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REVIEW

Research advances in plant root geotropism

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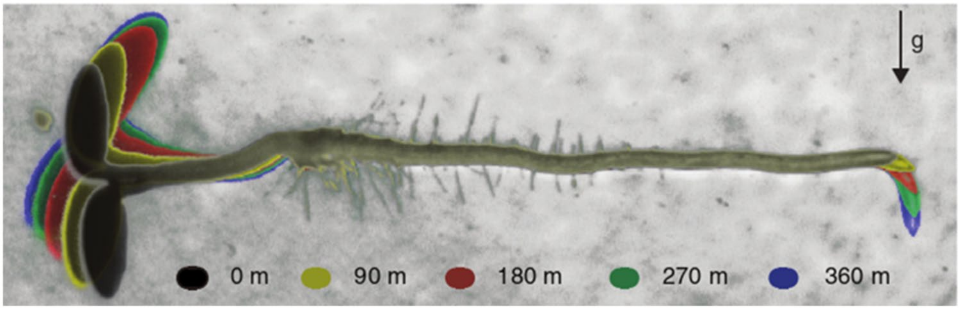
Abstract

Plants cannot grow or develop properly without the support of their roots. Gravity plays an essential role in the formation of the root structure, but it is not clear how roots respond to gravity signals or how downward growth occurs. The two best-known models for root gravity sensing affirm the importance of starch. After the hyper-sensitive root crown perceives a gravity signal, starch granules within the rootlet cells settle to the endoplasmic reticulum in the direction of the signal, where they bind to specific receptors or open ion channels and release downstream signaling molecules. This triggers a series of signal transduction mechanisms, and this process involves signaling molecules such as indole-3-acetic acid (IAA), reactive oxygen species, and calcium signaling, which ultimately induce groundward root growth. This review summarizes the mechanism of action underlying, and a research overview of, how plant roots sense and respond to gravity. The role of key signals such as starch, IAA, and calcium ions in root gravitropism is analyzed by integrating available information. The results provide a more complete theoretical basis for how roots grow toward gravity, which will contribute to our understanding of gravitropism and lay the foundation for discovering new directions of scientific research.

Graphical abstract



The graphics developed in this article are done by Microsoft Office PowerPoint 2010, Adobe Illustrator 2018 and ChemDraw 20.0.

Keywords Root · Starch grains · IAA · Ca^{2+} · ROS

Introduction

One of the differences between plants and animals is the way of movement. Plants generally cannot move and can only passively receive stimuli from the environment. Plants have, however, evolved excellent mechanisms to adapt to the terrestrial environment: When plants perceive an external stimulus, complex signal transduction mechanisms arise to eliminate or attenuate damage (Zhang et al. 2022b). These

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include the directional movements of higher plants, such as hydrotropism, phototropism, and gravitropism, which were acquired over time as they adapted to the natural environment (Fig. 1). Well-developed roots anchor plants in the soil for better nutrient uptake. The positive groundward motion of roots is necessary for plants to obtain nutrients and water, while their ultimate, long-term bending angle is the key to nutrient utilization by the root tip. The response of the root is complex when sensing changes in gravity vectors, obstacles, and other stimuli (Toal et al. 2018).

The process of root growth gravitropism is divided into three main components: gravity perception, signal transduction, and differential growth. In this review, we discuss the currently validated understanding of these three stages of root geotropism and summarize the findings of the molecular mechanisms involved in the formation of gravitropism in the incipient roots of higher plants. This paper provides a new perspective on root growth research by summarizing and analyzing the theory of root geotropism.

Gravity perception

Starch-equilibrium stone hypothesis

Beginning with Knight's (1806) proposal that gravity controls the direction of root growth, a theoretical system on root gravitropism has gradually been established. The amyloplast-equilibrium theory was first proposed by Haberlandt (1900), who discovered freely moving starch grains in the chloroplasts and white bodies of purple duck-toed grass stem nodule cells and called them otoliths or equilibrium stones. This theory suggests that starch grains sense gravity and are deposited in the endoplasmic reticulum. This triggers a signal transduction cascade reaction that allows the resulting signal molecules to be transmitted to gravity-sensing sites in the root elongation zone, ultimately achieving gravitational root growth (Němec 1900). Altered starch density affects the root's response to gravitational stimuli. Starch-deficient and starch-free mutants have now been discovered, including *Nicotiana plumbaginifolia* and *Arabidopsis thaliana*; the density of amyloplasts in these mutants is much lower than in the wild type (WT) (Lin et al. 1988; Kiss et al. 1989; Caspar and Pickard 1989; Masson PH et al. 1995). Moreover, few mutant amyloplasts are deposited at the bottom of the cell, which leads to a significantly weaker tendency for groundward root growth. In *Arabidopsis*, artemisinin can interfere with the response of roots to gravity by limiting the number of amylopectin grains in root tips (Yan et al. 2018). The application of 3-nitrophthalic acid or 1-naphthaleneacetic acid (1-NAA) to *Arabidopsis* seedlings leads to a significant increase in starch grain accumulation in the root tip relative to dimethyl sulfoxide treatment and to a faster rate of groundward growth (Zhang et al. 2019b). This evidence suggests that starch is important to the perception of gravity through the primitive root. The columnar cells in the root crown, with their dense starch granules, are the locus of the response of the vascular plant root to gravity (Morita 2010). This explains Barlow's (1974) suggestion that the perception of gravity in maize is diminished after the removal of the root crown.

Protoplasm hypothesis

Although most authors support the starch-equilibrium stone hypothesis, it remains controversial whether this theory is the only basis for the groundward growth of roots in higher plants (Richter et al. 2019; Ishikawa and Evans 1990) showed experimentally that the root tip is not the only gravity-sensing tissue, and it was found that plants could still sense gravity after the removal of the root crown (Blancaflor et al. 1998). This phenomenon was verified in maize seedlings (Edelmann et al. 2018). Wayne and Staves (1996) proposed the protoplast hypothesis, which holds that plant cells use the buoyancy in their protoplasts as a medium to sense gravity and that gravity can circulate protoplasts. As

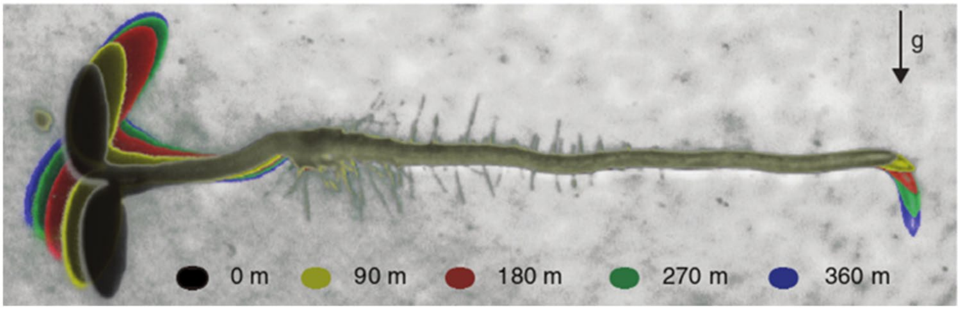

Fig. 1 *Arabidopsis* seedling root and hypocotyl develop opposite curvature responses to gravistimulation. Overlaid images of a 4-day-old *Arabidopsis* seedling (Col ecotype) responding to gravistimulation. Images were taken every 90 min. Overlaid images are false-colored differently with photoshop to better illustrate organ bending. (SU et al. 2017)

the flow of protoplasts in the gravitational field changes, the tension between the upper cell wall and the cell membrane is enhanced. The tension of the cell membrane then changes, which activates tension-sensitive ion channels on the plasma membrane (PM). This changes the concentration of Ca^{2+} in the cytoplasm, triggering downstream signaling and ultimately causing the gravity-bending growth of the root.

Gravity perception model

Perbal (1999) suggested that plants may have derived multiple gravity-sensing mechanisms during evolution and that the starch-equilibrium stone hypothesis and the protoplast hypothesis may act simultaneously during gravity perception in root growth. Researchers have experimentally tested two models to describe how physical signals are converted into chemical signals after deposition of amyloplasts in root column cells. One study suggested that the deposited amyloplasts exert pressure on sensitive PM in resting cells, thus opening mechanosensitive ion channels in the membrane and releasing signaling molecules such as calcium ions that trigger downstream signaling (Su et al. 2017). Another model, proposed by Limbach et al. (2005), suggested that the rootstock senses gravity not through starch deposition in the endoplasmic reticulum or pressure in the protoplasm but rather through some component of the surface of the deposited amyloplast that is in direct contact with the membrane-bound receptor; this is known as the ligand-receptor model.

In sum, starch is indispensable for the process of gravity perception in plant roots. In recent years, it has been found that, in addition to starch, IAA is also essential for gravity perception and starch accumulation in plant root tips (Zhang et al. 2019b). However, the establishment of the specific mechanisms of gravity perception requires further investigation.

Signal transduction

Column root crown cells sense gravity in roots, but the gravitropic response occurs in elongation zone cells (Han et al. 2021). Starch grains in higher plants move vectorially under the effect of gravity (Zhang and Friml 2019a). The gravity-stimulated deposition of starch grains leads to the release of a downstream signal from the endoplasmic reticulum, which causes gravity tropism of roots (Kiss et al. 1989; Evans et al. 1986). This downstream signal is IAA, which is synthesized in the developing leaf primordia and stem tip and then is transported to the target tissue. It is polarized and transported by a carrier. Quantitative biochemical analysis of IAA levels and in vivo expression analysis using IAA response or the biosensing of IAA levels have revealed the presence of a lateral IAA gradient in root tips subjected to gravity stimulation (Baldwin et al. 2013).

Transport of IAA in plant roots

In a previous study, labeling IAA with the IAA response elements DR5 and the IAA2 and IAA sensor DII 28 showed the location and differential accumulation of IAA distribution in roots under gravity (Brunoud et al. 2012). The Cholodny-Went theory suggests that the asymmetric distribution of IAA in plants causes geotropic bending growth in the roots (Mesland 1992). IAA is usually transported between cells in polar transport mode, which is primarily regulated by the IAA influx carrier AUX1 and the IAA efflux carrier protein PIN family in concert (Bennett et al. 1996; Han et al. 2021).

There are three members of the *AUX1/LAX* gene family in *Arabidopsis*: *AUX1*, *LAX2*, and *LAX3* (Swarup and Bhosale 2019). Only *AUX1* is expressed in the lateral root cap (LRC), columella, and epidermis, and it plays a root-directed role. The functions of these carriers are to sense, transmit, and respond to gravity (Swarup et al. 2001, 2004). When AUX1 protein is deficient, the rate of IAA transport is limited, and the gravitational perception of roots is diminished. In a previous study, this was alleviated by applying NAA to the *aux1* mutant (Marchant et al. 1999). By examining the local expression of an HA-epitope-tagged *AUX1* sequence (*HA-AUX1*) in *Arabidopsis* root tissues, Swarup et al. (2005) found that root-directed growth requires both the LRC and epidermal cells to express *AUX1*, which implies that both tissues have IAA transport functions. Measurement of the root bending amplitude of WT and *Osaux1* mutants in *Oryza sativa* has revealed that this angle is reduced in the absence of the *AUX1* gene (Taylor et al. 2021). This is further evidence of the important role of AUX1 for groundward root growth.

Genomic analysis of *Arabidopsis* has revealed eight major homologs of the *PIN* gene family, *PIN1–PIN8* (Chen et al. 1998) and some efflux carrier proteins have been found to be localized to the root tip (Müller et al. 2014). Among them, small column cells contain *PIN3*, *PIN4*, and *PIN7*, whereas LRC, epidermal, and cortical cells express *PIN2* (Friml et al. 2002; Blilou et al. 2005). In Band et al. (2012), DII-Venus, a novel IAA sensor, was combined with a mathematical modeling approach; IAA in the root was asymmetrically distributed when stimulated by gravity for a short period, and its concentration was significantly greater on the inner side of the curved root than on the outer side (Konstantinova et al. 2021). This may be because gravity stimulates *PIN3/7* to reposition to the earthward side of a columnar cell, which results in the initial lateral IAA gradient (Swarup et al. 2005).

PIN protein phosphorylation may be responsible for this asymmetric distribution. It depends on the small GTPase of the *auxin response factor* (*ARF*) associated with GNOM-type GDP/GTP exchange factor (Ganguly et al. 2012). Researchers have found that both PID/WAGs kinase activity and PIN phosphorylation regulate PIN3 protein relocalization in roots within the gravitational field. When PID/WAGs are downregulated, PIN3 localization is enhanced and roots grow in a geotropic bend (Grones et al. 2018). PIN2 induces asymmetric localization of IAA, allowing expression of the inward and outward flow promoters *AUX1* and *PIN2* and directing IAA from the root crown to the elongation zone (Luschnig et al. 1998; Chen et al. 1998). Moreover, AUX1 usually regulates root reorientation upstream of PIN2 (Liu et al. 2018). According to Blilou et al. (2005), *PIN2* expression in the distal elongation zone produces a protein that is localized to the epidermal cells at the root apex and LRC, which tugs on PIN2 to induce the movement of IAA. *PIN3/7* are expressed in mid-column sheath cells and transport IAA from the distal elongation zone to the root crown, which forms an IAA return loop (Fig. 2). This loop is important for root gravity. Differences in IAA concentrations lead to differential cell growth, and PIN-mediated IAA distribution controls cell division and elongation (Blilou et al. 2005; Sato et al. 2015). Wang et al. (2022b) demonstrated the importance of *PIN1* in *Oryza sativa*. Compared to WT, the roots of the ospin1b mutant grow non-geotropically, probably because *OsPIN1b* regulates root reversion through signals such as light and nutrients. This complements the study of PIN proteins in plant root-oriented heaviness.

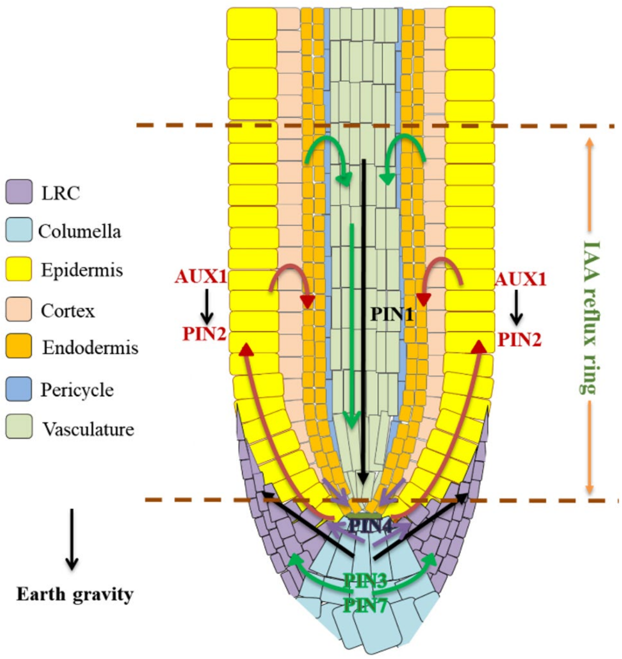

Fig. 2 Return pattern of root IAA transport. Plant root growth toward gravitropism is regulated by the IAA in-flow carrier AUX1 and the out-flow carrier PIN family of proteins. Under the effect of gravity, AUX1 promotes the expression of *PIN2* in epidermal cells and tracts PIN2 to induce IAA movement to the elongation zone; meanwhile, *PIN3/7* expression in the mid-column sheath changes the IAA concentration therein and transports IAA from the distal elongation zone to the root crown, finally forming a return loop of IAA to make the root growth in the direction of gravity

Regulation of plant root gravitropism by *LAZY1*

In addition to the PIN and *AUX1/LAX* gene families, the *LAZY1* gene family also has an important role in plant gravitropism (Jiao et al. 2021). In this family, *AtNGR1* (*LZY2*), *AtNGR2* (*LZY3*), and *AtNGR3* (*LZY4*) are expressed in rhizosphere cells (Yoshihara and Spalding 2017). In recent years, researchers have found that *ngr* mutant roots of *Medicago truncatula*, *Arabidopsis*, and *Lotus japonicus* exhibit negative geotropic growth (Ge and Chen 2016, 2019; Chen et al. 2020). Further studies of *atngr1;2;3* mutants have led to the conclusion that the counter-transportation of PIN3 in rootlet cells in the mutant to the cell membrane on the outer side in response to gravity stimulation may be the cause of this phenomenon. The *LAZY1* gene family may thus be the bridge between gravity-induced amyloplast migration and directional IAA transport (Nakamura et al. 2019; Furutani et al. 2020) further used a yeast two-hybrid screen with an interaction assay and found that the BRX structural domain of the RCC1-like (RLD) protein and the CCL structural domain of LZY in *Arabidopsis* interacted in vitro to regulate groundward root growth. LZY3 follows the gravitational direction of amyloplast deposition and enriches RLD1 polarity into the PM of small column cells. RLD may lead to asymmetric distribution of IAA by regulating the transport of PIN3.

Transcriptome analysis of root gravitropism mechanism

In the systematic study of root-directed growth gene regulation, there has been a breakthrough regarding the transcriptional level of root-directed growth. A *HUB* gene with high transcriptional activity in *Arabidopsis* was identified (Manian et al. 2021) and these genes are involved in cell wall Gene Regulatory Networks only in spaceflight microgravity. Network analyses suggest that Xyloglucan endoglycosyl transferases/hydrolases (*XTH*s) modify cell walls and mediate cell growth in *Arabidopsis* in a microgravity environment. In microgravity conditions, *XTH*s act on the cell wall to produce greater elongation, leading to cell swelling and root deflection. Aubry-Hivet et al. (2014) analyzed the early changes in *Arabidopsis* WT and mutant root transcriptome under microgravity, hyper-gravity, and other treatments, and found that 15 genes in the root responsive to IAA gene ontology (GO) classification were upregulated in WT and *pin2* mutants but not significantly in *pin3* mutants. This suggests that the regulation of IAA-responsive gene expression in

WT during transient microgravity depends on PIN3-mediated IAA flux. Fuji et al. (2018) subjected seedlings with waterward and gravity responses to transcriptome analysis of RNA-Seq gene expression. In all, 21 and 45 genes were asymmetrically expressed in the root under water and gravity induction, respectively, and 5 genes were identical. GO analysis revealed that key genes regulating IAA were significantly enriched in the concave side of the root compared to the convex side during root growth toward water or toward gravity (Fuji et al. 2018).

Geotropic growth of roots

Gravitropism of starch and roots

Starch is a macromolecular carbohydrate that is formed by the polymerization of glucose molecules. Altered starch density affects the sensitivity of the root to gravitational stimuli. With starch-deficient mutants as carriers, the plastids still contain limited amounts of starch, but their density increases somewhat. The amyloplasts at this point are not sufficient to allow for post-sedimentation response to gravity. However, when centrifugal forces are high, these amyloplasts continue to precipitate, and plants regain geotropism (Vitha et al. 2007). Conversely, mutations such as *Arabidopsis sex1*, which affect starch-degrading enzyme activity, may enhance gravity-sensing sensitivity by producing larger amyloplasts (Lin et al. 1988; Vitha et al. 2007). Although there is substantial evidence for the important role of starch grains in root geotropism, starch deposition may not be the only mechanism. Mancuso et al. (2006) found that the root of maize seedlings remains somewhat gravitropic after excision of the root crown, a response that could be enhanced by manipulating myosin activity or by disrupting actin filaments. Despite the absence of precipitated amyloplasts in this region, gravity sensing may occur through protoplast pressure (Su et al. 2017).

Gravitropism of calcium ions and roots

Calcium is abundant in plants. It is important in the composition of the body structure of the plant and has a key role in metabolism and signaling (White et al. 2002). One study found that Ca^{2+} is a secondary messenger that transmits gravity signals (Hepler et al. 1985). External stimuli affect cellular Ca^{2+} concentration balance by triggering transient changes in Ca^{2+} concentration in cytoplasm and subcellular structures (Kordyum 2003).

The large family of Ca^{2+}-sensing proteins in plants contains proteins composed of calcineurin B-like proteins (CBLs), calmodulin-like proteins (CMLs), and calmodulin (CaM) with CBL-interacting protein kinases, as well as Ca^{2+}-dependent protein kinases (CDPKs) and related kinases (Batistic and Kudla 2012; Wang et al. 2021; Harmon et al. 2000) found that *Arabidopsis* has 34 CDPK-encoding genes, and the CDPK family is among the largest Ca^{2+} sensor families. Ca^{2+} can stimulate CDPKs to decode and translate calcium signals (Cheng et al. 2002). The calcium-dependent ion channel protein located on the vesicle membrane releases Ca^{2+} from the vesicle to regulate abiotic stress responses in stomatal guard cells (Ja´slan et al. 2019). Flooding stress leads to root hypoxia in plants, and knocking down *ACA* (Ca^{2+}-ATPase) and *CAX* (Ca^{2+}/H^+ exchanger) has shown that *ACA* alleviates the damage to the root by knocking down its Ca^{2+} content (Wang et al. 2016). Within plant cells, changes in Ca^{2+} are sensed by major response proteins or sensors. Among them, CMLs, CaM, and CBLs can bind to free Ca^{2+} in the cytoplasm, which regulates their activity and thus triggers downstream physiochemical effects (DeFalco et al. 2010; Tian et al. 2020; Grenzi et al. 2021).

Ca^{2+} in plant cells is transported through specific transport sites (Fig. 3), and transient elevations initiate cellular responses to various environmental, developmental, and pathological stresses (White 2000). Amyloplast sedimentation can cause Ca^{2+} exocytosis from the endoplasmic reticulum to the cytoplasm, and external environmental stimuli and endogenous signals can also cause transient increases in cytoplasmic Ca^{2+} concentrations, which ultimately activate related proteins downstream directly or indirectly (Sander et al. 2002; Belyavskaya 1992) found that different stimuli result in elevated cytoplasmic Ca^{2+} levels and completely inhibit *Pisum sativum* seedling root geotropism, which provides evidence for the role of Ca^{2+} on root geotropism. Lee et al. (1983) reported asymmetric Ca^{2+} gradients in roots under gravity, such as those of *Pisum sativum* and *Zea mays*. Subsequently, Lee et al. (1984) found that the sensitivity of groundward root growth was reduced by applying Ca^{2+} chelate. The role of Ca^{2+} in the root gravity growth of higher plants was further verified. Ca^{2+} is involved in regulating the differential changes in extracellular pH around the elongation zone at the apical and bottom sides of gravity-stimulated roots in response to IAA, which leads to changes in root orientation (Su et al. 2017).

Plant hormones and root gravitropism

Plant hormones including IAA, cytokinin (CTK), gibberellin (GA), and ethylene (ET) are key signaling compounds that regulate plant growth, development, and adaptation responses to environmental stresses. Root system architecture (RSA) is affected by hormonal crosstalk and hormone-environment interactions that are integrated with plant biology (Liu et al. 2014). These factors integrate with the plant signaling system through specific downstream regulators, which leads to changes in plant signaling pathways

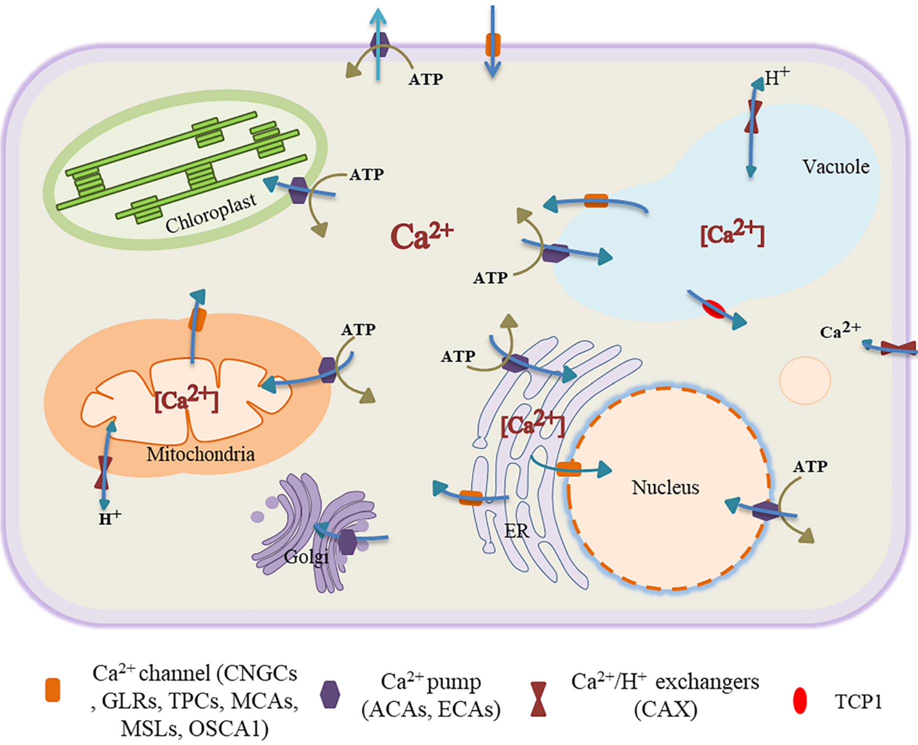

Fig. 3 Ca^{2+} transport pathway. Ca^{2+} transport in plants is achieved through Ca^{2+} transport channels and sites of action on the plasma membrane of organelles. Reference Tong et al. (2021) plotted

(Sengupta and Reddy 2018; Sharma et al. 2021). Šimášková et al. (2015) found that CTK induces the expression of *PIN1/7* through the CTK response factors *CRF2/6*, thereby regulating RSA. Brassinosteroids can alter the gravitropism of *Zea mays* roots by regulating reactive oxygen species (ROS) metabolism and other pathways (Trevisan et al. 2020).

IAA can modulate plant perception and response to gravity (Zhang et al. 2019b). Approaches based on plant physiology, genetics, and cell biology revealed that the signal mediating the gravimetric response is IAA (Friml et al. 2002). Following gravity sensing, PIN2 and AUX1 control IAA transport aboveground, while PIN3/7 shift to the gravity-facing side of the columnar cells and mediate IAA repositioning (Bennett et al. 1996; Utsuno et al. 1998; Luschnig et al. 1998; Kleine-Vehn et al. 2010). This promotes high IAA concentrations on the groundward side, which inhibits differential cell growth and leads to a groundward root curvature. The asymmetric IAA gradient in plant roots is regulated by several IAA signaling molecules, including *ARF*, the *Auxin/IAA* (*Aux/IAA*) family, and *small auxin-upregulated RNA* (*SAUR*), among others (Luo et al. 2018). Among these, the ubiquitination of Aux/IAA proteins can inhibit the activity of ARFs, thus regulating IAA activity (Yu et al. 2022). The *arf10/16* double mutant of *Arabidopsis* significantly suppresses the positive gravitropism of its roots compared to WT, perhaps because *ARF10* and *ARF16* control root crown formation by limiting cell division and differentiation, thereby altering the sensitivity of their roots to gravity (Wang et al. 2005). *ARF7* can induce the asymmetric distribution of downstream methyltransferase, which converts IAA from inactive methylindole-3-acetate to biologically active IAA, thereby enhancing the concentration gradient of IAA in the hypocotyl and creating a different growth curvature to gravity (Zhang et al. 2022a).

ET can regulate root growth by affecting gravity-induced lateral transport of IAA to alter root orientation. This process may interfere with the transport of IAA to alter the adaptation to gravitational stimuli (Lee et al. 1990). Root elongation is inhibited by ET in the transport of IAA through PIN2. The intrinsic mechanism is the involvement of the ET-responsive HD-Zip gene *HB52* in ET-induced primary root elongation in *Arabidopsis*. *HB52* inhibits root growth by regulating the expression of the IAA transporter-related genes *WAG1*, *WAG2*, and *PIN2* (Miao et al. 2018) (Fig. 4).

The PIN transporter within the root tip has been shown to alter local IAA concentration changes, which induces the expression of downstream key genes for starch synthesis (*ADG1*, *SS4*, and *PGM*) and ultimately alters the strength of gravity perception (Zhang et al. 2019b). GA is essential for the germination, growth, and development process of plant seeds (Richards et al. 2001). Abscisic acid (ABA) can block GA biosynthesis and inhibit seed growth (Meng et al. 2016). An embryo synthesizes biologically active GAs, which are then transported to the dextrin layer during germination. GA-induced cGMP catalyzes the synthesis of the α-amylase gene by regulating the transcription of GAMYB to enable its expression. Finally, to hydrolyze

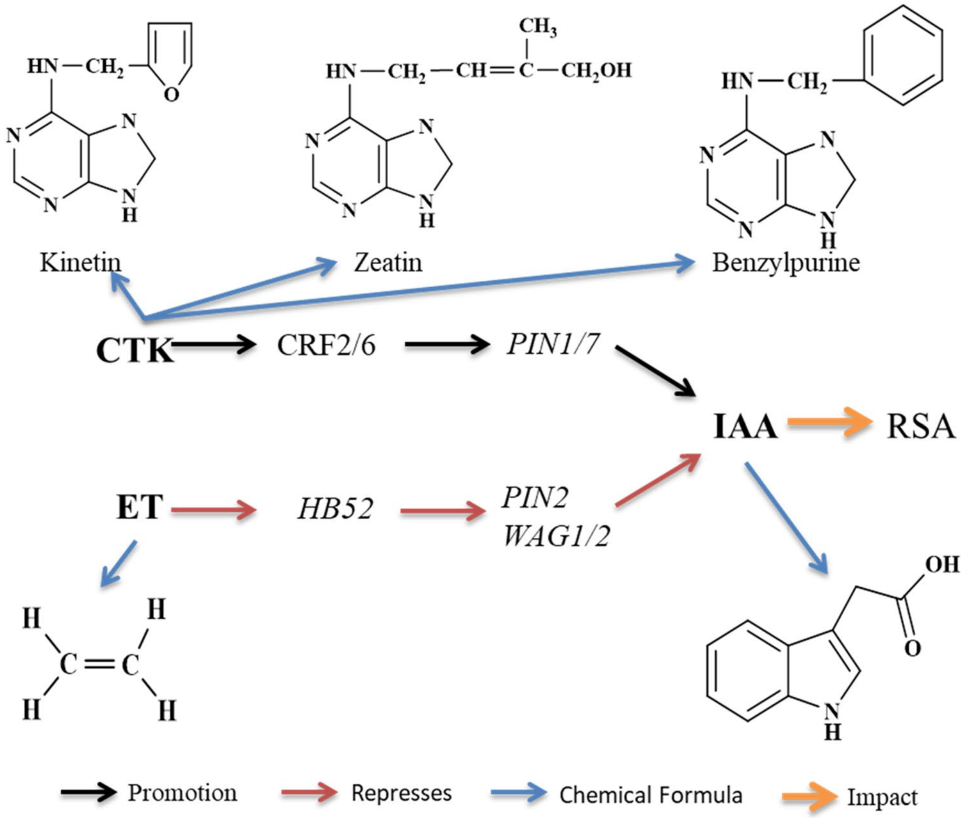

Fig. 4 Plant hormone interactions affect root growth. The action of plant hormones on RSA. CTK (KT, ZT, 6-BA) induces the expression of *PIN1/7* through the cytokinin response factor CRF2/6; *HB52*, the gene of ET response to HD-Zip, inhibits root growth by regulating the expression of IAA transport-related genes *PIN2*, *WAG1*, and *WAG2*. Both CTK and ET ultimately act on the RSA by altering the IAA.

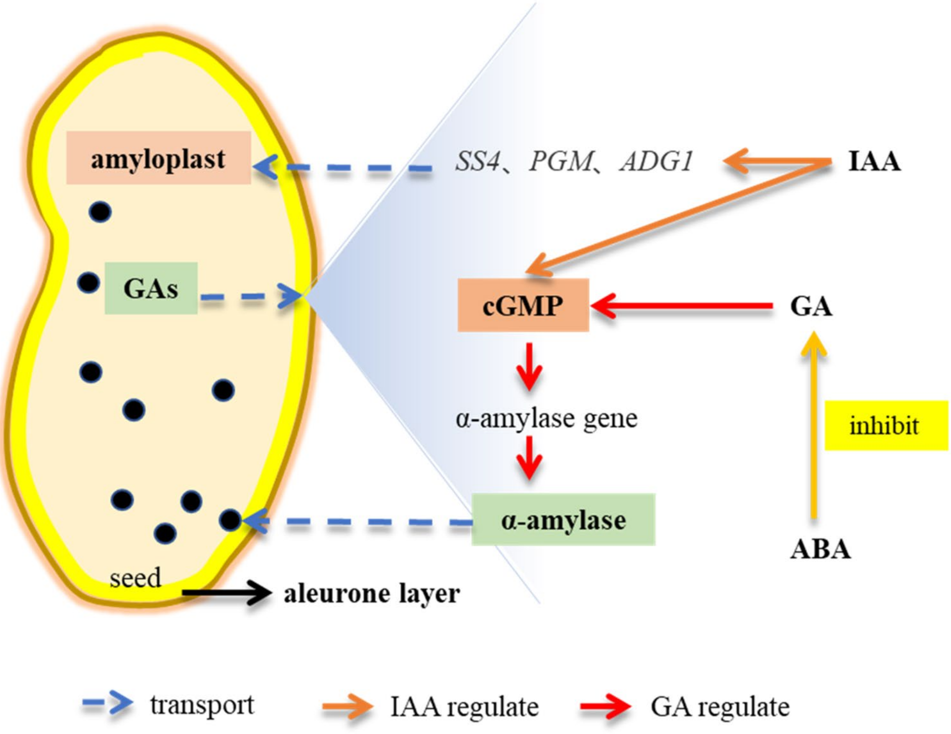

Fig. 5 Regulation of starch metabolism. Starch metabolism in plant seeds. When IAA concentration changes, the expression of its downstream starch synthesis genes (*SS4*, *PGM*, and *ADG1*) is induced, thus altering the starch content. When seeds germinate, biologically active GAs are synthesized in the embryo and transported to the dextrin layer. GA regulates the transcription of GAMYB through the cGMP pathway to enable the expression of α-amylase genes, which catalyze their synthesis. Finally, α-amylase in the paste layer is secreted into the endosperm, thereby altering the starch content. ABA acts on starch by blocking GA biosynthesis

starch, α-amylase is secreted into the endosperm (Kaneko et al. 2002), thus affecting changes in starch quantity and leading to changes in the direction of root growth (Fig. 5).

Cell wall and root gravitropism

The cell wall is an important structure that protects plant cells. It is mainly composed of cellulose, hemicellulose, lignin, and other components. Cell growth is constrained by the cell wall, and differences in cell size and shape in the root elongation zone can lead to changes in the growth phenotype of the plant body, such as the gravity growth of roots. Voids in the cell wall can be rapidly expanded by acidification with IAA, which activates cell wall localization proteins and loosens the cell wall; this growth mechanism follows acid growth theory (McQueen-Mason et al. 1992).

It has been theorized that IAA induces proton efflux by activating the p-type H^+-ATPase proteins located at PM, which leads to ectoplasmic acidification (Hager 2003). Increased H^+ concentration activates the cell wall by expanding the activity of H^+, which leads to cell elongation (McQueen-Mason et al. 1992). Receptor-like kinases (RLKs) have an important role in regulating the growth and development physiology of higher plants (Walker and Zhang 1990). RLKs are in the LRR XI subfamily. Most of their functions have been verified, but three have not been characterized. The researchers found an increase in the number of cells in the apical meristem of RLKs triple mutants and an increase in the size of cells in the mature and elongated regions (Wang et al. 2022a).

ROS and root gravitropism

ROS are a class of metabolites with high reactive activity produced by the progressive reduction of O_2 (Mittler et al. 2011). H_2O_2, a major component in the ROS system, plays a critical role in the root-directed growth pathway. H_2O_2 in plants maintains its balance through production and removal pathways (Fig. 6); it can mediate the signaling pathway of ABA to induce stomata closure and, through NADPH oxidase, can enable ABA to activate H_2O_2 synthesis (Pei et al. 2000), lateral root development (Potikha et al. 1999), and cell wall expansion (Su et al. 2006). The process of IAA regulation of the gravitonic response is also mediated by H_2O_2 (Neill et al. 2002).

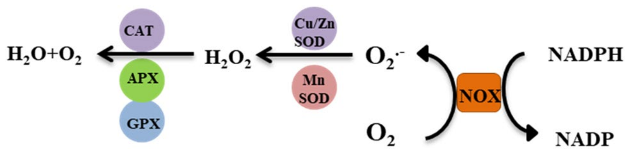

Fig. 6 Production and removal of hydrogen peroxide. CAT: catalase, NOX: NADPH oxidase, SOD: superoxide dismutase, APX: ascorbate peroxidase, GPX: glutathione peroxidase, NADPH: nicotinamide adenine dinucleotide phosphate, NADP: nicotinamide adenine dinucleotide phosphate. O_2 forms $O_2.^-$ by NOX and converts NADPH to NADP, $O_2.^-$ to H_2O_2 by SOD, and finally to H_2O and O_2 by CAT, APX, and GPX.

Li et al. (2007) found that exogenous H_2O_2 promotes adventitious root formation in mung bean and cucumber seedlings and increases the germination rate of *Pisum sativum* by interacting with phytohormones (Barba-Espin et al. 2010). Subsequent studies have found that treatment of sallow seeds with H_2O_2 results in non-terrestrial differential growth of the primary roots of seedlings (Jiang et al. 2012; Li et al. 2015) treated *Pisum sativum* seeds with H_2O_2 to verify this phenomenon and found that primary root development was caused by the uneven distribution of hormones (IAA, GA_3) on both the inner and outer sides of the curved root. Appropriate exogenous H_2O_2 can regulate Ca^{2+} concentration and IAA distribution in *Arabidopsis* root tip cells during early germination to alter primary root growth (Zhou et al. 2018).

Many plant hormones produce ROS when regulating growth and developmental mechanisms (Vivancos et al. 2010). ROS and hormone interactions not only regulate plant growth and development but can also improve stress tolerance (Xia et al. 2015). H_2O_2 downregulates ABA biosynthesis while upregulating GA biosynthesis (Shu et al. 2015, 2018). This in turn regulates α-amylase activity (Kaneko et al. 2002), which leads to changes in the number of starch grains and alters the gravitational sensitivity of plant roots. IAA induces ROS accumulation during the induction of gravity growth of roots, and groundward bending depends on ROS. In Joo et al. (2001), in the early stages of the groundward response, the IAA concentration in the concave surface of the maize root was higher while there was a transient increase in ROS concentration in the root. This asymmetric ROS distribution is necessary for the gravitational growth of roots, which is diminished by the treatment of maize roots with ROS scavengers. Signaling between ROS and IAA occurs during the gravity growth of roots oxidizing active IAA into the inactive and non-transported form oxIAA (Peer et al. 2013). H_2O_2 may be involved in the regulation of calcium signaling; for example, the involvement of H_2O_2 produced by tobacco cell inducers increases the concentration of Ca^{2+}, probably due to the activation of H_2O_2-sensitive Ca^{2+} channels in PM (Lecourieux et al. 2002). NADPH oxidase regulates the expansion of plant cells through the activation of hyperpolarized Ca^{2+} channels by ROS, thereby regulating cell development (Foreman et al. 2003).

Conclusion

This paper reviews the response pathways and interrelationships among key signaling molecules during root gravitropism in higher plants to provide a reference for the study of root gravitropism. Under gravity stimulation, amyloplasts settle in horizontally placed plant root tip cells, resulting in PIN3/7 re-localization in the rootlet cells. At the same time, PIN2 is degraded asymmetrically on both sides of the root, prompting the flow of IAA from the root crown to the elongation zone, leading to a high IAA concentration that inhibits lower cell growth (Muller et al. 2018). Furthermore, starch deposition causes fluctuations in cytoplasmic Ca^{2+} content, which are positively correlated with changes in IAA and trigger downstream plasma ectodomain ROS production and changes in pH (Sato et al. 2015). Cells on both sides of the root are induced to grow asymmetrically, and the root thus bends toward gravity (Fig. 7). The signal transduction mechanisms involved in the occurrence of gravity growth of roots contain complex physiological and biochemical responses, and the following questions still need to be explored to clarify their interactions and links to gravity growth of roots:

(1) How is thephysical signal of gravity translated into intracellular chemical signals?
(2) Is the rootperception of groundward growth triggered by one mechanism or multiplemechanisms interacting with each other?
(3) How areunknown pathways involved in the signal transduction process of root growthtoward gravity carried out, and how can they be verified?

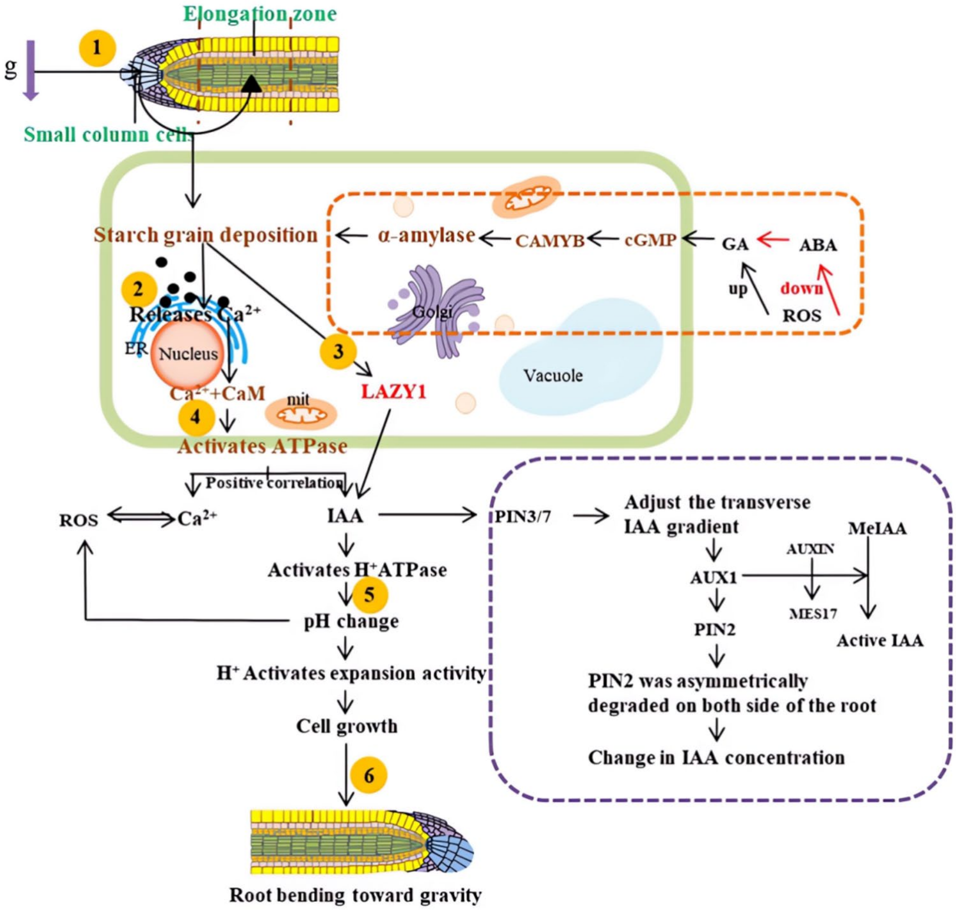

Fig. 7 Model diagram of gravimetric growth mechanism of plant roots. Mechanism of gravity growth signal transduction in plant roots. ① When plant roots are placed flat, the root crown senses gravity, and then starch grains are deposited in the direction of gravity (the initiation of downstream signaling may be the result of the interplay of multiple models of gravity perception). ② When starch is deposited into the endoplasmic reticulum of the cell, it causes the release of Ca^{2+} from it into the cytoplasm, changing the Ca^{2+} concentration in the cell. ③ At the same time, starch deposition alters the activity of LAZY1, causing the asymmetric distribution of IAA on both sides of the root under the action of endocytic and efflux carriers. ④ And Ca^{2+} in the cytoplasm can CaM binding activate the activity of ATPase on the plasma membrane, open ion channels and transmit the signal molecules to the outside of the cell. ⑤ The acid growth theory suggests that IAA activates the p-type H^+-ATPase protein to cause proton efflux, which subsequently triggers changes in extracellular ROS and pH; an increase in H^+ concentration can activate cell wall extension and activate the cell wall, thus altering cell growth. ⑥The effect of gravity differentiates the IAA concentrations on both sides of the transversely placed roots, resulting in different H^+ concentrations, asymmetric cell growth, and eventually root growth toward heavy curvature

(4) Exogenous H_2O_2application causes different ground-oriented responses in the primary roots ofdifferent species of plants (Li et al. 2016); *Leguminosae* root grows non-geotropically under certainconcentrations, while *Zea mays* doesnot: What is the reason for this? Is it due to the difference in the mechanismfor gravity sensing in the roots due to species variability or to a differencein root resistance?

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Data availability Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

Declarations

Competing interest The authors have no relevant financial or non-financial interests to disclose.

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