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Review

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Gravity sensing and responses in the coordination of the shoot gravitropic setpoint angle

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Summary

Gravity is one of the fundamental environmental cues that affect plant development. Indeed, the plant architecture in the shoots and roots is modulated by gravity. Stems grow vertically upward, whereas lateral organs, such as the lateral branches in shoots, tend to grow at a specific angle according to a gravity vector known as the gravitropic setpoint angle (GSA). During this process, gravity is sensed in specialised gravity-sensing cells named statocytes, which convert gravity information into biochemical signals, leading to asymmetric auxin distribution and driving asymmetric cell division/expansion in the organs to achieve gravitropism. As a hypothetical offset mechanism against gravitropism to determine the GSA, the anti-gravitropic offset (AGO) has been proposed. According to this concept, the GSA is a balance of two antagonistic growth components, that is gravitropism and the AGO. Although the nature of the AGO has not been clarified, studies have suggested that gravitropism and the AGO share a common gravity-sensing mechanism in statocytes. This review discusses the molecular mechanisms underlying gravitropism as well as the hypothetical AGO in the control of the GSA.

I. Introduction

Plants use various environmental signals, including light, temperature, and gravity, to adapt to the surrounding environment. Gravity is a fundamental force on Earth under which all living organisms evolved. Many such organisms, including plants, recognise and respond to gravity to optimise their growth and development. In plants, gravity information is recognised as a force and sensed as a directional cue. In this review, we focus on gravity as a directional cue with which plants optimise directional organ growth to achieve reproductive success, that is the process known as gravitropism (Kiss, 2000; Morita, 2010). In general, when a plant shoot senses a tilt from a gravity vector, a primary shoot stem grows upwards against gravity in a process known as negative gravitropism. By contrast, plant roots grow downwards according to gravity in a process known as positive gravitropism. Gravitropism is considered the result of the following sequential processes: (1) gravity sensing, in which plants recognise gravity vectors in specialised gravity-sensing areas; (2) gravity signalling, in which the gravity information is converted into biochemical signal transduction within gravity-sensing cells; (3) intercellular signal transduction, in which gravity information is shared within tissues and organs via signalling molecules, including the phytohormone auxin; (4) asymmetric organ growth, in which the cellular machinery is driven to achieve gravitropism via differential cell division/elongation; and (5) termination of asymmetric organ growth due to the regulation of auxin feedback after sufficient bending. Collectively, these processes contribute to plant gravitropism in the shoots and roots.

As described below, gravitropism affects the growth direction of lateral organs, thereby reflecting plant architecture, which is often linked to plant reproductive traits. For instance, during local adaptation to the surrounding environment, adaptive divergence in shoot gravitropism in the Australian wildflower *Senecio lautus* has been selected in the evolution of hybrid sterility (Wilkinson *et al.*, 2021). In another example, leaf and branch growth angles directly affect crop productivity; therefore, they are a target for the genetic improvement of crops (Waite & Dardick, 2021). In addition to gravity information, other environmental signals, such as light, affect the growth direction of plant organs (Fankhauser & Ulm, 2011). Typically, shoots grow toward the light, whereas roots grow away from the light. Shoot phototropism optimises light capture in the leaves to maximise photosynthesis. In the roots, water and nutrients also affect growth angles (Kobayashi *et al.*, 2007; Huang *et al.*, 2018; Yamazaki *et al.*, 2020). Environmental cues, including gravity and light, are integrated to optimise plant architecture (Moulia *et al.*, 2022).

Among the various inputs that affect the growth angle of organs, we focus on gravity information in the present review. Primary shoots and roots tend to grow vertically according to the gravity vector, whereas lateral organs, such as lateral branches and lateral roots, tend to grow at specific nonvertical angles according to the gravity vector, which is termed the gravitropic setpoint angle (GSA) (Digby & Firn, 1995). As a hypothetical growth component that counteracts gravitropism to determine the GSA, the anti-gravitropic offset (AGO) has been proposed (Roychoudhry *et al.*, 2013; Roychoudhry & Kepinski, 2015). According to this concept, the GSA is considered to be balanced between two antagonistic growth components, that is gravitropism and the AGO. Although the nature of the AGO has yet to be clarified, several studies have suggested that gravity-sensing cells are important in the control of the AGO and gravitropism. Consequently, plant architecture in the shoots and roots is affected by gravity. In this review, we focus on the early steps of the process, that is gravity sensing and signal transduction processes in the gravity-sensing cells of shoots under gravitropism, and comparatively assess the similarity and uniqueness of the process with that of root gravitropism. We also discuss the enigmatic AGO and the potential links among gravitropism, the AGO and environmental cues in relation to determining the GSA.

II. Gravity-sensing cells in shoots

In plant organs responsive to gravistimulation, such as the roots and hypocotyl, plastids containing dense starch granules, known as amyloplasts, are commonly observed. Upon gravistimulation achieved via the reorientation of such organs, these amyloplasts sediment along the new gravity vector. The starch–statolith hypothesis proposes that amyloplast sedimentation triggers gravity sensing in specialised cells known as statocytes (Haberlandt, 1900; Nériec, 1900; Sack, 1991). In the roots, sedimentable amyloplasts are often observed in the columella cells in the root cap (Fig. 1a,e). In addition to early physiological experiments, modern studies involving cell ablation techniques have demonstrated that the columella cells in the root cap are responsible for gravity sensing (Hart, 1990; Blancaflor *et al.*, 1998; Tsugeki & Fedoroff, 1999). Consistent with these findings, for the loss-of-function mutants of two auxin response factors (ARFs), ARF10 and ARF16, the daughter cells of the initial columella cells failed to differentiate into columella cells with starch-filled amyloplasts, resulting in abnormal root gravitropism (Table 1; Wang *et al.*, 2005).

Sedimentable amyloplasts are observed in several shoot tissues, including the bundle sheaths and cells of the inner cortex in hypocotyls, the inflorescence stems of dicots, and the coleoptiles and leaf sheath pulvinus of monocots (Brock *et al.*, 1989; Hart, 1990). In *Arabidopsis*, the gravity-sensing tissue in shoots has been identified as the endodermis (Fukaki *et al.*, 1996, 1998; Fig. 1a–c). *shoot gravitropism* (*sgr*) *1* and *sgr7* mutants have completely lost gravitropism in the inflorescence stems, whereas their roots are still responsive to gravistimulation. Furthermore, *sgr1* and *sgr7* lack an endodermal cell layer in the hypocotyl and inflorescence stem and are allelic to the *scarecrow* (*scr*) and *short-root* (*shr*), respectively, which were reported as radial pattern mutants unable to form root endodermal cells (Table 1; Scheres *et al.*, 1995; Di Laurenzio *et al.*, 1996; Fukaki *et al.*, 1998; Helariutta *et al.*, 2000). The causal gene *endodermal-amyloplast less1* (*eal1*), an agravitropic mutant in the inflorescence stem (Fujihira *et al.*, 2000), was also mapped on the SHR locus, and the mutation caused a single amino acid deletion in SHR protein (Table 1; Morita *et al.*, 2007). However, *eal1* still maintains the ability to form an endodermal-like cell layer, indicating that it is a hypomorphic mutant allele of *sgr7*/*shr*. The

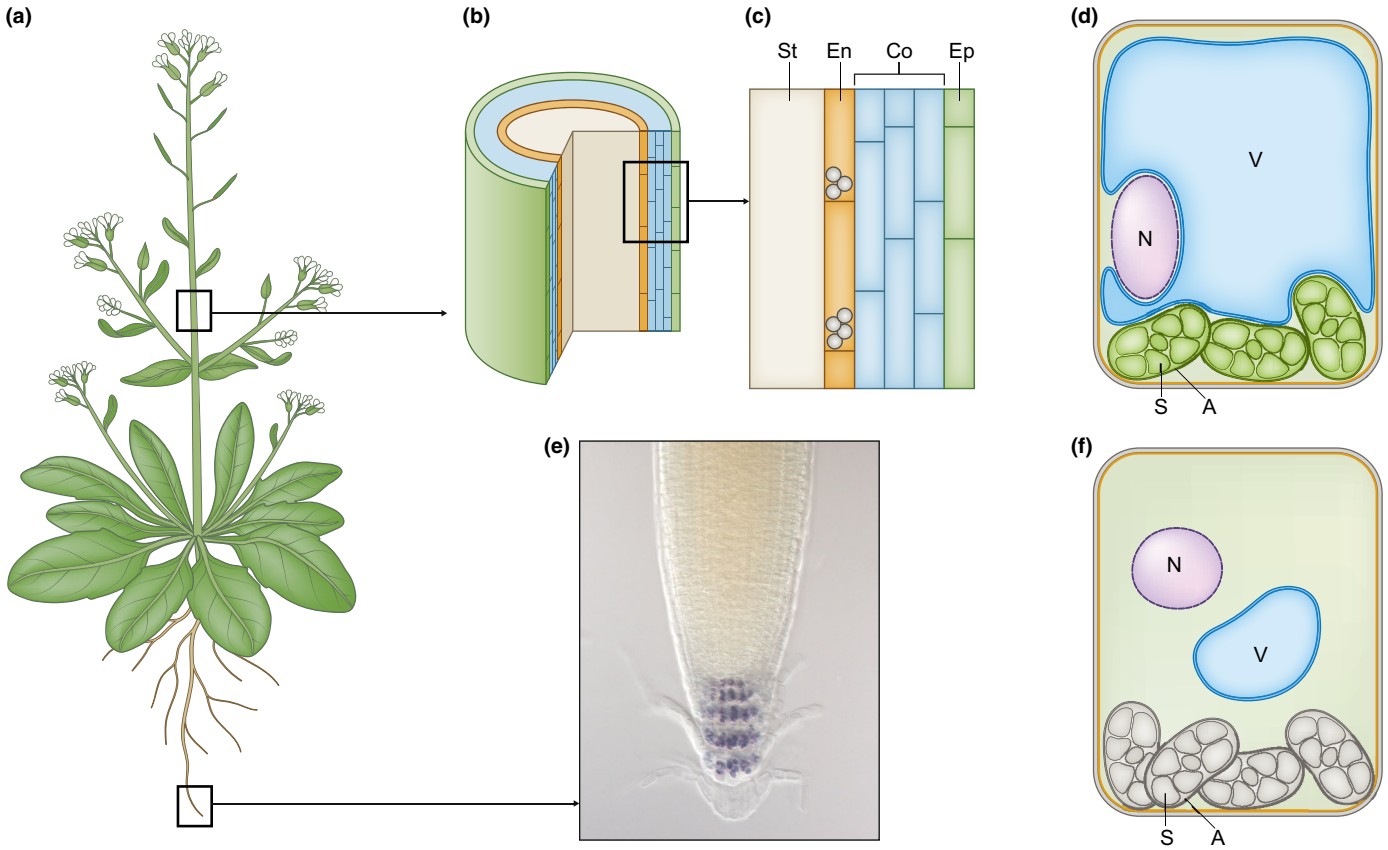


Fig. 1 Gravity-sensing locations in the shoots and roots. (a) Illustration showing the whole *Arabidopsis* shoots and roots, including the lateral organs. (b) Schematic structure of the *Arabidopsis* inflorescent stem region, as indicated by the upper dashed box in (a). (c) Layer structure of the *Arabidopsis* inflorescent stem, as indicated by the dashed box in (b). From the outer most layer (right to left): Ep, epidermis; Co, cortex; En, endodermis; and St, stele. (d) Cellular features of endodermal cells. Amyloplasts sediment toward the bottom of the cell according to the gravity vector. The cell is occupied by a large central vacuole. (e) Photograph showing a primary root tip of *Arabidopsis* as indicated by the lower dashed box in (a). Columella cells contain amyloplasts (stained purple). (f) Cellular features of columella cells. Amyloplasts sediment toward the bottom of the cell according to the gravity vector. Nucleus is in the upper part of the cell. In (d, f): N, nucleus; V, vacuole; A, amyloplast; S, starch granule.

endodermal-like cells of *eal1* contain starchless plastids, suggesting their incomplete differentiation as statocytes.

III. Characteristics of shoot statocytes

In *Arabidopsis*, the endodermis and columella cells are where gravity vectors are sensed in the shoots and roots, respectively (Fig. 1). As statoliths, these statocytes contain starch-filled, round-shaped and sedimentable plastids known as amyloplasts. By definition, the term amyloplast describes nonpigmented leucoplasts that store starch. Although the amyloplasts in root columella cells are leucoplasts, those in shoots have a thylakoid membrane and photosynthetic pigments (Morita *et al.*, 2002; Niihama *et al.*, 2009). Therefore, the amyloplasts in the shoot endodermis are not leucoplasts but rather chloroplasts that accumulate starch. In this review, endodermal statoliths are referred to as amyloplasts according to the convention.

A notable difference between the shoot statocytes and root columella cells is a large central vacuole (Fig. 1d,f). Based on the observation that amyloplasts are surrounded by a vacuolar membrane with thin cytoplasm, the possible role of the vacuolar membrane in gravity sensing had been suggested (Clifford *et al.*, 1989). Genetic analyses of a series of *Arabidopsis sgr* mutants with reduced shoot gravitropism have clarified the role of the vacuole in shoot statocytes. *SGR2* encodes a phospholipase A1-like protein that localises in the vacuole membrane (Table 1; Kato *et al.*, 2002). *SGR3* and *SGR4/ZIG* encode SNAREs, syntaxin SYP21/AtVAM3, and AtVTI11, respectively, which function in membrane trafficking to the vacuole (Table 1; Kato *et al.*, 2002; Yano *et al.*, 2003). *SGR8/GRV2/KAM2* encodes a protein containing a DnaJ domain and IWN repeats, similar to those of *Caenorhabditis elegans* receptor-mediated endocytosis 8, and this protein is involved in protein sorting to the vacuole (Table 1; Silady *et al.*, 2004; Tamura *et al.*, 2007). *SGR6* encodes an unknown protein harbouring HEAT repeat motifs that localise in the vacuole membrane (Table 1; Hashiguchi *et al.*, 2014). A common feature observed in the loss-of-function mutants of these *SGR* genes is the impairment of amyloplast sedimentation in endodermal cells. Endodermis-specific expression of *SGR2*, *SGR3*, *SGR4/ZIG*, and *SGR6* rescues the gravitropic phenotype of the corresponding mutants. Live cell imaging analyses of wild-type endodermal cells demonstrated that the large central vacuole exhibits dynamic and

Table 1 Genes involved in gravitropism and control of gravitropic setpoint angle.

	Genes	Proteins	Molecular function	Plant species	Organs	References
Formation of statocytes	*SGR1/SCR*	GRAS family transcription factor	Transcriptional regulation	*Arabidopsis*	Shoot	Fukaki *et al*. (1998)
	SGR7/SHR/EAL1	GRAS family transcription factor	Transcriptional regulation	*Arabidopsis*	Shoot	Fukaki *et al*. (1998); Fujihira *et al*. (2000); Morita *et al*. (2007)
	ARF10, *ARF16*	ARF family transcription factor	Transcriptional regulation	*Arabidopsis*	Root	Wang *et al*. (2005)
Gravity sensing	*PGM*	Phosphoglucomutase	Starch biosynthesis in plastid	*Arabidopsis*	Shoot, root	Caspar & Pickard (1989); Kiss *et al*. (1989); Kiss *et al*. (1997)
	SGR2	Phospholipase A1-like	Related to vacuolar function	*Arabidopsis*	Shoot	Kato *et al*. (2002)
	SGR3/SYP21/AtVAM3	Syntaxin	Related to vacuolar function	*Arabidopsis*	Shoot	Yano *et al*. (2003)
	SGR4/ZIG	Qb-SNARE	Related to vacuolar function	*Arabidopsis*	Shoot	Kato *et al*. (2002)
	SGR5/IDD15	IDD family transcription factor	Transcriptional regulation	*Arabidopsis*, rice	Shoot	Morita *et al*. (2006); Tanimoto *et al*. (2008); Cui *et al*. (2013)
	SGR6	HEAT repeat motif protein	Related to vacuolar function	*Arabidopsis*	Shoot	Hashiguchi *et al*. (2014)
	SGR8/GRV2/KAM2	DnaJ and IWN repeat protein	Related to vacuolar function	*Arabidopsis*	Shoot	Silady *et al*. (2004); Tamura *et al*. (2007)
	SGR9	RING E3 ubiquitin ligase	Related to actin cytoskeleton	*Arabidopsis*	Shoot	Nakamura *et al*. (2011)
	RMD	Actin-binding protein	Related to actin cytoskeleton	Rice	Shoot, root	Huang *et al*. (2018); Song *et al*. (2019)
Gravity signalling	*ARG1/RHG1*	DnaJ-like, coiled-coil domain protein	Membrane trafficking?	*Arabidopsis*	Hypocotyl, root	Fukaki *et al*. (1997); Sedbrook *et al*. (1999); Boonsirichai *et al*. (2003)
	ARL2	DnaJ-like, coiled-coil domain protein	Membrane trafficking?	*Arabidopsis*	Hypocotyl, root	Guan *et al*. (2003)
	MAR1/TOC75-III	Subunit of translocon complex	Protein translocation at chloroplast outer membrane	*Arabidopsis*	Root	Stanga *et al*. (2009)
	MAR2/TOC132	Subunit of translocon complex	Protein translocation at chloroplast outer membrane	*Arabidopsis*	Root	Stanga *et al*. (2009)
	LZY family	Unknown protein with conserved C-terminal domain	Unknown	*Arabidopsis*, rice, maize, *Medicago*, wheat, *Lotus*	Shoot, root	Li *et al*. (2007); Yoshihara & Iino (2007); Dong *et al*. (2013); Uga *et al*. (2013); Yoshihara *et al*. (2013); Howard *et al*. (2014); Ge & Chen (2016); Taniguchi *et al*. (2017); Yoshihara & Spalding (2017); Ashraf *et al*. (2019); Chen *et al*. (2020)
	OsBRXL4	BRX-like domain protein	Unknown	Rice	Shoot	Li *et al*. (2019)
	RLD family	PH, RCC, FYVE, BRX domain-containing protein	Membrane trafficking?	*Arabidopsis*	Root	Furutani *et al*. (2020)

Table 1 (Continued)

	Genes	Proteins	Molecular function	Plant species	Organs	References
GSA	*WEEP*	SAM domain protein	Unknown	*Prunus persica* (peach)	Shoot	Hollender *et al*. (2018a)
	EGT2	SAM domain protein	Unknown	Barley, wheat	Root	Kirschner *et al*. (2021)
	TAC1	Unknown protein with conserved C-terminal domain	Unknown	*Arabidopsis*, rice, maize, *Prunus persica* (peach)	Shoot	Yu *et al*. (2007); Ku *et al*. (2011); Dardick *et al*. (2013)
Autostraightening	*Myosin XI*	Myosin	Motor protein that moves along actin filament	*Arabidopsis*	Shoot	Okamoto *et al*. (2015)

flexible membrane structures, whereas the dynamic features are lost for *sgr2* and *sgr4*/*zig*, probably leading to the impairment of amyloplast movement (Saito *et al*., 2005; Toyota *et al*., 2013). Taken together, these findings indicate that proper formation of vacuoles in endodermal cells is required for amyloplast sedimentation during gravity sensing.

In addition to the vacuole, thick actin bundles affect amyloplast sedimentation in shoot statocytes. *SGR9* encodes a C3H2C3-type RING E3 ubiquitin ligase, which is localised in amyloplasts in endodermal cells (Table 1; Nakamura *et al*., 2011). The mutation in *SGR9* causes excessive dynamic movement of amyloplasts. Pharmacological and live cell imaging analyses have suggested that the interactions between the amyloplasts and thick actin bundles are enhanced in *sgr9* mutants, resulting in less sedimentation. As E3 ubiquitin ligase activity is required for SGR9 function, SGR9 may control amyloplast–actin filament interactions via protein degradation. Although thin actin mesh has been observed in root statocytes (Blancaflor & Hasenstein, 1997), a close relationship exists between the regulation of the actin cytoskeleton and amyloplast sedimentation. Loss-of-function of DISTORTED 1/ACTIN-RELATED PROTEIN 3 causes the amyloplasts to be surrounded by thick actin bundles as well as insufficient amyloplast sedimentation (Zou *et al*., 2016). Additionally, the *rice morphology determinant* (*rmd*) mutant with enhanced root gravitropism exhibits faster sedimentation of amyloplasts upon gravistimulation in root columella cells. Given that *RMD*-encoded type-II formin FH5 localises on the surface of amyloplasts and that the actin filaments surrounding amyloplasts are reduced in the *rmd* mutant, RMD seems to function as a link between the actin cytoskeleton and amyloplasts (Table 1; Huang *et al*., 2018).

SGR5/*INDETERMINATE DOMAIN15* (*IDD15*) encodes a member of the *Arabidopsis* IDD transcription factors and is likely required for the full development of the shoot endodermis. *SGR5* expression is observed in shoot endodermal cells but not in columella cells in the roots, consistent with reduced gravitropism found only in the shoots of the *sgr5* mutant (Table 1; Morita *et al*., 2006). The accumulation of starch in amyloplasts is reduced in the endodermis of the *sgr5* mutant, resulting in a deceleration of amyloplast displacement upon gravistimulation (Tanimoto *et al*., 2008). Furthermore, the IDD family transcription factors IDD14, SGR5/IDD15, and IDD16 control auxin biosynthetic genes that encode YUCCA5 and auxin efflux carrier PIN-FORMED (PIN) proteins (Cui *et al*., 2013). SGR5 may control multiple steps in gravitropism, including the formation of auxin asymmetry in the shoots. In rice, an IDD gene was reported as a causal gene of the *loose plant architecture 1* (*lpa1*) mutation, which affects tiller and leaf angle (Wu *et al*., 2013). In the *lpa1* mutant, amyloplast sedimentation in the parenchyma cells of coleoptiles is slower than that in the wild-type. Based on phenotypic similarity, *LPA1* seems to be the functional ortholog of *Arabidopsis SGR5*. However, some distinct features exist between these two genes. For example, the *sgr5* mutant has specific defects in shoot gravitropism, whereas the *lpa1* mutant has pleiotropic phenotypes, including the development of internodes, leaves, and grains, as well as shoot gravitropism.

IV. Gravity-sensing mechanisms

Based on several lines of evidence, the classical starch–statolith hypothesis is widely accepted. Amyloplasts containing dense starch granules are heavier than the surrounding cytoplasm, resulting in settling in the statocytes upon gravistimulation. The *Arabidopsis phosphoglucomutase* (*pgm*) mutant, which fails to synthesise starch, shows reduced gravitropism in the shoots and roots (Table 1; Caspar & Pickard, 1989; Kiss *et al*., 1989, 1997; MacCleery & Kiss, 1999). However, the hypocotyl of the *starch excess 1* mutant, which contains larger amyloplasts with excess starch due to a defect in starch mobilisation, is more sensitive to gravistimulation (Vitha *et al*., 2007). The importance of starch in gravitropism has also been demonstrated in rice. Several starchless rice mutants lacking ADP-glucose pyrophosphorylase or LA2 exhibit reduced gravitropism and wider tiller angles (Okamura *et al*., 2015; Huang *et al*., 2021). However, the starch levels in the statocytes of these mutants are unknown because shoot statocytes have not been identified in rice shoots (Wang *et al*., 2022).

Researchers have questioned how the perception of gravity as a physical process in amyloplast displacement is converted into a biochemical signal in the statocyte. Several mechanotransduction models have been proposed based on mechanosensitive channels and/or cytoskeleton networks that are sensitive to the force/pressure exerted by amyloplast sedimentation (Yoder *et al*., 2001; Perbal & Driss-Ecole, 2003; Leitz *et al*., 2009; Fig. 2a,b). However, a link between mechanoreceptive channels and gravitropism has not yet been reported, although a series of studies have reported on these channels in plants in recent years. A transient increase in the cytosolic Ca^{2+} level has been detected in seedlings immediately

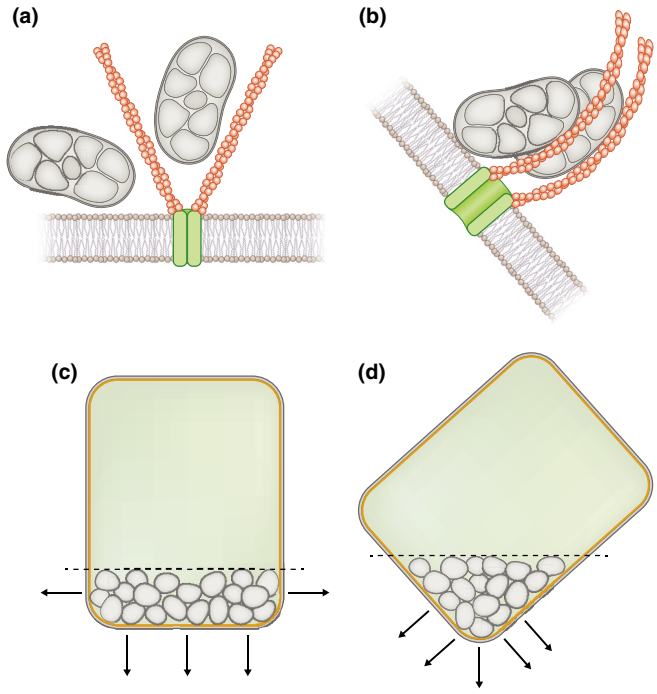


Fig. 2 Schematic presentation of two proposed gravity-sensing models in the statocytes. (a, b) Mechanotransduction model. The actin filaments link to the stretch-activated Ca^{2+} channel. In the steady state, amyloplasts do not trigger the channel by pressing actin filaments (a). Once the amyloplasts move in response to gravistimulation, they provide a mechanical tension on the actin filaments to activate the channel (b). (c, d) Position sensor model. The proximity or contact sites between the amyloplasts and plasma membrane induces local auxin flow in the cell, as indicated by the arrows. The sum of these local flows determines the direction of gross auxin flux.

after gravistimulation (Plieth & Trewavas, 2002; Toyota *et al.*, 2008). However, due to insufficient spatial resolution, it is unclear whether the change in the Ca^{2+} level is derived from the statocytes. Analysis using calcium indicators did not detect a change in the Ca^{2+} level upon gravistimulation in root columella cells (Legué *et al.*, 1997). A study under microgravity conditions in the International Space Station provided controversial results: cytoplasmic Ca^{2+} levels in the root columella cells of *Brassica napus* were monitored using a pyroantimonate precipitation method, and the change in the Ca^{2+} level was detected at the onset and removal of gravistimulation, without significant displacement of amyloplasts, by controlling 1 ***g*** centrifugation (Bizet *et al.*, 2018). It is expected that these results will be confirmed using modern approaches, such as live cell imaging analysis with high-sensitive Ca^{2+} sensors, to demonstrate the link between the change in Ca^{2+} precipitates and gravitropic signaling.

Given that amyloplasts transmit forces to cellular components, such as membranes and cytoskeletons, the gravitropic response should be sensitive to the magnitude of the gravitational force. However, physiological experiments combining centrifugal hypergravity and clinostats showed that shoot gravitropism depends not on the magnitude of the gravitational force but the angle of inclination in several angiosperm species (Chauvet *et al.*, 2016). This has led to the position sensor hypothesis, which suggests that statocytes sense the inclination, in a manner similar to that of a clinometer, via the intracellular position of the amyloplasts rather than through the magnitude of the gravitational force (Pouliquen *et al.*, 2017). In cuboid-like shoot statocytes, an avalanche pile of sedimented amyloplasts is caused by inclination, which is followed by a horizontal ridge line of the pile of amyloplasts (Fig. 2c,d). The position hypothesis proposes that the lateral difference in the areas of certain cellular components or structures at the sides of the cell to which amyloplasts are in close proximity leads to the recognition of the direction of gravity. Compared with liquids, granular materials, such as sand and amyloplasts, are not as sensitive to tilt because, due to interactions among granules, the granules do not cause avalanches unless the tilt angle is above a certain threshold. Nevertheless, plant organs can respond to a low-level tilt. This discrepancy can be explained as follows, based on the analyses of amyloplast behaviour in statocytes and experiments involving biomimetic cells consisting of microfluidic cavities filled with a suspension of heavy particles (Bérut *et al.*, 2018): if the particles are agitated to some extent, an avalanche of particles is more likely to occur, that is it is more sensitive to tilt. Indeed, amyloplasts are constantly agitated due to actin cytoskeletons (Sack *et al.*, 1986; Nakamura *et al.*, 2011), which possibly renders statocytes highly sensitive to tilt. The position sensor hypothesis could be a fascinating concept in relation to connecting amyloplast sedimentation with biochemical signal transduction in gravitropism.

Amyloplast sedimentation is indeed critical for gravitropism in angiosperms. However, starchless mutants still show reduced gravitropism in the roots and shoots, suggesting that plants do not rely only on starch accumulation in amyloplasts for gravity sensing (Caspar & Pickard, 1989; Kiss *et al.*, 1989; Huang *et al.*, 2021; Song *et al.*, 2021). Thus, either starchless amyloplasts somehow trigger gravitropism or unknown gravity-sensing machinery may function in parallel with amyloplast sedimentation.

In root gravitropism, from an evolutionally perspective based on analyses of the rhizoids or roots of various plant species representing lineages of mosses, lycophytes, ferns, gymnosperms, and angiosperms, it has been suggested that seed plants have developed root apex-specific gravity perception to acquire fast gravitropism (Zhang *et al.*, 2019). All roots except for moss rhizoids contain amyloplasts, and the roots of lycophytes have amyloplasts in cells above the root apex but not in cells within the root cap. Amyloplasts were observed in the root cap cells and the cells above the root apex in ferns, but they are specifically accumulated in cells at the root apex, including the root cap, in seed plants. Furthermore, amyloplast sedimentation is observed only in seed plants (Zhang *et al.*, 2019). According to these observations, amyloplast sedimentation is a relatively new gravity-sensing mechanism in the evolution of plants. However, a classic evolution-type gravity-sensing mechanism that contributes to slowing gravitropism may function in parallel with amyloplast sedimentation in seed plants, including *Arabidopsis*.

In maize roots, secondary gravity-sensing sites outside the root cap have been proposed in studies that used a unique device for imaging analysis combined with feedback control of the rotating stage (Wolverton *et al.*, 2002). This device keeps the angle of a small segment of the root tip constant during organ curvature. When the distal elongation zone was kept inclined, the root

curvature continued after the root cap reached a vertical position, that is when overshooting of the root was observed, suggesting that cells without amyloplasts in the distal elongation zone can sense organ inclination/gravity, although the contribution to gravitropism as a whole is minimal. This result can be explained using the protoplast-pressure hypothesis, which was proposed based on the observation of gravitropism in Chara internodal cells without statoliths and rice roots grown in medium with various densities (Staves *et al.*, 1992, 1997). In this hypothesis, the cells sense gravity as the differential pressure from the whole protoplast on the membrane or cell wall between the upper and lower sides of the cell. Slow root gravitropism in mosses, lycophytes, and ferns without amyloplast sedimentation might involve this type of gravity sensing, which could be related to the gravity-resistant response, in which plants alter their cell elongation in response to the magnitude of the gravitational force through the modification of cell wall properties (reviewed by Soga, 2013). It has been suggested that the mechanosensitive channel MCAs are involved in the gravity-resistant response in *Arabidopsis* hypocotyls (Hattori *et al.*, 2020; Yoshimura *et al.*, 2021). In the moss *Physcomitrium*, growth responds to the magnitude of the gravitational force (Takemura *et al.*, 2017). The protoplast-pressure hypothesis could be applied to explain sensing of the magnitude of gravity in general cells that developed in the early stages of evolution, after which the starch–statolith system may have evolved and increased the speed of gravitropism.

V. Gravity signalling leading to the regulation of auxin transport

After sensing the directional change of the gravity vector, information is converted to biochemical signals, leading to differential auxin flow. During this process, PIN proteins, mainly PIN3, become repolarised on the plasma membrane, leading to the redirection of auxin flow in the statocytes (Friml *et al.*, 2002; Harrison & Masson, 2008; Kleine-Vehn *et al.*, 2010; Rakusová *et al.*, 2011). However, the mechanisms underlying the control of PIN repolarisation due to gravity information have not been revealed. Genes involved in gravity signalling should be expressed and function in statocytes, and the loss-of-function mutations of such genes should affect the state of PIN proteins but not amyloplast sedimentation. Below, we outline the genes involved in gravity signalling, based primarily on findings in the roots.

VI. *ALTERED RESPONSE TO GRAVITY 1*

It was reported that *ALTERED RESPONSE TO GRAVITY 1* (*ARG1*) encoding the type-II DnaJ protein containing a J domain, hydrophobic domain, G/F region, and coiled–coil domain was the causal gene for the *altered response to gravity 1* (*arg1*) mutant, which shows reduced gravitropism in *Arabidopsis* roots and hypocotyls (Table 1; Fukaki *et al.*, 1997; Sedbrook *et al.*, 1999; Rajan & D'Silva, 2009). Although ARG1 is expressed ubiquitously, root cap-specific or endodermis-specific expression is sufficient to rescue the *arg1* phenotype in the roots and hypocotyls, respectively (Boonsirichai *et al.*, 2003). Among three closely related genes in *Arabidopsis*, *ARG1* and *ARG1-LIKE 2* (*ARL2*) are involved in gravitropism (Table 1; Guan *et al.*, 2003; Rajan & D'Silva, 2009). Asymmetric auxin signalling was not detected with a DR5:GUS reporter in *arg1* and *arl2* mutant roots, whereas starch accumulation was normal in these mutants (Harrison & Masson, 2008). In vertically growing root columella cells, PIN3 is uniformly localised in the plasma membrane; however, upon gravistimulation, PIN3 rapidly relocalises in the lateral side, that is the new bottom side, of columella cells (Friml *et al.*, 2002). In vertically growing *arg1* and *arl2* mutants, the PIN3 localisation pattern is indistinguishable from that of the wild-type. However, upon gravistimulation, the relocalisation of PIN3 in columella cells was impaired in *arg1* and *arl2* mutants (Harrison & Masson, 2008). ARG1 and ARL1 are peripheral membrane proteins localised in the plasma membrane, cell plates, and endomembrane compartments (Boonsirichai *et al.*, 2003; Harrison & Masson, 2008). A biochemical experiment suggested that a portion of ARG1 associates with the actin cytoskeleton (Boonsirichai *et al.*, 2003). Therefore, ARG1 and ARL2 may be involved in PIN3 relocalisation via a membrane trafficking pathway. Interestingly, it was also reported that a possible functional link exists between ARG1/ARL2 and amyloplasts, that is the mutants of the translocon of the outer membrane of chloroplasts (TOC) complex were isolated as enhancers of *arg1*, named *modifier of arg1* (*mar1* and *mar2*) (Table 1; Stanga *et al.*, 2009). *MAR1* and *MAR2* encode different components of the TOC complex, namely TOC75-III and TOC132, respectively. *mar1* and *mar2* single mutants enhance the *arg1* phenotype, whereas the single mutants of *mar1* and *mar2* do not have a gravitropic phenotype. Starch accumulation and amyloplast movement were normal in the double mutants, suggesting that MAR1 and MAR2 function in gravitropic signalling processes but not in amyloplast sedimentation, although it is not clear whether phenotypic enhancement via the *mar* mutations can be attributed to the function of the TOCs in the statocytes. Because ARG1 and ARL2 do not localise in the plastid, the physical interaction with the TOC complex does not affect gravitropism directly. Given that translocons are involved in protein transport across the membrane, clients of the TOC complex in amyloplasts and cargo proteins in ARG1 and ARL2-mediated vesicle trafficking to the plasma membrane may interact to transduce gravitropic signalling. As discussed in detail in the following section, possible candidates for clients of the TOC complex include the LAZY family proteins. Indeed, MAR1 was identified as an interacting protein of LZY2 and LZY3 through coimmunoprecipitation coupled with LC–MS/MS (Furutani *et al.*, 2020). This is an attractive hypothesis to be investigated in future studies.

VII. LAZY1 family proteins

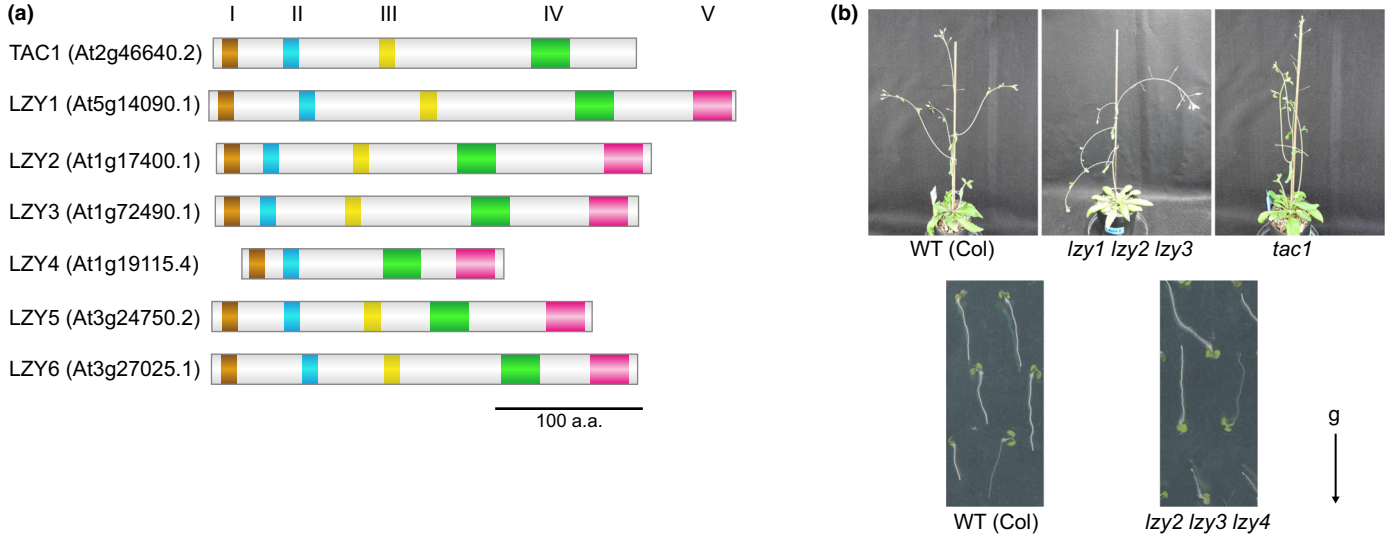
1. Structure and function

The recent findings related to *LAZY1* family genes have been vital in advancing our understanding of the signal transduction process of gravitropism. *LAZY1* was originally identified in rice as a causal gene for the 'lazy' phenotype or prostrate shoot growth mutants (Table 1; Li *et al.*, 2007; Yoshihara & Iino, 2007). Later, based on

sequence similarity, six *LAZY1* family genes in *Arabidopsis* were reported (Table 1; Yoshihara *et al.*, 2013) (Figs 3a, 4). Various names have been given to the LAZY1 family genes by several research groups because of their mutant phenotypes. Here, we use LZY to represent *Arabidopsis* and the original names for the other plant species, according to previous nomenclature (Taniguchi *et al.*, 2017; Nakamura *et al.*, 2019). Although the extent of the contribution of each gene differs, *LZY1*, *LZY2* and *LZY3* function redundantly in shoot gravitropism, whereas *LZY2*, *LZY3*, and *LZY4* function in root gravitropism (Ge & Chen, 2016; Taniguchi *et al.*, 2017; Yoshihara & Spalding, 2017; Fig. 3b). The statocyte-specific expression of *LZY* genes can restore gravitropic responses in *lzy* mutants (Taniguchi *et al.*, 2017). Collectively, these results indicate that the LZY family proteins that function in statocytes are likely to contribute to shoot gravitropism. Although the *lzy1 lzy2 lzy3* triple mutant is agravitropic in the shoots, amyloplast sedimentation in the endodermis is not impaired in this mutant, suggesting that the LZY proteins function in the signalling process following amyloplast sedimentation. As mentioned above, the repolarisation of PIN3 upon gravistimulation leads to asymmetric auxin distribution in the roots and hypocotyl. Asymmetric expression of DR5rev:GFP was observed in the wild-type but not in the *lzy1 lzy2 lzy3* mutant after reorientation. In the roots of the *lzy2 lzy3 lzy4* triple mutant, auxin accumulation in the upper flank of roots was increased according to analysis involving DR5rev:Venus and DII:Venus (Yoshihara & Spalding, 2017; Ge & Chen, 2019). These results indicate that LZY proteins function between the processes of gravity sensing and the establishment of asymmetric auxin distribution.

The functional importance of *LZY* family genes in gravitropism has been reported in various plant species, including maize, *Medicago*, *Lotus*, and wheat species (Table 1; Dong *et al.*, 2013; Uga *et al.*, 2013; Howard *et al.*, 2014; Ge & Chen, 2016; Salojärvi *et al.*, 2017; Ashraf *et al.*, 2019; Chen *et al.*, 2020). Although the functional importance of *LZY* family genes has yet to be investigated in other plant species, they are also found in moss, *Physcomitrium*, and Selaginella (Guseman *et al.*, 2017; Kitomi *et al.*, 2020; Waite & Dardick, 2021; Xia *et al.*, 2021). Phylogenetic studies indicate that the *LZY* family genes can be classified into four subgroups: the LZY1 group, LZY/DRO group, TAC1 group, and another group (Kitomi *et al.*, 2020; Waite & Dardick, 2021; Fig. 4).

Among the LZY family proteins, known functional domains have not been found, although multiple alignment revealed that five conserved regions exist within these proteins (Fig. 3a). Because of a well conserved sequence motif (GXL(A/T)IGT) in region II,



(c)

	Region I	Region II	Region III	Region IV
	***	* *	**	***
TAC1	MTIFNWVQKKLHQ	NWFDGVLTIGTFGFDTLN	---TDHF---GS-	IKK---MRQMIKRMLKKKIHPDVD
LZY1	MKFWGWMHHKFRE	DFFDGFLAIGTLGGETLL	KFPLQEYF-FGSL	KKK---FQKMVQV-FHRKVHPEES
LZY2	MKFFGWMQNKLNG	DWPHALLAIGTFGTTSNS	NLPLDRFLNCPSS	ESR---MEKLLKMMLHKKINAQAS
LZY3	MKFFGWMQNKLHG	DWPHGLLAIGTFGNKKQT	NLPLDRFLNCPSS	ETR---MEKLLRMMLHKKVNTQAS
LZY4	MKIFSWVQRKLSG	QDEETFLAIGTLGNNIFP	----------	NTR---MEKMLRTILNKKIHPQRS
LZY5	MEIFQWLFKLGRS	LWCRKDVAKACFSSTFTL	KIKAQGGEEQVTS	NRR------KLKMM--REVNEEES
LZY6	MKLLSWMRTIKPN	DEFCGFLAIGTLGTDPET	ECPLQDYDLFRSS	SKKKKDLKKNV-QTCRRKVHPVLC

Fig. 3 Structure of LZY/TAC1 family proteins in *Arabidopsis* and loss-of-function phenotypes. (a) Structure of the *Arabidopsis* LZY family. Because several splicing variants are found in the database, the representative variants shown here were selected for analysis. (b) The loss-of-function phenotype of the *lzy1 lzy2 lzy3* and *tac1* mutations in the shoots and *lzy2 lzy3 lzy4* mutation in the roots. Arrow indicates the gravity vector. (c) Sequence alignment of four conserved regions in LZY family proteins. Asterisks (*) indicate the mutagenised amino acids in LZY1 (Yoshihara & Spalding, 2020).

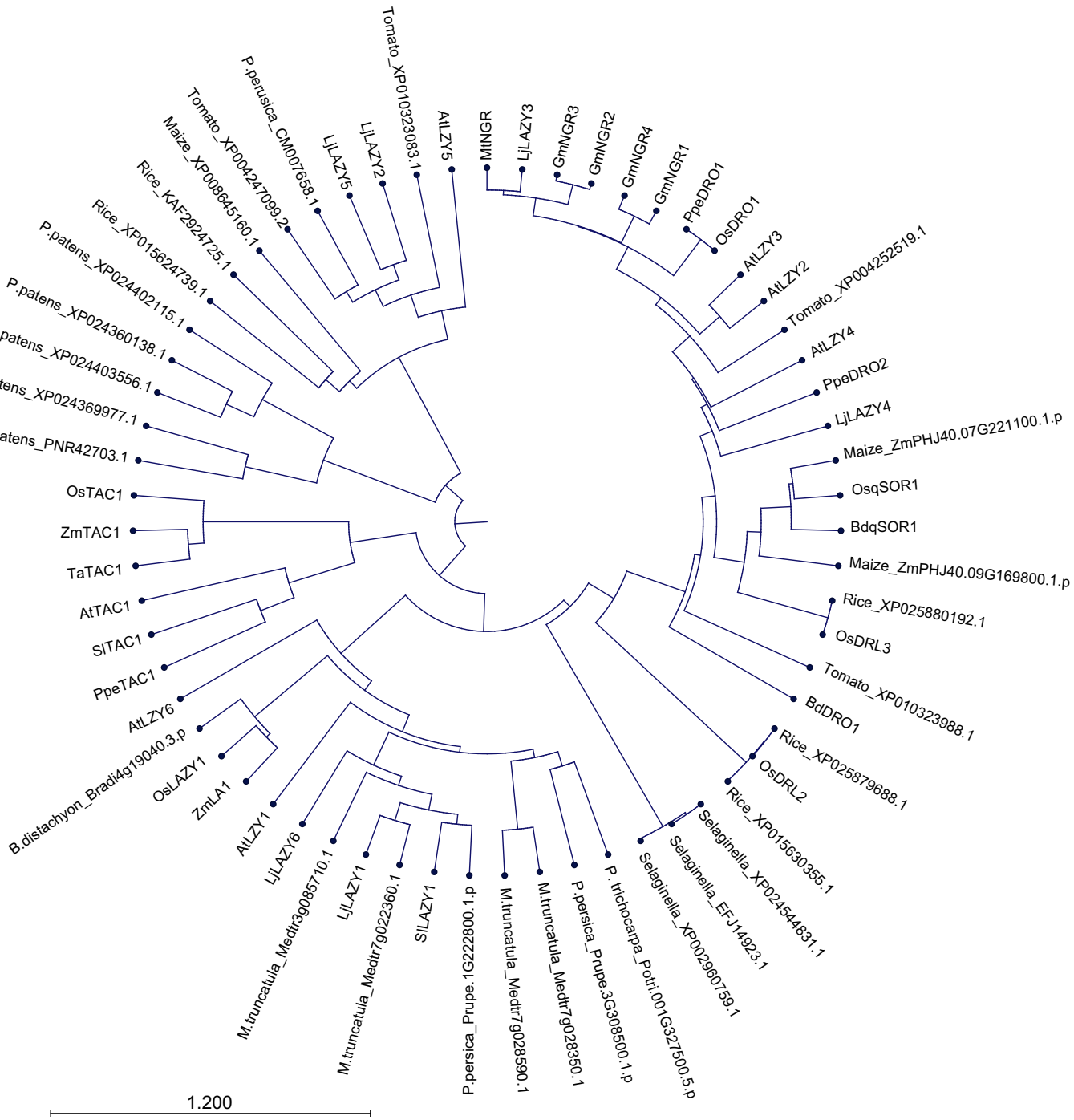


Fig. 4 Phylogenetic tree of LZY/TAC1 family proteins based on genome information from *Arabidopsis thaliana*, *Lotus japonicus*, *Medicago truncatula*, *Glycine max*, *Solanum lycopersicum*, *Oryza sativa*, *Zea mays*, *Triticum aestivum*, *Brachypodium distachyon*, *Physcomitrium patens*, *Selaginella moellendorffii*, *Prunus persica* and *Populus trichocarpa*. Sequences were analysed using ClustalW, and the circular phylogenetic tree was visualised using CLC sequence viewer.

LZY family genes are also referred to as IGT family genes together with TAC1 (Dardick *et al.*, 2013; Fig. 3c). To investigate the functional importance of the five conserved regions of LZY family proteins, mutational analyses have been performed (Yoshihara & Spalding, 2020; Figs 3c, 5a). A mutation in region I diminishes LZY1 function to complement the *lzy1* phenotype of the lateral branch angle. Similar results were reported in the region II and V variants of LZY1. However, region III and IV variants could rescue the *lzy1* phenotype slightly, although not to the level of wild-type LZY1. These two regions are not highly conserved compared with the conservation of other regions (Yoshihara *et al.*, 2013; Taniguchi *et al.*, 2017; Nakamura *et al.*, 2019), which may have minor effects on function. Mutations in region V, also known as the conserved C-terminus in LAZY1 family proteins (CCL), have major effects on

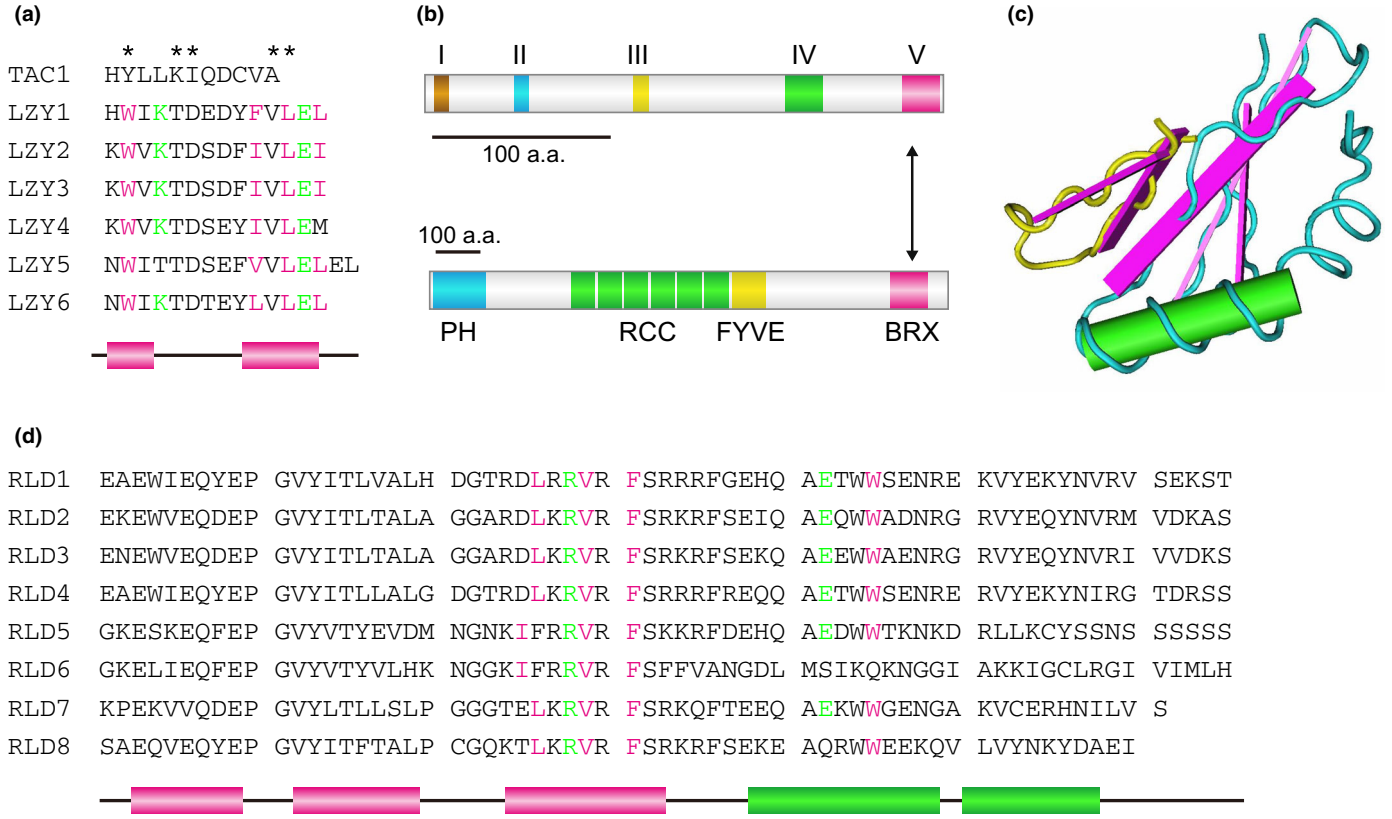


Fig. 5 Interaction between LZY–RLD family proteins. (a) Sequences of the region V CCL in LZY family proteins. Magenta boxes indicate β-sheets. Asterisks (*) indicate the mutagenised amino acids in LZY1 (Yoshihara & Spalding, 2020). (b) Schematic illustration of the domain structure of LZY3 and RLD2. Double arrows indicate the interaction domains between LZY3 and RLD2. (c) Crystal structure of the LZY3–CCL and RLD2–BRX complex. Backbones in yellow and cyan indicate LZY3–CCL and RLD2–BRX, respectively. β-Sheets and α-helixes are presented in magenta and green, respectively. Modified from PDB: 6L0V. (d) Sequence alignment of the BRX domain from *Arabidopsis* RLD proteins. Magenta and green boxes indicate β-sheets and α-helixes, respectively. Texts in magenta and green indicate the key amino acids for hydrophobic interactions and salt bridge interactions, respectively.

LZY1 function (Taniguchi *et al.*, 2017; Yoshihara & Spalding, 2020).

2. Nuclear localisation of LZY family proteins and functions

The sequence of the CCL is weakly similar to that of the ethylene-responsive element binding factor-associated amphiphilic repression motif, which is found in numerous transcriptional repressors (Ohta *et al.*, 2001; Dardick *et al.*, 2013). To investigate the subcellular localisation of LZY1, GFP-tagged LZY1 was generated under the control of its promoter in the *lzy1* mutant. However, N-terminal and C-terminal GFP fusions failed to complement the *lzy1* phenotype and detect a GFP signal (Yoshihara *et al.*, 2013). To ensure that the function of LZY1 was not disrupted, GFP was inserted between the conserved region IV and region V CCL. Although this LZY1–GFP fusion protein rescued the *lzy1* phenotype, the GFP signal was not visible. According to ectopic expression using *Nicotiana benthamiana* and transient overexpression in *Arabidopsis*, the LZY1 protein is localised in the plasma membrane and nucleus. In a previous study, to clarify the functional importance of nuclear localisation or plasma membrane localisation of LZY1, the predicted nuclear localisation signal was disrupted. Therefore, mutated LZY1 was observed only in the plasma membrane and fully complemented the *lzy1* phenotype. Although the possibility that a small number of nuclear-localised LZY1 functions in gravitropism cannot be excluded, the aforementioned study suggested that plasma membrane-localised LZY1 functions in gravitropism (Yoshihara *et al.*, 2013).

Rice LAZY1 also localises in the nucleus and plasma membrane, similar to *Arabidopsis* LZY1 (Yoshihara *et al.*, 2013; Li *et al.*, 2019). A Brevis Radix (BRX) domain-containing protein, BRX-like 4 (OsBRXL4), was identified as a rice LAZY1-interacting protein (Table 1; Li *et al.*, 2019). OsBRXL4 contains three BRX domains that are required for the interaction with the C-terminal part of LAZY1, and this interaction prevents the nuclear localisation of LAZY1 (Fig. 6; Table 2). The overexpression of OsBRXL4 leads to wider tiller angles, similar to those of the rice *lazy1* mutant. Therefore, OsBRXL4 might control tiller angles by interfering with LAZY1 nuclear localisation. Additionally, the wheat LAZY1 family protein TaDRO1 interacts with the wheat orthologue of TOPLESS, a transcriptional corepressor protein (Ashraf *et al.*, 2019). The maize LZY1, ZmLA1, is also localised in the plasma membrane and nucleus (Howard *et al.*, 2014) and interacts with IAA17 in the nucleus (Dong *et al.*, 2013; Fig. 6; Table 2).

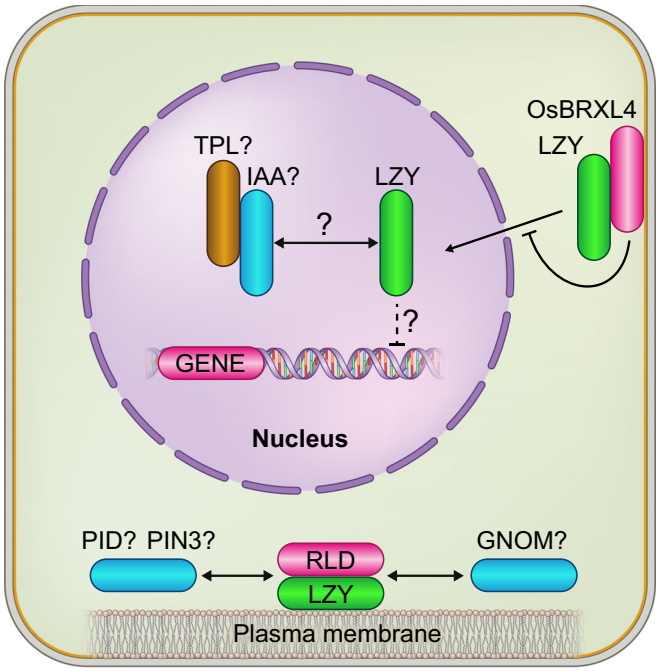


Fig. 6 Schematic illustration of LZY function in the nucleus and plasma membrane. According to a study on rice, nuclear-localised LAZY1 is functional, and its nuclear localisation is inhibited by plasma membrane-localised OsBRXL4 (blunt-ended arrow; Li *et al*., 2019). In the nucleus (dashed circle), maize ZmLA1 interacts with IAA17 and wheat TaDRO1 interacts with TPL (double-headed arrow, Dong *et al*., 2013; Ashraf *et al*., 2019). While the interactions and nuclear localisation were reported, involvement of ZmLA1 in transcriptional regulation is open question (dashed blunt-ended arrow). In the plasma membrane, *Arabidopsis* LZY3 interacts with RLD1 on the bottom side of the cell (Furutani *et al*., 2020). Some evidence suggests that the LZY–RLD complex interacts with GNOM and PID (double-headed arrows, Dong *et al*., 2013; Furutani *et al*., 2020; Wang *et al*., 2022). In addition, Table 2 lists the details of these interactions.

However, the functional importance of the nuclear localisation of TaDRO1 and ZmLA1 in gravitropism is not clear. All these localisation studies used ectopic or transient expression systems; therefore, *in vivo* localisation studies in shoot statocytes are required to clarify where LZY1 functions in shoot gravitropism.

3. Plasma membrane localisation of LZY family proteins and their function

In *Arabidopsis*, plasma membrane-localised LZY1 is likely to function in shoot gravitropism (Yoshihara *et al*., 2013). Localisation studies using *Arabidopsis* protoplasts showed the localisation of C-terminally mCherry-tagged LZY3 (LZY3-mCherry) in the plasma membrane but not in the nucleus (Taniguchi *et al*., 2017). Furutani *et al*. (2020) reported that LZY3-mCherry is localised to the plasma membrane asymmetrically in the columella cells of young lateral roots. By contrast, Waite *et al*. (2020) reported that Venus-tagged LZY3 localises in the nucleus in the elongation zone of primary and lateral roots but that the signal is undetectable in columella cells. However, it is unclear whether the nuclear localisation of LZY3 in the elongation zone is important for gravitropism. In young lateral root columella cells, LZY3 was localised on the bottom of the plasma membrane. To date, intracellular localisation of LZY family proteins has been reported only at the site of function, that is polar localisation of LZY3 in the plasma membrane of columella cells. Upon gravistimulation via reorientating of the lateral roots, LZY3 relocalised in the new bottom of the plasma membrane within 30 min. This rapid gravistimulation-induced LZY3 relocalisation suggests that the protein may connect the gravity-sensing and gravity-signalling processes. However, due to the weak signal of LZY3-mCherry, the behaviour of LZY3 according to gravistimulation was only observed in fixed and cleared samples. Live imaging of LZY family proteins in gravity-sensing cells remains challenging and requires further investigation.

4. Unique features of LZY1

Among the LZY family proteins in *Arabidopsis*, LZY1 has some unique features. N-terminal and C-terminal fusions of fluorescent

Table 2 List of known interactions of LZY family proteins.

Plant species	Interactions	Methods	Localisation	References
Oryza sativa	LAZY1-OsBRXL4	Yeast two hybrid Co-IP BiFC	Plasma membrane (rice protoplast)	Li *et al*. (2019)
Zea mays	ZmLA1-IAA17	Yeast two hybrid BiFC	Nucleus (tobacco leaf epidermis)	Dong *et al*. (2013)
Zea mays	ZmLA1-PKC	Yeast two hybrid BiFC	Plasma membrane (tobacco leaf epidermis)	Dong *et al*. (2013)
Triticum aestivum	TaDRO1-TaTPL	Yeast two hybrid BiFC	Nucleus (tobacco leaf epidermis)	Ashraf *et al*. (2019)
Arabidopsis thaliana	LZY3-RLD1	Yeast two hybrid Co-IP	Plasma membrane (*Arabidopsis* columella cells)	Furutani *et al*. (2020)
Arabidopsis thaliana	LZY3-GNOM	Co-IP	Unknown	Furutani *et al*. (2020)
Arabidopsis thaliana	RLD2-GNOM	Yeast two hybrid Co-IP BiFC	Golgi apparatus, endosome (tobacco leaf epidermis) (*Arabidopsis* stomatal lineage cells)	Wang *et al*. (2022)

proteins interfere with LZY1 function in gravitropism (Yoshihara *et al.*, 2013), whereas such interference of LZY3 functionality has not been observed (Furutani *et al.*, 2020; Waite *et al.*, 2020). Additionally, only LZY1 localises in the nucleus and plasma membrane. The other LZY family proteins localise in the plasma membrane alone or the nucleus alone (Yoshihara *et al.*, 2013; Taniguchi *et al.*, 2017; Furutani *et al.*, 2020; Waite *et al.*, 2020). Additionally, in maize, ZmLA1 is involved in gravitropism as well as inflorescence development (Dong *et al.*, 2013). Although the results are only clear in maize currently, such dual localisation of LZY1 suggests that LZY1 has multiple functions in gravitropism and development in different cellular compartments. Based on phylogenetic tree construction, LZY1 group proteins are separated from the other LZY family proteins, which may reflect the functional uniqueness of LZY1 group proteins.

VIII. Regulator of chromosome condensation 1-like domain family proteins

Regulator of chromosome condensation 1 (RCC1)-like domain (RLD) family proteins are conserved among land plants and share a pleckstrin homology (PH) domain, RCC1-like motif repeats, a Fab/YGL023/Vps27/EEA1 (FYVE) domain, and a BRX domain from the N-terminus (Fig. 5b). The PH and FYVE domains of RLD1 have been reported to bind to several phospholipids (Jensen *et al.*, 2001; Heras & Drøbak, 2002). Among the eight *RLD* family genes in *Arabidopsis*, *RLD1–4* are isolated as LZY interactors and expressed in various tissues, including the columella cells. The *rld1 rld4* double mutant has a wider growth angle of the lateral root tip than that of the wild-type, and the gravitropic phenotype is rescued by columella-specific expression of *RLD1* (Table 1; Furutani *et al.*, 2020). Asymmetric expression of DR5rev:GFP does not occur in the roots of the *rld1 rld4* mutant or those of the *lzy1 lzy2 lzy3* triple mutant. Furthermore, the loss of RLD1 and RLD4 leads to reduced PIN3-GFP levels in the columella cells of the lateral roots. RLD1–4 interact with LZY family proteins via the BRX domain and CCL (Fig. 5). A mutational study of the LZY3 CCL sequence indicated the functional importance of the LZY3–RLD1 interaction in the control of the root GSA. In columella cells, LZY3 changes its polar distribution in the plasma membrane upon gravistimulation, leading to the recruitment of cytoplasmic RLD1 into the plasma membrane. Taken together, these findings suggest that LZY3 recruits RLD1 in the direction of gravity in columella cells during gravity signal transduction (Fig. 6). Due to severe developmental defects, it was impossible to analyse the shoot gravitropism of the *rld* quadruple mutant. However, based on interaction studies between the LZY1 CCL and RLD BRX domains and given the functional importance of the LZY1 CCL (Furutani *et al.*, 2020), we can speculate that LZY1 may also interact with RLD1–4 in the endodermal cells of the shoots and may recruit to the bottom of cells. In further studies, the contribution of RLD family proteins in shoot gravitropism should be investigated using modern molecular genetic tools, such as CRISPR-Cas9-based tissue-specific knockout systems (Decaestecker *et al.*, 2019; Rojas-Murcia *et al.*, 2020).

IX. Possible PIN regulation mediated by LZY–RLD during gravitropism

Researchers have investigated the underlying mechanisms by which LZY and RLD proteins regulate auxin flow in statocytes. The RCC1-like domain containing a fragment of RLD1/PRAF1 has the catalytic activity of guanine nucleotide exchange against Rab8a *in vitro* (Jensen *et al.*, 2001), and Rab8a is a member of the RAB8/RABE class involved in membrane trafficking post-Golgi to the plasma membrane. Localisation analyses revealed that RLD family proteins associate with the Golgi, TGN/EE, endosomes, and the plasma membrane in *Arabidopsis* epidermal cells (Wang *et al.*, 2022). The *rld* quadruple mutant phenotype also provides insights. For instance, the embryonic defect in the quadruple mutant *rld1 rld2 rld3 rld4* resembles that of the *gnom* mutant (Mayer *et al.*, 1991, 1993; Furutani *et al.*, 2020). Consistently, an interaction between RLD1 and GNOM has been reported during the polarity establishment process in stomatal development (Wang *et al.*, 2022). GNOM was included in coimmunoprecipitates with LZY2 and LZY3, suggesting that it is a new candidate component in the LZY–RLD protein complex (Furutani *et al.*, 2020). GNOM encodes an ARF-GEF protein involved in membrane trafficking and controls root gravitropism through PIN3-mediated auxin flow (Kleine-Vehn *et al.*, 2010). According to the collective evidence, the most feasible scenario is that the LZY–RLD–GNOM signalling module regulates the trafficking of PIN3 in the statocytes during root gravitropism (Fig. 6).

Numerous studies have suggested that the polar localisation and auxin transport activity of PINs are controlled by their phosphorylation state. It has been reported that AGCVIII-type Ser/Thr protein kinases, PINOID (PID), WAVING AGRAVITROPIC ROOTs (WAGs), D6 PROTEIN KINASES, and PROTEIN KINASE ASSOCIATED WITH BRX (PAX) are involved in the phosphorylation of PINs (Barbosa *et al.*, 2018; Marhava *et al.*, 2018). The overexpression of PID interferes with gravity-induced PIN3 polarisation in the endodermal cells of the hypocotyl, whereas the loss-of-function mutant of PID and its closest homologues of WAG1 and WAG2 induce PIN3 polarisation, resulting in a hypergravitropic response in the hypocotyl (Rakusová *et al.*, 2011). These findings suggest that PIN3 phosphorylation mediated by PID kinase plays an inhibitory role in PIN3 polarisation in gravitropism. A possible functional relationship between the LZY family proteins and kinases has been suggested, that is maize ZmLA1 interacts with a protein kinase similar to PID in the plasma membrane in tobacco epidermal cells (Dong *et al.*, 2013; Fig. 6; Table 2). It has also been reported that, during the process of protophloem sieve element differentiation, AtBRX harbouring double BRX domains interacts with PAX and colocalises with PINs in the plasma membrane in a PAX-dependent manner. PAX activates PIN-mediated auxin transport via phosphorylation, and this activity is inhibited by AtBRX. Auxin induces the dissociation of AtBRX from the plasma membrane, leading to PAX activation (Marhava *et al.*, 2018). Assuming that the function is similar to that of the BRX domain, the LZY–RLD module may induce PIN3 relocalisation upon gravistimulation by interfering with the activity of PID/WAG kinases.

X. Termination of gravitropic bending

Termination of gravitropic bending is considered important for maintaining the posture of plant organs and the whole plant architecture (Bastien *et al.*, 2013; Moulia *et al.*, 2019). After sufficient gravitropic bending, plant organs terminate bending to maintain the straightness of organs. This phenomenon has been termed autotropism or autostraightening (Tarui & Iino, 1997; Stanković *et al.*, 1998) and modelled as proprioception (Bastien *et al.*, 2013), which is also involved in phototropism. However, the organ straightening mechanisms that underlie the maintenance of plant architecture are largely unknown. Asymmetric auxin distribution mediated by PIN3 triggers organ bending by stimulating cell elongation. After bending, this asymmetry must be terminated and the symmetric distribution must be re-established. Indeed, after organ bending, auxin feedback terminates the asymmetric auxin distribution pattern (Rakusová *et al.*, 2016). Gravistimulation-mediated polarisation of PIN3 establishes an auxin gradient in the hypocotyl, and subsequent auxin feedback induces PIN3 polarisation toward the inner membrane at the lower flank. Accordingly, the authors concluded that the initial auxin flow from the upper to lower flank contributes gravitropism, and the subsequent opposing auxin flow terminates organ bending by dissipating the auxin asymmetry. During this process, GNOM-mediated PIN3 trafficking and nuclear auxin signalling are required (Rakusová *et al.*, 2016; Han *et al.*, 2020).

Another possible mechanism underlying the termination of organ bending involves the dynamics of the cytoskeleton. In *Arabidopsis*, Okamoto *et al.* (2015) reported that the myosin XI mutant (*myosin xif xik*) has an organ straightening defect in the primary inflorescence stem, hypocotyl, and roots after gravitropic bending (Table 1). In addition to gravitropism, the *myosin xif xik* double mutant also has a defect in the hypocotyl and petiole in the straightening process of phototropism. The expression of myosin XIk, driven by the myosin XIf promoter, in the xylem fibre cells and interfascicular fibre cells but not in the endodermal cells is sufficient to complement the myosin *xik* and myosin *xik xif* phenotypes. Such cell type-specific expression suggests that organ straightening driven by myosin XIf and XIk is gravity-sensing independent. Myosin XI proteins function in actin organisation and dynamics in *Arabidopsis* and *Physcomitrium* (Peremyslov *et al.*, 2010; Ueda *et al.*, 2010; Vidali *et al.*, 2010). In the fibre cells, longitudinal very-long actin cables were observed, which may serve as a type of tension sensor. Indeed, the semidominant actin 8 mutant *fiz1* has a similar overbending phenotype, as observed in the myosin *xif xik* double mutant (Kato *et al.*, 2010; Okamoto *et al.*, 2015). The detailed mechanisms underlying myoxin XI–mediated organ straightening are still under investigation; however, cytoskeleton dynamics contribute to organ straightening outside gravity-sensing cells.

XI. Anti-gravitropic offset

As mentioned earlier, lateral organs, such as lateral roots and shoot branches, maintain specific growth angles relative to a gravity vector, which is known as the GSA (Digby & Firn, 1995). Studies on gravitropism have mainly focused on the responses of elongating primary roots and primary shoots upon gravistimulation by the reorientation. However, lateral branches and lateral roots continuously grow at a specific growth angle. Continuous and constant gravity cues could trigger gravitropism of the lateral organs during their inclined growth, yet they grow straight at a constant angle without continuous bending, as if they were not subjected to gravistimulation. Accordingly, the concept of the AGO has been proposed to interpret this phenomenon. The GSA is thought to be determined by the balance between gravitropism and the AGO (Roychoudhry & Kepinski, 2015). The molecular mechanisms underlying gravitropism have been well studied, but our knowledge of the AGO, including its enigmatic molecular nature, is limited. It was reported that auxin signalling is important in the control of the AGO (Roychoudhry *et al.*, 2013). Lateral roots and lateral branches change their growth direction to upwards and downwards, respectively, during clinorotation under pseudomicrogravity conditions (De Vries, 1872; Roychoudhry *et al.*, 2013). This anti-gravitropic growth is thought to reflect the AGO. NPA treatment blocks the anti-gravitropic growth of lateral branches and lateral roots, suggesting that auxin transport is required for the AGO. Analyses using various auxin-related mutants also demonstrated that auxin transport and auxin signalling are involved in the AGO. Interestingly, the endodermis-specific expression of dominant-negative *bdl* (Hamann *et al.*, 2002) enhanced the AGO, resulting in the horizontal growth of lateral branches (Roychoudhry *et al.*, 2013). Similar cell type-specific expression of stabilised IAA17 (Swarup *et al.*, 2005) indicated the importance of auxin signalling in columella cells in the root AGO. Collectively, these results suggest that auxin signalling in statocytes is important for the AGO.

In various plant species, *LZY* family genes contribute to the GSAs of the primary roots, lateral roots and shoot branches by controlling gravitropism. The *lzy2 lzy3 lzy4* mutant exhibits an opposite gravitropic response in the primary roots, and its lateral roots grow upwards; however, the shoot branches of the *lzy1 lzy2 lzy3* mutant grow downwards, and its lateral roots grow horizontally or upwards (Ge & Chen, 2016; Taniguchi *et al.*, 2017; Yoshihara & Spalding, 2017). The peculiar phenotypes of *lzy* multiple mutants are termed 'anti-gravitropic' phenotypes, and it is assumed that they are due to the manifestation of the AGO caused by the loss of gravitropism (Kawamoto *et al.*, 2020). Ge & Chen (2019) found that genetic and pharmacological disruption of polar auxin transport through mutations in *PIN* genes and auxin transport inhibitor NPA treatment, respectively, randomised the directional root growth of the *lzy2 lzy3 lzy4* mutant. This finding also highlights the importance of auxin transport in the control of the AGO.

Genetic analyses have been performed to characterise the 'anti-gravitropic' phenotypes and reveal the nature of the AGO. For example, by combining the *sgr1* and *eal1* mutant, which have defects in endodermal specification, with the *lzy1 lzy2 lzy3* triple mutant, the importance of the endodermis to the 'anti-gravitropic' phenotype of the *lzy1 lzy2 lzy3* mutant was investigated, and both quadruple mutants were found to be agravitropic (Kawamoto *et al.*, 2020). Consistent with previous research (Roychoudhry

et al., 2013), the AGO requires the endodermis in the shoots as it is required for gravitropism. To investigate the gravity-sensing mechanism underlying the AGO, the starchless *pgm* mutation was introduced into *lzy1 lzy2 lzy3* and *lzy2 lzy3 lzy4* mutants, respectively. The *pgm* mutation randomised the growth angles of the primary roots in the *lzy2 lzy3 lzy4 pgm* mutant compared with in its parental *lzy* triple mutant, but this effect was limited in the lateral branches of the *lzy1 lzy2 lzy3 pgm* mutant. Therefore, the starchless amyloplasts reduced the 'anti-gravitropic' effect, and gravitropism and the AGO apparently share a similar gravity vector sensing mechanism involving the use of starch-filled amyloplasts as statoliths. Taken together, these findings suggest that gravitropism and the AGO require endodermal cells in the shoots and starch-filled amyloplasts in statocytes for gravity sensing in the shoots and roots.

XII. Similarity and uniqueness of the GSA in the shoots and roots

The physiological properties of the AGO have been revealed gradually; however, the molecular nature of the AGO remains elusive. A candidate for the key regulator gene in the shoot AGO is *TILLER ANGLE CONTROL 1* (*TAC1*), which was reported originally in rice as a quantitative locus trait of the tiller angle and later in peach trees (*Prunus persica*), maize, and *Arabidopsis* (Table 1; Yu *et al.*, 2007; Ku *et al.*, 2011; Dardick *et al.*, 2013; Hollender *et al.*, 2018a). In rice, the loss of *TAC1* results in a narrower tiller angle, whereas its overexpression causes a wider tiller angle. Loss-of-function *TAC1* mutations cause the vertically oriented growth of shoot branches in peach trees and *Arabidopsis*. *TAC1* encodes a plant-specific protein similar to the LZY family proteins except for its C-terminal (Dardick *et al.*, 2013; Nakamura *et al.*, 2019). LZY family proteins have a conserved C-terminal CCL, which is essential for their function in gravitropism because of its interaction with RLD family proteins (Furutani *et al.*, 2020; Yoshihara & Spalding, 2020); however, the TAC1 protein lacks a CCL. This difference may represent functional diversification between LZY family proteins and TAC1 (Fig. 5a). In the *lzy1 tac1* double mutant, *lzy1* is epistatic to *tac1* (Hollender *et al.*, 2020), implying that there is another contributor (or contributors) in the AGO beside TAC1. For example, it has been reported that WEEP, a sterile alpha motif (SAM) domain-containing protein, is responsible for the weeping phenotype of shoot branches in peach trees (Table 1; Hollender *et al.*, 2018b). A WEEP-related SAM domain-containing protein, ENHANCED GRAVITROPISM 2 (EGT2), which controls the root growth angle in barley and wheat, was reported (Table 1; Kirschner *et al.*, 2021). EGT2 is expressed in the whole root tip, including the root cap, meristem and elongation zone. Because of its expression pattern, EGT2 is thought to contribute to the signal transduction process of gravitropism rather than gravity sensing or differential cell elongation (Kirschner *et al.*, 2021). Accordingly, some factors contribute in a shoot- or root-specific manner, whereas other factors function in the shoots and roots. Therefore, in addition to molecule-oriented studies, such as the characterisation of TAC1, unbiased forward genetic screening should be conducted to deepen our understanding of the AGO.

XIII. Interaction with environmental cues in coordination of the GSA

In addition to gravity information, many environmental factors affect plant architecture. For example, light is an important environmental factor for plant growth and development. ELONGATED HYPOCOTYL 5 (HY5), a basic leucine zipper transcription factor, promotes plant photomorphogenesis via transcriptional regulation of its target genes (Gangappa & Botto, 2016) and affects root gravitropism (Oyama *et al.*, 1997). Together with HY5, PHYTOCHROME INTERACTING FACTORs (PIFs), members of the basic helix–loop–helix transcription factor family, controls hypocotyl and root gravitropism through the transcriptional regulation of *LZY3* (Yang *et al.*, 2020). *TAC1* is also controlled transcriptionally by light and photosynthetic signals, thereby modulating plant architecture (Waite & Dardick, 2018). In addition to light signalling, environmental temperature is important for plant adaptation (Posé *et al.*, 2013; Jung *et al.*, 2016; Legris *et al.*, 2016). SGR5, an IDD transcription factor involved in shoot gravitropism, reportedly has two splicing variants, SGR5α and SGR5β; higher temperature induces SGR5β expression, which in turn interferes with SGR5α activity by forming nonfunctional heterodimers. Consequently, shoot gravitropism is lost under high temperature (Kim *et al.*, 2016). In the later steps of gravitropism, asymmetric auxin distribution is a driving force of differential organ growth. Together with auxin signalling, auxin biosynthesis is a key process. Furthermore, the TGA class bZIP transcription factor OsbZIP49 controls rice tiller angle through the transcriptional regulation of auxin biosynthetic genes (Ding *et al.*, 2021).

Below ground, root architecture is also affected by environmental factors. In response to water and nutrients, plants change the growth angle of their roots toward these resources. The former response is known as hydrotropism, and MIZ1, a domain of unknown function (DUF617) protein, and MIZ2/GNOM are involved in *Arabidopsis* hydrotropism (Kobayashi *et al.*, 2007; Miyazawa *et al.*, 2009). The latter repose is known as nutritropism, and NH_4^+ attracts the lateral roots of rice (Yamazaki *et al.*, 2020). Phosphate is also an important nutrient for plants, and it affects the growth angle of the crown roots in rice (Huang *et al.*, 2018). The actin-binding protein RMD controls amyloplast sedimentation in root columella cells to change the root growth angle. A loss-of-function mutation of RMD, amyloplast-associated actin-binding protein, increases the speed of root gravitropism. It has also been suggested that RMD is regulated to adjust the growth angle in response to phosphate conditions. In the shoots, RMD contributes to gravitropism by regulating actin dynamics in a light-dependent manner (Song *et al.*, 2019). The PIF-like transcription factor OsPIL16 possibly controls RMD expression negatively. In summary, various environmental cues are integrated transcriptionally and post-transcriptionally to coordinate the GSA.

XIV. Perspectives

During the past several decades, the identification of some key genes has deepened our understanding of the molecular mechanisms underlying gravitropism and the AGO. Previous studies have proposed several fascinating concepts related to gravity sensing, signal transduction and control of the GSA. Other knowledge gaps should also be addressed, such as how the polar localisation of LZY family proteins is controlled and how LZY–RLD modules control PIN3 polar localisation. Filling these knowledge gaps might allow us to elucidate the mechanisms underlying plant gravitropism. Gravitropism and the AGO are two sides of the same coin in terms of the control of the GSA. As well as characterising the AGO itself, the mechanisms underlying gravitropism must be elucidated to deepen our understanding of the control of the GSA in the shoots and roots. For instance, although LZY family proteins and TAC1 share similar sequences except for the C-terminus, their loss-of-function phenotypes are opposites. Therefore, further characterisation of TAC1 might reveal the enigmatic nature of the AGO while providing valuable information on gravitropism. Importantly, such findings could contribute to improving crop production by facilitating the modification of the GSA. Indeed, in the plant breeding, the plant architecture is one of the target traits for improving crop productivity. Especially, in rice, upright tiller angle phenotypes have been selected during domestication processes (Yu *et al.*, 2007; Dong *et al.*, 2016; Inagaki *et al.*, 2021). In wheat and maize, tiller, and leaf angles are also target traits for breeding (Ku *et al.*, 2011; Marone *et al.*, 2020).

Unlike monocots, weeping growth habits in woody species, such as apple and peach, are target traits for horticulture (Dougherty *et al.*, 2018; Hollender *et al.*, 2018a). Because woody plants have rigid stems surrounded by lignified cell walls, they develop reaction woods with specialised cell wall properties to achieve gravitropism (Gerttula *et al.*, 2015; Groover, 2016). Although the mechanisms that control gravitropic bending differ among woody plants and herbaceous plants, several common key players, including LZY, TAC1 and WEEP, contribute to GSA control. Further understanding of gravitropism and the AGO could expand the possibilities of plant breeding and accelerate the process to obtain plant ideotypes by coordinating the GSA in the shoots and roots.

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