6/RabF1 RabA1a, RabA1b, RabA1c, RabA1d AhRabG, OsRabG/ OsRab7 and OsRabA/OsRab11	endosomes		Salinity stress response Required for salinity stress tolerance	Arabidopsis	Ebine et al. (2011) Asooka et al. (2013)
	PtRabE1b	Root		Responsive to abiotic stresses	Rice	Sui et al. (2017); Chen and Heo. (2018)
	RabA2b	plasma membrane		Maintain great root growth status under salt stress Improve drought resistance	Arabidopsis	Zhang et al. (2018)
	RabE1c	in guard cells	Pyrabactin Resistance1-like protein (PYL)	Acting as a positive regulator in ABA signaling and drought stress response	Arabidopsis	Ambastha et al. (2021)
	CaRabC	leaves		Response to salinity stresses	Chickpea	Zhao et al. (2008)
	ZmRabD1 and ZmRabD2c	Endoplasmic reticulum	Prenylated Rab Receptor 1, ZmPRA1, C1	Response to heat stress	Maize	Khassanova et al. (2019) Xie et al. (2022)

(continued on next page)

**Table 1 (continued)**

	Rab GTPases	Location	Effector	Function	Species	References
Fruit softening process	RabE1b	plastids		Crucial for protein translation	Arabidopsis	<a href="#">Li et al. (2018)</a>
	SlRabA11a	fruit		Regulate fruits softening process	Tomato	<a href="#">Lu et al., 2001</a>
	RabA3 and RabA4	fruit		Regulate fruits softening process	Mangoes	<a href="#">Lawson et al. (2020)</a>
	VvRabA	fruit		Regulate fruits softening process	Vitis vinifera	<a href="#">Abbal et al. (2008)</a>
	PpRABA1-1, PpRABA2, PpRABD2-1, PpRABD2-2, and PpRABC2	fruit		Regulate fruits softening process	Peach	<a href="#">Falchi et al. (2010)</a>

are dependent on the integrity of the F-actin cytoskeleton ([Preuss et al., 2004](#)). Further exploration found that RabA4b is localized in the vesicles appearing from TGN and that this Rab GTPase plays an important role in regulating the transport of polarized membranes in root hair cells ([Kang et al., 2011](#)). As part of this regulation, AtRabA4b exhibits the ability to recruit lipid kinases PI4K $\beta$ 1 and PI4K $\beta$ 2, and these proteins coordinate to regulate polarized expansion in root hairs. When the polarization position of AtRab4b changes or is absent, it can lead to deficiencies in the delivery of cell wall molecules to the cell wall, as demonstrated by the root hair development mutants *rhd1-1*, *rhd2-1* and *rhd3-1* ([Preuss et al., 2004](#)).

Similarly, RabA2 in *Phaseolus vulgaris* has also been associated with root hair development. A reverse genetic approach revealed that silencing RabA2 leads to a decrease in the number and length of root hairs, without affecting the directionality of growth ([Blanco et al., 2009](#)). RabA2 also functions in nodule organogenesis. It is required for the rhizobial-activated signal transduction pathways that lead to the induction of gene expression in the root ([Blanco et al., 2009](#)). Interestingly, the role of plant RabA family members is not limited to tip-targeted cell wall deposition, but also related to cytokinesis ([Berson et al., 2014](#)). RabA1d localizes in the trans-Golgi network and early endosomal compartments, and it accumulates on the growing cell plates during cytokinesis ([Shi et al., 2023](#)). The expansion of cell plate is largely supported by the mechanism of secretion and endocytosis. At the initial stage of cell plate formation, RabA1d forms a disc-like structure on the equatorial plane, exhibiting a steady increase in fluorescence intensity. This observation strongly suggests that RabA1d regulates the delivery of goods and membranes from early endosomes/TGN to the cell plate during cytokinesis.

Another Rab associated with root hair in *N. benthamiana* is NbRabE1 (a new RabE isoform), which mainly expresses in young tissues containing actively dividing cells and in stomata guard cells. The ectopic expression of dominant-negative NbRabE1 in Arabidopsis yields a pleiotropic phenotype, including a delayed growth rate of both shoot and root, accompanied by defective root hair formation. Dysfunction of NbRabE1 may hinder the transport and local release of polarized membrane materials and membranes, thereby interfering with the protection of cell cytoplasmic division and root hair development, leading to defects in cell plate assembly and polarized cell expansion ([Ahn et al., 2013](#)).

### 3. Control of the shape of plant organs

The morphogenesis of plant cells depends on the coordinated control of cell division planes and the differential growth of polyhedral cells on distinct surfaces ([Uyttewaal et al., 2012](#)). Some studies have found that cytoskeleton plays a pivotal role in cell morphogenesis, and its dynamic behavior is regulated by Rab GTPases. In mammals, Rab8 and Rab14 have a strong influence on cell morphogenesis by reorganizing actin-/microtubules, as well as regulating the process of microtubule acetylation ([Peranen, 2011](#)). However, this regulatory approach has not been reported in plants. In addition to cytoskeleton, membrane organization also plays an important role in shaping plant cells.

During the process of organogenesis in Arabidopsis, the

endomembrane system involves an important cellular spatial domain—geometric edge located directly below the plasma membrane at the cell edge, and the formation of this domain depends on RabA5c. The pattern of RabA5c accumulation at the cell edges presents in young lateral roots and young leaf primordia, and is lost in older cells. Inhibition of RabA5c activity causes radial swelling and a loss of tensile strength in growing cell walls, resulting in the gradual development of severely disordered cell shapes in the lateral roots of germinated seeds ([Kirchhelle et al., 2016](#)). RabA5c thus meets a requirement to specify this cellular spatial domain during organogenesis. In addition, recent reports also provide some insight on RabC1, the counterpart of mammalian Rab18, in the regulation of stomatal morphogenesis. RabC1 is highly expressed in young stomata and has been identified as a key regulatory factor required to regulate lipid droplet dynamics and lipid metabolism. Subcellular localization and Co-IP analyses indicate that activated RabC1 is targeted to the surface of lipid droplets, where it interacts with ER-localized SEIPIN2 and SEIPIN3, thereby regulating lipid droplet mobilization and ensuring the availability of lipids to establish functional stomata ([Ge et al., 2022](#)).

RabG/Rab7 protein in Arabidopsis also has a notable impact on vacuoles morphology. Expression of a dominant-negative RabG/Rab7 mutant induces the formation of enlarged prevacuolar compartments, disrupting vacuole morphology, inhibiting vacuolar trafficking and ultimately leading to seedling death ([Cui et al., 2014](#)). Moreover, Rabe1d localizes in the Golgi apparatus and plasma membrane of Arabidopsis mesophyll cells and plays a fundamental role in the secretion of extracellular matrix molecules. It interacts with phosphatidylinositol 1-4-phosphate 5-kinase 2 (PIP5K2) to stimulate the production of PtdIns (4,5) P2 (temporally and spatially localized) at the plasma membrane ([Camacho et al., 2009](#)). Downregulation of its expression level results in a significant alteration in leaf morphogenesis and a reduction of plant volume ([Speth et al., 2009](#)).

RabH1b is essential for maintaining Golgi morphology and modulating the trafficking of cellulose synthase complexes from endosomal compartments to plasma membrane ([McFarlane et al., 2014](#)). In plant cells, cellulose is produced through a cellulose synthase complex located in the plasma membrane, which is transported to the PM by RabH1b. The loss of RabH1b function leads to impaired exocytosis of CESA6, accumulation of vesicles around the abnormal Golgi apparatus, and an increase in the number of cisternae, thereby resulting in defects in the homeostasis of the pools, a decrease in cellulose content, and seedlings exhibiting short and fragile yellowing hypocotyls ([He et al., 2018](#)).

### 4. Role of rab GTPase in fruit ripening

#### 4.1. Fruit softening

The fruit development and ripening process is a carefully designed physiological process in plants that changes fruit characteristics such as color, texture and flavor compounds, making it more attractive to seed-spreading organisms. As previously reported, fruit ripening is controlled by complex mechanisms driven by hormones, developmental factors and environmental stimuli ([Herrera-Ubaldo, 2022](#)). To improve and maintain fruit quality, researchers have established a multi-level gene

regulatory network for fruit ripening using tools such as genome editing, genomics, metabolomics and transcriptomics (Brumos, 2021; Ma et al., 2022; Deng et al., 2023). Fruit softening is a ripening-related process that is closely related to the breakdown of cell walls. It has been shown that cell-wall-modifying enzymes are the main factor affecting fruit softening. Therefore, many groups attempt to maintain cell hardness and prolong fruit shelf life by inhibiting the expression of cell wall synthesis/modification enzymes (Jiang et al., 2019). Despite the success of these technologies at the genetic level, these technologies typically produce minor phenotypical alterations in the softening process.

In the past two decades, Rab GTPase has attracted widespread attention due to its diversity and ripening-related expression in fruit. Some Rab members have been proven to play an important role in fruit ripening (Table 1), regulating the fruit softening process by secreting

and targeting enzymes that alter cell wall components (Lunn et al., 2013). As an important model system for studying fruit ripening, tomatoes contain 56 Rab GTPases, whose expression patterns are shown in Table 2. Among them, LeRab11a (Solyc07g055290) has been proven to regulate the softening process of fruits. Using antisense technology to silence tomato SlRabA11a, transgenic lines had lower levels of polygalacturonase (PG) and pectinesterase (PE) and significantly stronger fruits than untransformed lines (Lu et al., 2001). However, Lunn et al. suggest that SlRab11a reduced fruit softening by changing cell wall deposition rather than cell wall hydrolytic enzymes (Lunn et al., 2013). During fruit development, the cell wall undergoes complex compositional and structural changes. SlRab11a is highly expressed during fruit development, which is related to the period when pectin flows into the wall, and SlRab11a antisense fruit had a decreased proportion of pectin

**Table 2**  
Rab GTPase expression levels (RPKM) in different tissues and ripening processes of tomato.

	bud	flower	leaf	root	1 cm_fruit	2 cm_fruit	3 cm_fruit	MG	Br	Br+10
Solyc01g086850	20.99	17.665	7.36	18.35	4.335	6.78	5.305	17.025	13.61	20.51
Solyc01g088560	49.395	30.785	49.355	57.62	75.665	81.355	47.985	71.57	65.4	64.93
Solyc01g090170	58.89	55	40.075	60.11	56.81	52.275	56.52	54.84	48.285	51.535
Solyc01g096220	12.54	4.995	13.81	25.68	57.5	19.36	4.655	12.28	2.465	10.48
Solyc01g103370	140.71	103.21	86.155	132.23	133.585	85.68	71.23	89.14	73.78	66.91
Solyc01g103380	22.82	17.51	15.55	18.555	29.455	28.12	14.36	31.585	19.795	20.435
Solyc01g109520	67.365	78.1	72.905	145.805	155.64	132.01	153.94	183.85	220.8	221.505
Solyc02g036450	44.365	42.36	34.24	51.43	30.34	28.875	26.725	36.465	28.52	24.805
Solyc02g069370	52.085	54.51	56.41	132.56	25.14	35.015	34.215	23.885	28.27	31.2
Solyc02g072180	33.665	10.54	14.885	35.77	52.665	32.44	14.66	12.58	4.24	1.64
Solyc02g081380	28.445	26.705	17.095	33.905	28.4	38.355	20.92	29.67	22.12	29.075
Solyc02g093530	27.33	24.49	31.795	20.865	33.795	33.215	38.215	27.1	35.88	42.035
Solyc03g064020	2.15	1.2	0.11	0.06	0.065	0	0	0.075	0	0
Solyc03g078570	77.39	64.29	73.59	66.11	87.115	63.92	91.04	60.595	47.465	43.175
Solyc03g079900	7.18	1.355	0	0	0.085	0.09	0.14	0.17	0.065	0.655
Solyc03g118820	4.925	5.165	4.535	7.13	15.62	25.55	16.945	16.64	29.14	34.89
Solyc03g120750	60.065	49.13	43.75	48.815	47.29	38.425	19.41	30.83	38.475	43.74
Solyc04g011360	62.42	65.58	41.72	79.6	66.41	62.875	70.795	75.985	69.16	85.875
Solyc04g012180	25.555	22.76	21.42	31.47	45.34	39.795	40.365	45.92	45.39	48.63
Solyc04g051700	11.53	8	10.73	10.57	13.37	11.53	8.1	10.63	8.01	9.08
Solyc04g064510	48.265	48.5	34.06	74.805	45.54	43.52	33.295	47.705	59.36	75.81
Solyc04g072060	32.84	33.925	23.63	43.3	40.19	27.835	15.9	22.225	18.2	17.225
Solyc05g045660	26.565	76.115	0.05	0.105	0	0	0.1	0.185	0.05	0
Solyc05g051570	90.21	92.855	4.96	28.495	30.015	50.14	66.015	82.51	85.96	25.655
Solyc05g052070	100.99	123.22	31.83	59.67	60.82	68.75	85.375	48.62	48.19	36.71
Solyc05g053940	95.975	86.545	74.87	116.02	103.125	100.525	69.875	86.41	100.01	87.235
Solyc05g054150	20.83	18.595	14.39	15.9	8.94	13.855	15.29	16.285	7.22	0.61
Solyc06g005350	7.195	4.52	5.42	3.515	7.19	7.335	11.71	5.695	2.635	1.705
Solyc06g005810	31.46	33.915	13.625	61.225	14.86	7.91	4.18	6.85	17.3	9.44
Solyc06g060210	0.92	0	0	0	0	0.105	0	0.105	0	0
Solyc06g076450	35.76	35.995	1.71	9.335	1.04	2.32	2.615	8.305	8.85	13.235
Solyc07g053480	27.58	9.83	11.785	28.595	67.575	33.575	19.39	14.145	2.425	2.8
Solyc07g055290	19.695	52.17	27.19	41.695	28.72	30.08	18.13	22.865	24.64	25.22
Solyc07g056150	30.255	35.895	24.655	45.605	32.825	50.4	42.525	45.91	27.92	33.75
Solyc07g064290	15.29	15.1	11.445	36.675	7.91	6.685	8.72	10.145	8.95	14.53
Solyc08g078070	73.75	95.27	40.395	117.34	28.695	32.215	16.795	69.495	119.545	136.51
Solyc09g008460	11.895	7.99	17.425	43.95	26.045	19.525	26.265	31.4	7.37	0.39
Solyc09g010370	102.52	110.865	39.65	184.29	99.235	105.23	98.78	103.39	68.685	44.555
Solyc09g056340	9.675	5.83	12.955	23.395	23.71	16.675	9.135	26.37	25.78	32
Solyc09g097900	14.115	12.14	11.125	10.45	16.125	16.55	9.02	10.77	9.015	4.445
Solyc09g098170	13.16	15.07	19.475	28.255	41.345	36.06	32.775	31.535	33.1	27.795
Solyc10g007700	30.99	30.82	32.55	70.225	44.835	47.865	50.665	52.765	59.065	20.915
Solyc10g008840	5.05	1.14	0	0.35	0	0	0.095	0.055	0.19	0.04
Solyc10g045550	34.855	21.84	29.595	37.76	65.265	51.69	19.555	33.13	22.615	23.95
Solyc10g086310	1.92	0.56	2.25	8.86	0.95	0.615	0.935	0.19	0	0.12
Solyc10g086350	75.24	60.25	61.345	97.43	55.975	49.42	68.04	79.76	67.845	73.065
Solyc11g008020	4.44	15.22	7.335	12.98	12.635	12.02	17.57	22.465	27.855	16.75
Solyc11g008430	71.195	84.005	60.465	60.19	54.73	63.86	55.205	70.235	63.62	57.47
Solyc11g010100	26.21	22.025	29.57	44.82	67.495	48.235	34.78	63.06	46.32	44.46
Solyc11g012460	74.76	52.8	14.33	27.97	13.395	25.15	49.095	30.13	20.425	10.65
Solyc11g073050	90.05	69.41	62.285	137.69	101.41	68.39	43.45	44.5	19.415	25.025
Solyc12g005840	72.285	155.715	1.94	16.16	30.58	21.955	21.325	14.84	0.055	0
Solyc12g010790	84.16	67.695	51.965	71.705	97.42	57.72	91.075	97.93	69.1	50.88
Solyc12g011130	31.74	29.83	17.125	17.065	18.735	24.16	15.825	17.645	19.25	38.66
Solyc12g014080	43.515	45.005	28.89	40.785	55.18	55.45	35.44	42.345	38.74	39.88

Data from The Tomato Genome Consortium.

in the cell wall compared with the wild type. However, during the fruit ripening process (from MG to Br+9), there are other Rab GTPase expression levels higher than those of SlRab11a, such as Solyc09g056340 (Table 2). Its role in fruit softening is worth exploring.

Recently, Lawson et al. utilized a comprehensive in silico approach to identify Rab (23 genes) in mangoes and classified them into eight subfamilies through sequence alignment and similarity tree analysis. RNA-Seq and RT-qPCR analysis showed that some members of RabA, RabC, RabD, RabE and RabF expressed differentially between the unripe (UR) and ripe (R) stages. In particular, the expression levels of most RabA genes in the UR stage were higher than those in the P stage. More noteworthy is the significant negative correlation between the expression levels of RabA3 and RabA4 genes and the fruit hardness during the immature stage of mangoes (Lawson et al., 2020). A total of 26 genes encoding Rab proteins were identified in *Vitis vinifera*, and they were expressed at all stages of fruit development. In particular, VvRabA is developmentally regulated and strongly accumulates during the ripening stage (Abbal et al., 2008). Similarly, the significant fluctuations of PpRab transcripts during fruit development and ripening also present in peach (Falchi et al., 2010). As mentioned above, accumulating evidence supports the involvement of tRab GTPases in the regulation of fruit ripening process, and they are thought to exert their functions by mediating the transport of enzymes to the cell wall.

#### 4.2. Fruit abscission

Mature fruit abscission is another natural event related to fruit ripening. Despite there being two independent developmental and genetic processes, the former significantly affects the yield, quality and postharvest storage of fruits. The presence of a differentiation abscission zone (AZ), localized between the stem and fruit, is a prerequisite for abscission to occur (Olsson and Butenko, 2018). Only after the fruit is mature and the preformed AZ cells are activated will the fruit loosen. It will not shed until the surrounding floral organs fall off. Immature fruit do not go through abscission under normal conditions, even if AZs are formed (Briegas et al., 2020). The process of fruit ripening and abscission is the result of cell wall modification, which involves a wide range of structural proteins and hydrolytic enzymes with distinct functions in the tissues.

Many global transcriptome studies on mature fruit abscission are well documented, suggesting that, in addition to hormones and environment, vesicle formation and transport are also necessary for the changes in deposition of wall material. In melon fruit-AZ, the majority of genes displayed different expression patterns in both early and late induction of abscission, among which 22 Rab-GTPases upregulated at 38 DAP and 8 Rab11 (Raba) were expressed strongly (Corbacho et al., 2013). At the same time, Briegas et al. characterized the transcriptomes of the olive AZ. They link the wall modification process with the upregulation of Rab family members and found that in the fruit AZ Rab11, Rab18, Rab7 and ARA6 were significantly up-regulated and associated with gene-encoding members of the  $\alpha$ -galactosidase and  $\beta$ -hexosaminidase, which strengthens the possibility that Rab GTPase regulated endosome transport participating in abscission signaling (Briegas et al., 2020). Thus, Rab-GTPase is thought to regulate mature fruit abscission by mediating the delivery of cell wall depolymerases (required for cell expansion and cell wall relaxation) to extracellular vesicles.

#### 5. Role of RABs in plant biotic and abiotic stress tolerance

Environmental stressors can directly cause the change of membrane fluidity, polarizability and sodium chelating capacity in the plant cell, triggering cellular stress sensing (Zhang et al., 2022). To resist environmental pressure, plants have evolved a complex molecular mechanism that enables them to respond and adapt to the environment in a timely manner. Significantly, numerous biochemical and molecular studies have identified several Rabs as crucial regulatory factors

participating in the stress response (El-Esawi and Alayafi, 2019).

##### 5.1. Biotic stress

Plants engage in different ecological relationships with organisms in their surroundings, including beneficial interactions (symbiosis or reciprocity) with their partners and pathogenic interactions where fungi or bacteria infect and colonize the host. A number of studies have confirmed the important role of Rab GTPase in these interactions. In leguminous plants, a mutualistic interaction is established between plants and Rhizobia, enabling legumes to obtain assimilable forms of nitrogen from bacteria in exchange for photosynthetic products. The formation of root nodule involves the growth and breakdown of cell wall. During this process, Rab GTPases are necessary for the development of functional nitrogen-fixing nodules. Previous reports have found that sRAB1 and sRAB7 influence nodule development in leguminous plants by affecting the number of bacteroids in the cytoplasm and vacuoles (Cheon et al., 1993). In addition, PvRabA2, a member of the RABA/Rab11 subgroup, plays a vital role in reorienting the polar growth of root hairs, causing them to curl around rhizobia microbiota and form infection bags (Cheon et al., 1993). Rab11f was also shown to be expressed in the nodules of *Medicago sativa* (Schiene et al., 2004).

In response to pathogens that pose a threat to plant growth and reproduction, plants employ two branches of immune system, including (1) recognizing and responding to various common microorganisms, and (2) reacting to virulence factors of pathogens directly or through their impact on host targets (Blanco et al., 2009). Multiple lines of evidence have confirmed the role of Rab GTPase in plant disease defense responses. Firstly, Rab GTPase is critical for stomatal closure induced by microbial patterns. Some pathogenic fungi specialize in using stomata as an entry route such as the rusts. It has been confirmed that many plants close their stomata when sensing microbes, which can reduce the severity of infection (Melotto et al., 2008). The dynamics of actin filaments are related to stomatal movement, forming different actin arrays within guard cells: radial orientation of open stomata and longitudinal orientation of closed stomata (Wang et al., 2017). RabG3b has been identified to be involved in FLS2-triggered guard cell actin reorganization (Hawkins et al., 2023). It interacts with NETWORKED4 (NET) as a bridge connecting actin filaments and vacuole membranes, regulating the remodeling process of actin cytoskeleton during stomatal closure. *rabg3b* mutants are unable to close stomata normally under the induction of flg22, and their phenotype is similar to that of two *net4* mutants (Hawkins et al., 2023).

RabG3b as a component of autophagy plays a positive role in autophagy and promotes hypersensitive cell death in response to avirulent bacterial pathogens in *Arabidopsis* (Kwon et al., 2013). Autophagy is vital for the direct elimination of pathogens, and its role in plant basal immunity to virulent pathogens has been determined. Apart from RabG3b, AtRabD2a and PagRabE1b positively regulate autophagosome biogenesis in *Arabidopsis* and poplar (Kwon et al., 2013; Liu et al., 2021). Rab GTPases also participate in defense signaling pathways by regulating intracellular vesicular trafficking. According to reports, OsRabA/OsRab11 along with OsGAP1 and OsGDI3 synergistically regulate vesicular transport from the TGN to the PM or vacuole in *Oryza sativa* (Li et al., 2011). They are widely expressed in plants and can be induced by jasmonic acid (JA) and elicitor treatments. Hong et al. identified OsOPR8 as one of the targets of OsRabA/OsRab11. It is a key enzyme in JA accumulation in response to environmental stress. OsRabA/OsRab11-overexpressing *Arabidopsis* transgenic plants clearly exhibited enhanced resistance to the pathogen *P. syringae* by regulating OsOPR8 and enhancing its NADPH-dependent reductase activity (Hong et al., 2013). Hence, OsRabA/OsRab11 plays an important role in JA-mediated defense signaling. When pathogens attack plants, plant cells can strengthen cell walls through the deposition of glucan polymer callose to thwart pathogen infiltration. In *Arabidopsis*, the interaction between RabA4c and its effector PMR4 (callose synthase) regulates the

biosynthesis of the callose and enhances the deposition of callose at the early stage of infection, which prevents fungal ingress into epidermal cells (Ellinger et al., 2014). In addition, some studies have found that small GTPase participates in ROS production and signaling in plant immunity, such as MtRop9, Rop6 and OsRac1 (Wang et al., 2020; Ganatra et al., 2023). The relationships between Rab GTPase and ROS in plant are poorly understood. However, there are also some Rab GTPases that negatively regulate plant disease resistance. For example, the Arabidopsis AtRABE subfamily contains five members, which are membrane proteins associated with the endomembrane system and participate in vesicle transport process (Zheng et al., 2005). Among these, AtRabE1a, AtRabE1b and AtRabE1d interact with the Arabidopsis RTNL proteins AtRTNLB1–4 and virulence protein VirB2 of *Agrobacterium tumefaciens*. The high expression levels of *rabe1a*, *rabe1b* and *rabe1d* in Arabidopsis increased the susceptibility of plants to *Pst DC3000* infection (Huang et al., 2021).

## 5.2. Abiotic stress

At present, various genetic, biochemical and molecular studies have identified numerous Rab GTPases as imperative components required for regulating abiotic stress tolerance across a diverse array of plant species.

### 5.2.1. Salt stress

Soil salinization is increasingly a problem for agriculture worldwide. The increase in salt concentration reduces the ability of plants to absorb water, and the large absorption of  $\text{Na}^+$  and  $\text{Cl}^-$  have a negative impact on growth by damaging metabolic processes and reducing photosynthetic efficiency (Hassani et al., 2021). To resist the effects of salt stress, plants can modify the composition, localization and turnover of protein and lipid components of the plasma membrane via coordinating endocytosis, secretion and endosomal trafficking pathways (Gonzalez et al., 2022).

A recent study indicated that AtRabG3e is involved in salt stress tolerance. AtRabG3e showed a basal level expression in different Arabidopsis organs and could be induced by high but not low concentration of  $\text{H}_2\text{O}_2$ . During salt stress, transgenic plants overexpressing AtRabG3e showed increased tolerance to salt and osmotic stresses by accelerating endocytosis, increasing sodium accumulation in the vacuole and reducing generation of ROS (Mazel et al., 2004). Plant-unique ARA6/RabF1 also has a functional role in the salinity stress response. It regulates SNARE complex formation comprising VAMP727 and SYP121 at the plasma membrane, and participates in direct transport from the endosome to the plasma membrane. This trafficking pathway involving ARA6/RabF1 modulates the salt response, since ARA6/RabF1 loss-of-function conferred salt hypersensitivity (Ebine et al., 2011). Heterologous expression of AtARA6 in soybeans directly enhances plant salt tolerance by participating in the regulation of soybean SNARE complexes in vesicular transport pathways (Hong et al., 2022). Unlike ARA6/RabF1, members of RABA1 (RabA1a, RabA1b, RabA1c, RabA1d) are required for salinity stress tolerance, but they are not responsible for the regulation of sodium content and distribution (Asaoka et al., 2013). In *Melilotus albus*, researchers found that members of the MaRab family were widely involved in the abiotic stress response, among which MaRab1, MaRab3, MaRab5, MaRab6, MaRab11, MaRab12, MaRab17, MaRab19, MaRab22, MaRab23 and MaRab55 responded to salt stress, while the details of the regulatory mechanisms involved in the MaRab-mediated drought signal response remain an area of active investigation (Zhang et al., 2022). Furthermore, AhRabG, OsRabG/OsRab7 and OsRabA/OsRab11 are also known to be responsive to abiotic stresses, and their overexpression in transgenic peanut and rice has demonstrated elevated salinity tolerance compared with wild-type plants (Sui et al., 2017; Chen and Heo, 2018).

In the case of perennial woody plants, Rab GTPases are also crucial for development and environmental response. For instance, in poplar, a

total of 67 PtRab GTPases were identified and categorized into eight subfamilies. Among them, PtRabE1b was related to salt stress response, and the overexpression of the constitutive activated mutant form of PtRabE1b (Q74L) maintained healthy root growth status under salt stress conditions by upregulating the expression of genes related to trafficking, stress responses and developmental processes (Zhang et al., 2018).

### 5.2.2. Drought stress

Drought stress is another major abiotic stress that profoundly hampers the growth, development and yield of crops all over the world. Plants subjected to water stress employ various mechanisms to avert desiccation. These include the regulation of transpiration by means of stomata closure and the augmentation of cuticle thickness, optimizing water transport within the plant, enhancing succulence for water storage, bolstering cellular elasticity and accumulating protective substances, such as dehydrated proteins (Razi and Muneer, 2021). It is generally accepted that maintaining the integrity and stability of the membrane is a major component of plant drought resistance.

O'Mahony and Oliver (O'Mahony and Oliver, 1999) were the first investigators to report the relationship between Rab protein and drought stress. They found that the transcriptional level of the RabB/Rab2 gene increased during dehydration in desiccation-tolerant grass *Sporobolus stapfianus*, followed by a decrease after rehydration, which indicates that SsRab2 is involved in short-term responses and later recovers from desiccation. Since then, research has revealed associations between genes encoding Rab proteins and various stressors in numerous plant species. In Arabidopsis, RabA2b was reported to be involved in the drought resistance response. It is highly upregulated under drought stress and can be induced by osmotic stress and stress hormone ABA. Overexpression of RabA2b in Arabidopsis was strikingly drought resistant. Further investigation revealed that, under drought stress, RabA2b can alter the proteome of PM, enrich stress-coping proteins and modify cell wall/stratum corneum, thereby reducing the permeability of leaf stratum corneum and improving drought resistance in Arabidopsis (Ambastha et al., 2021). Similarly, RabE1c also is highly induced by ABA and drought stress. It has been identified as one of the abundant proteins in guard cells and has been shown to bind to ABA receptors, including Pyrabactin Resistance1-like (PYL) protein, in the plasma membrane of Arabidopsis (Zhao et al., 2008). In the loss-of-function *rabe1c*, the sensitivity of stomatal closure, endoplasmic reticulum signaling and whole plant drought stress response to ABA treatment decreased, indicating that RabE1c acts as a positive regulator in ABA signaling and drought stress (Chen et al., 2021).

Interestingly, CaRabC is also involved in response to salinity stresses. A total of 54 isoforms of CaRab genes were identified in chickpea, and all isoforms of CaRabC were strongly expressed. However, they were downregulated under the slowly developing drought, and very strongly upregulated in rapidly dehydrated leaves (Khassanova et al., 2019). They were involved in drought resistance regulation pathways different from those previously reported. In addition, PgRab7 (from *Pennisetum glaucum*), the homolog OsRab7 (from rice) and AtRab7 (from Arabidopsis) are implicated in intracellular vesicle trafficking from late endosome to the vacuole. Their overexpression has been found to enhance tolerance to mannitol and NaCl in transgenic tobacco, rice and Arabidopsis, respectively (Nahm et al., 2003; Agarwal et al., 2008). It is of interest that the transcript of PgRab7 not only increases under stress conditions but is also upregulated by auxin IAA. Consequently, it is worth further exploring whether PgRab7 has the function of balancing plant growth and stress response.

### 5.2.3. Temperature stress

Temperature stress (cold/heat stress) is also an important factor influencing the geographical distribution of plants and threatening food security. The perception of temperature signals and the activation of response genes are crucial for the tolerance of plants to temperature

stress (Ding and Yang, 2022). Heat stress severely disrupt intracellular protein homeostasis, leading to the accumulation of abnormally folded proteins, especially in the ER. As a receptor protein for Rab GTPase, the Prenylated Rab Receptor 1 (PRA1) domain protein is located in the endoplasmic reticulum, Golgi apparatus and endosomes/prepolar compartments, and is an important factor in regulating vesicular transport (Alvim et al., 2008). For instance, PRA1\_F4 regulates protein excretion from the Golgi apparatus in *Arabidopsis* (Lee et al., 2017), while PRA1\_A in tomatoes reduced the localization of pattern recognition receptors in the endosomes, effectively alleviating ER stress (Pizarro et al., 2018). In maize, ZmPRA1\_C1 interacts with ZmRabD1 and ZmRabD2c and ensures their retention in the membrane of cognate organelles. ZmPRA1\_C1 was not regulated by high temperature at the transcriptional level, but the soluble form of ZmPRA1\_C1 rapidly decreases under heat stress conditions. Heat upregulated gene 1 (ZmHUG1) has been reported to thermally stabilize ZmPRA1\_C1 and prevent its aggregation in ER. In the *zmhug* mutant, the secretion of secGFP from the ER to the apoplast was impeded and the plant experienced more severe ER stress (Xie et al., 2022).

Apart from the pivotal role in vesicle transport, Rab GTPase contributes to plant heat tolerance by regulating protein translation. RabE1b, also known as the translation elongation factor Tu (EF Tu), is a GTP-binding protein crucial for protein translation in prokaryotic, eukaryotic mitochondria and plastids (Berisio et al., 2010). Under heat stress, RabE1b is one of the most abundant aggregates in *Arabidopsis thaliana* plastids (Li et al., 2018). Knockdown of Rabe1b increased heat sensitivity, which was associated with inhibited induction of HsfA2 and its target genes under heat stress. Thus, it not only affects plastid protein translation under normal conditions/heat stress, but also affects the expression of nuclear heat response genes (Li et al., 2018). In addition, OsRab7 could improve rice tolerance to drought and heat stress conditions. Rice overexpressing OsRab7 exhibits greater tolerance to drought and heat stress effects by improving gas exchange, enhancing osmolytes and chlorophyll content, and inducing antioxidant enzyme activities under drought and heat stress (El-Esawi and Alayafi, 2019). These results provide a new molecular regulatory pathway for Rab to improve plant heat tolerance.

## 6. Conclusion and perspectives

At present, the importance of vesicle transport has been widely confirmed, but the molecular mechanism of this process is mostly unknown. It is now clear that Rab GTPase, as a regulatory switch, can recruit effector molecules in the active GTP-bound form, thereby controlling various aspects of vesicle transport in mammalian and yeast cells. Compared with yeast/mammals, plant Rab GTPase appears to follow different evolutionary pathways, and the diversity and specificity of plant Rabs have sparked interest in exploring its function. Accumulating evidence shows that Rab GTPases play an important role in various life activities of plants, including tip growth, plant development, biotic/abiotic stress response and fruit ripening. Our manuscript mainly summarizes the Rab GTPases that play an important role in these vital movement and the molecular pathways they may participate in.

Due to the extensive functions of Rab GTPase, the identity and function of a large number of effector molecules in plants are currently unclear. Fortunately, emerging technologies such as BioID, combined with methods such as yeast hybridization and Co-IP, will greatly expand the number of effectors. Therefore, screening the interacting proteins of functional Rab GTPase is also a focus of future work. In addition, Alphafold2 has been applied to predict protein spatial structure and predict interactions between two proteins (Tunyasuvunakool et al., 2021). The conservation of Rab-GTPase protein space provides the possibility of using structural alignment strategies to screen more Rab and its interacting proteins. Overall, numerous studies on the functional analysis of Rab GTPase have suggested that it can regulate plant morphology and fruit maturation by affecting the transport and

composition of cell -wall-modifying enzymes and cell wall polysaccharides, as well as regulating plant immunity and development by coordinating lipid transport, cell plate origin, etc. These reflect the critical requirements of Rab GTPase for plant life.

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## CRediT authorship contribution statement

**Yao Lu:** Writing – review & editing, Writing – original draft, Visualization. **Ke Cheng:** Writing – original draft, Conceptualization. **Hui Tang:** Software, Data curation. **Jinyan Li:** Visualization, Formal analysis. **Chunjiao Zhang:** Software, Conceptualization. **Hongliang Zhu:** Data curation, Conceptualization.

## Declaration of competing interest

This manuscript has not been published or presented elsewhere in part or in entirety and is not under consideration by another journal. We have read and understood your journal's policies, and we believe that neither the manuscript nor the study violates any of these. There are no conflicts of interest to declare.

## Data availability

Data will be made available on request.

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