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REVIEW

Auxins and environmental factors regulate root gravitropism

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Abstract

Roots are important for plant anchoring, water and nutrient absorption, and other physiological processes. Gravity is a primary determinant of the spatial distribution of plant roots in the soil. Therefore, in-depth understanding of the molecular mechanisms and biochemical networks of root responses to gravity has both theoretical and practical significance in guiding the genetic improvement of plants. Gravitropism, the process through which plants sense the direction of gravity and respond by making the roots grow downward and the stem grow upward, has been widely studied in roots. The perception of gravity and the gravitational growth of roots, key steps in root growth and development, are regulated by auxins and other factors. Here, we review the latest progress in the regulation of root gravitropism by hormone signals and environmental factors from a molecular perspective, and look forward to the direction of future research on root gravitropism.

Keywords: environmental factors, phytohormones, positive and negative gravitropism.

Introduction

Plants sense external environmental signals, such as light, water, temperature, and gravity, and adjust their growth accordingly to a changing environment (Kazan 2013, Oh *et al.* 2018, Zhang *et al.* 2022a). Among these signals, gravity is important for regulating plant growth, development, and morphogenesis. In gravitropism, plants relocate their growth after sensing a gravity stimulus to maintain an optimal angle between the organs and the direction of gravity (Firn and Digby 1997). For seeds sown in soil, regardless of the orientation of the embryo, the root grows downward (consistent with the direction of gravity) in a process termed positive gravitropism and the bud (stem) grows upward (in the opposite direction of gravity), which is termed negative gravitropism. Furthermore, the underground stems of some plants (such as reeds) grow in a horizontal direction, in a process called diagravitropism. Gravitational movement occurs only in growing areas of the plant. For example, when lodging occurs in rice and wheat plants, the upper part of the plant can stand upright again. Root gravitropism is especially important insofar as the roots of newly germinated seedlings must immediately enter the soil (*i.e.*, grow in the direction of gravity) to ensure access to water and nutrients (Bailey *et al.* 2002).

Here, to enable researchers to better understand root gravitropism research, we present a systematic review of research fields related to root gravitropism.

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Abbreviations: ABA - abscisic acid; ARF - auxin response factor; CCs - columella cells; CK - cytokinin; IAA - indole-3-acetic acid; $InsP_3$ - inositol 1,4,5-trisphosphate; PGM - phosphoglucomutase; ROS - reactive oxygen species.

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Four stages of the root gravity response

In the root, gravity is sensed in the columella cells (CCs) of the root cap, however, the response to gravity occurs in the root elongation zone. Therefore, there are obvious physical zones between the area in the root that senses gravity and the area that responds to gravity. The root gravity response can be divided into four stages: the perception of gravity (the conversion of physical forces into biochemical signals), the transduction of gravity signals (the output of biochemical signals), the asymmetric distribution of auxin, and the bending of roots during growth (Baldwin *et al.* 2013).

Gravity perception: The root cap is the main site where plant roots detect gravity. Early experiments found that removing the root cap leads to the loss of root geotropism (Blancaflor and Masson 2003). Further experiments using techniques such as laser excision of root cap cells, gene knockout, and heavy ion microbeam irradiation showed that CCs throughout the root cap are gravity-sensing sites (Blancaflor *et al.* 1998, Tsugeki and Fedoroff 1999). In *Arabidopsis thaliana*, the central S2 zone of CCs is most important for the geotropism of roots (Blancaflor *et al.* 1998). The nucleus is located at the top of each CC, the endoplasmic reticulum forms a cup-shaped structure at the bottom of the cell, and the bottom of the cytoplasm is occupied by numerous amyloplasts (Hashiguchi *et al.* 2013).

At present, it is generally accepted that the mechanism by which plants sense gravity can be described by the starch-statolith hypothesis. According to this proposal, when the direction of gravity changes, starch grains in the cell settle along the direction of gravity, leading to changes in various signaling molecules. These changes affect the transport of auxin, causing it to be distributed asymmetrically in the direction of gravity stimulation, which results in the bending of roots during growth (Sack 1997, Ottenschläger *et al.* 2003). Mutation of the gene *PGM* causes loss of function of glucophosphomutase, the key enzyme in starch synthesis, and the loss of amyloplasts. As a result, *Arabidopsis pgm* mutant cannot sense the gravity signal and they are therefore deficient in gravitropism (Wolverton *et al.* 2011). Although the *pgm-1* mutant is less sensitive to gravity than the wild type, however, the roots could still bend after prolonged gravity stimulation (the bending angle became smaller). This suggests that plants might have a variety of gravity-sensing mechanisms.

When the osmotic pressure of the external environment changes, the root bends to varying degrees, but sedimentation of the starch grains is not affected. This has led to the proposal that the protoplast itself can sense changes in gravity (the protoplast hypothesis). According to this hypothesis, protoplasts can sense gravity *via* changes in their own mechanical buoyancy. Under gravity stimulation, protoplasts settle to the cell wall or extracellular matrix. The resulting pressure difference between the plasma membrane and extracellular matrix activates gravity receptors and transmits gravity signals (Staves *et al.* 1997). Therefore, the mechanisms described by the starch-statolith and the protoplast hypothesis are coordinated to enable gravity sensing.

Additional hypotheses to describe root gravitropism include the bifurcation theory and the cytoskeleton theory. The amyloplast theory states that in the roots of higher plants, balanced cells can sense gravity through interactions of both bound and unbound amyloplasts with the cytoskeleton. When amyloplasts are bound to the cytoskeleton through cell membrane-related receptors or proteins, sedimentation of the amyloplasts under gravity stimulation alters cytoskeletal tension, the receptors on the cell membrane are activated, and downstream signals are also triggered to respond to gravity stimulation. When not bound to the cytoskeleton, the amyloplasts can move freely with changes in the direction of gravity and eventually settle onto the endoplasmic reticulum on the lower side of the cell. This triggers downstream signal transduction and gravity sensing (Baluska and Hasenstein 1997). The bifurcation theory, meanwhile, proposes that the nucleus and cytoskeleton are particularly critical in gravity sensing and signal transduction, and a gravity-sensitive window switches in cells to sense gravity signals (Mesland 1992).

Transduction of gravity signals: After amyloplasts are deposited in the cell, the cytoskeleton might rearrange itself, and the stimulation might be transferred to the endoplasmic reticulum or cell membrane to induce the opening of ion channels. Ca^{2+}, inositol 1,4,5-trisphosphate ($InsP_3$), pH, and other signaling molecules are used as second messengers to participate in the gravity response (White 2001, Taufiq-Ur-Rahman *et al.* 2009). Indeed, exogenous calcium channel inhibitors and Ca^{2+}-ATPase activity inhibitors can block the gravity response, and the use of calcium analogs can enhance the gravity responses of hypocotyls and roots (Masson 1995, Laohavisit *et al.* 2012, Yuan *et al.* 2014, Hazak *et al.* 2019, Tanaka-Takada *et al.* 2019). These findings indicate that changes in Ca^{2+} content are activated in response to gravity stimulation, thereby regulating the plant response to gravity.

Not only the content of Ca^{2+} in cells change under gravity stimulation, but also the content of the second messenger $InsP_3$ increases (Keizer *et al.* 1995). Application of the steroid U73122, which inhibits the formation of $InsP_3$ in roots, attenuated the gravitational response of roots (Andreeva *et al.* 2010). The lack of enzymes to degrade $InsP_3$ in the *5pt13* mutant caused $InsP_3$ accumulation, resulting in an enhanced response to gravity. Phosphatidylinositol monophosphate-5-kinase (PIP5K) is the synthetic precursor of $InsP_3$. In *pip5k* roots, the gravity response is delayed, and the ability of auxin transport carriers to flow between vesicles and the plasma membrane is weakened. These observations suggest that $InsP_3$ regulates the locations of transport carriers by regulating vesicle transport, thereby participating in the regulation of the root gravity response (Roderick and Bootman 2003, Perera *et al.* 2006).

Under stimulation by gravity, the pH of the proximal side of the root decreases, and the corresponding pH value of the distal side increases. This asymmetric change in pH mainly depends on the activities of Ca^{2+} channels (Monshausen *et al.* 2011). These findings indicate that a variety of signaling molecules function in gravity signal transduction.

Asymmetric distribution of auxin and root curving during growth: Perception of gravity occurs in CCs, but response to gravity is completed in the root elongation zone. The Cholodny-Went hypothesis explains this phenomenon through the proposal that during gravity sensing, sedimentation of starch granules leads to the transmission of the gravity signal to the response area of gravity, the elongation zone, *via* auxin. The major endogenous auxin is indole-3-acetic acid (IAA). Following gravity stimulation, auxin is asymmetrically distributed in the root, resulting in the asymmetric growth of cells on both sides of the root that leads to root curving during growth (Perrin *et al.* 2005). Analysis using the auxin response reporter gene constructs *proDR5*:*GFP* and *proDR5*:*GUS* revealed that, under gravity stimulation, the distribution of the signal in the distal and proximal sides of the root was asymmetric, indicating that auxin was distributed in an asymmetric manner (Abel 2007). Therefore, auxin is important in a plant's reaction to gravity. Indeed, mutants in auxin biosynthesis, transport, and signal transduction can exhibit abnormal gravity responses (Palme and Nagy 2008, Rakusová *et al.* 2011, Baster *et al.* 2013).

Effects of auxin transport on the gravity response: The auxin transport pathway is important in regulating the gravity response (Rakusová *et al.* 2019). The asymmetric distribution of auxin transport carriers leads to an asymmetric distribution of auxin. This, in turn, leads to the asymmetric growth of cells on both sides of the root, resulting in root bending (Leyser 2003, Gallavotti 2013).

AUX1, the first influx carrier identified for auxin, is crucial in the response of plants to gravity (Marchant *et al.* 1999). Auxin transport is abolished in the roots of the *Arabidopsis aux1* mutant, and the response to gravity in its roots is weakened (Swarup *et al.* 2001). The gravitational response of roots depends on the transport of auxin from the lateral root cap to the epidermis of the elongation zone, a process mediated by AUX1 in the lateral root cap and epidermal cells (Swarup *et al.* 2005, Schoenaers *et al.* 2018). AXR4, located in the endoplasmic reticulum, regulates the AUX1 cycle in cells. The accumulation of AUX1 in the endoplasmic reticulum and the loss of its asymmetric distribution in the epidermal cells of the root means that the *axr4* mutant shows a weakened gravity response in the root. This suggests that the auxin transport pathway is associated with the gravity signal transduction pathway to regulate the gravity response of roots (Dharmasiri *et al.* 2006, Hobbie 2006, Navarro *et al.* 2006).

Auxin is exported primarily by members of the PIN-FORMED (PIN) and ABCB/MDR/PCP protein families. The PIN protein family comprises eight members, PIN1 to PIN8. PIN2, PIN3, and PIN7 are directly involved in regulating root gravity response (Ganguly *et al.* 2014). The asymmetric distribution of these three proteins on the cell membrane results in asymmetric distribution of auxin, which leads to the asymmetric growth of cells and the growth of curved roots (Wiśniewska *et al.* 2006). Under gravity stimulation, PIN2 is degraded by the ubiquitin-proteasome system, resulting in the asymmetric distribution of PIN2 protein on the two sides of the root. This, in turn, affects the distribution of auxin (Kleine-Vehn *et al.* 2008, 2010). In *pin3* mutants, the gravitational responses of the roots and hypocotyls are weakened (Friml *et al.* 2002). Under gravity stimulation, PIN3 protein localizes to the bottoms of CCs along the direction of gravity stimulation, resulting in an asymmetric distribution of auxin on the near and distal sides of the root (Friml and Palme 2002, Rakusová *et al.* 2011, 2019). The function of PIN7 is similar to that of PIN3. A change in the polar localization of PIN7 in cells affects the redistribution of auxin and helps regulate the gravity response (Kleine-Vehn *et al.* 2010). The gravity response is weakened in the roots of the *pin7* mutant, and the gravity response of the *pin3pin7* double mutant is severely impaired, indicating that PIN3 and PIN7 are functionally redundant in regulating the root gravity response (Friml *et al.* 2002, Kleine-Vehn *et al.* 2010).

Members of the ABCB/MDR/PCP protein family are also important auxin export carriers and are widely involved in the response of plants to gravity. In the *pgp4* mutant, the rate of auxin transport from the root to the base is significantly reduced, and the response of the root to gravity is also weakened. The root gravity responses of *pgp1* and *pgp19* single mutants and *pgp1pgp19* double mutants are enhanced, likely because of decreased auxin polar transport, resulting in enhanced lateral auxin transport. This, in turn, increases the asymmetric distribution of auxin on both sides of the root, thereby enhancing the root gravity response (Bouchard *et al.* 2006, Cecchetti *et al.* 2015).

Post-transcriptional modifications, such as phosphorylation and dephosphorylation, regulate the polar localization of PIN proteins and participate in the root gravity response. PID phosphokinase phosphorylates the hydrophilic rings of PIN proteins and is important in their polar localization. The abnormal response to gravity of *pid1* roots may be caused by altered PIN localization, which affects the polar transport of auxin (Friml *et al.* 2004, Sukumar *et al.* 2009, He *et al.* 2019). Specifically, PID might regulate the gravitational response of roots by affecting the polar localization of PIN2 on the plasma membrane (Sukumar *et al.* 2009). Altering the phosphorylation site of PIN3 affected the gravity response mediated by this protein (Ganguly and Cho 2012, Ganguly *et al.* 2012). Members of the D6PK protein kinase family also regulate the gravity response of roots by altering the phosphorylation state of PIN proteins (Willige *et al.* 2013, Barbosa *et al.* 2014).

Effects of auxin signaling on the gravity response: Under gravity stimulation, the auxin signal transduction pathway specifically induces the differential expression of auxin response genes in the distal and proximal lateral cells of roots. This promotes the asymmetric distribution of auxin and leads to growth of curved root.

A mutant of the auxin receptor TIR1 is less sensitive to auxin, and its roots show a weaker response to gravity than the wild type (Han *et al.* 2020). Mutations of the *AUX/IAA* gene family members *AXR5/IAA1*, *SHY2/IAA3*, *AXR2/IAA7*, *SLR1/IAA14*, *AXR/IAA17*, *IAA20*, *IAA30*, and *IAA31* led to the loss or weakening of the response to gravity in *Arabidopsis* roots and hypocotyls (Berleth *et al.* 2004). In addition, a gain-of-function mutation of *IAA28* led to a weakened gravity response in roots. By contrast, mutation of *MSG2/IAA19* led to the loss of the gravity response of hypocotyls, but did not affect the root gravity response (Tatematsu *et al.* 2004). *ARF* gene mutations lead to abnormal auxin responses, which will affect the plant's gravity response. Thus, the *arf7-1arf1-19*, *arf10arf16*, and *msg2-1arf19-1* double mutants all show weakening of the root gravity response (Okushima *et al.* 2005, Muto *et al.* 2006).

Plants can adjust the growth direction according to gravity and ultimately control the structure of stems and roots. Gravitropism is a dynamic process. In this process, gravistimulation induces asymmetric distribution of plant hormone auxin, leading to asymmetric growth and organ bending, and then the auxin distribution returns to the original state before gravistimulation. During the reaction to gravity, the differential accumulation of auxin depends on the activity of polarly localized PIN auxin-efflux carriers. In particular, the time of this dynamic response is regulated by PIN2, and the membrane associated kinase regulator2 (MAKR2) controls the speed of the root to gravity response. During gravitropism, MAKR2 acts as a negative regulator of cell surface signaling mediated by the receptor-like kinase transmembrane kinase1 (TMK1) and is required for PIN2 asymmetry. In addition, auxin itself can antagonize the inhibitory effect of MAKR2 on TMK1 signaling, thereby triggering the rapid dissociation of MAKR2 in a TMK1 dependent manner. It was shown that the time of root to gravity reaction was coordinated by reversible inhibition of TMK1 signaling pathway on the cell surface (Marquès-Bueno *et al.* 2021).

Environmental factors regulating root gravitation

Effects of salt stress on root gravity response: Salt stress alters the response to gravity by controlling the direction of growth of primary roots. Root structural morphology is highly plastic during plant growth to allow plants to adapt to various environmental stresses. The structures of roots growing in soil can be adjusted according to the environment, such as high salinity, dry soil, and nutrient-deficient soil. In particular, salt stress has strong effects on root structure in *Arabidopsis*, among other species. Although salt stress is known to inhibit root elongation and reduces root number, many questions remain about the mechanisms underlying the effects of salt stress on root growth. Various experiments suggested that salt stress inhibits root growth by weakening the gravity response. Salt stress causes a sharp decrease in the number of starch grains in root CCs of *Arabidopsis*. This change is related to strongly altered expression and localization of *PIN2* mRNA. Moreover, several mutants of genes in the salt overly sensitive (SOS) regulatory pathway show a significantly reduced gravity response, indicating that salt stress alters both geotropism in roots and the salt balance in plants. SOS pathway mutants also show reduced content of starch grains in the CCs of root tips and reduced expression of *PIN2*. These findings suggest that under salt stress, the transcription of *PIN2* in *Arabidopsis* decreases through a process involving SOS pathway proteins, thereby reducing the effects of salt stress on geotropism (Sun *et al.* 2008).

Effects of H_2O_2 on gravitropism: When plants are stressed by drought (Ramachandra Reddy *et al.* 2004), low temperature (Kidokoro *et al.* 2022), salinity (Shalata *et al.* 2001), pathogens (Mur *et al.* 2005), ozone (Evans *et al.* 2005), or heavy metals (Romero-Puertas *et al.* 2004), hydrogen peroxide (H_2O_2) is rapidly produced in plant cells and released into the cytoplasm. H_2O_2 is a second messenger involved in many physiological and biochemical reactions in plants, such as stomatal movement induced by abscisic acid (ABA), auxins, and cytokinins (CK) (Pei *et al.* 2000, Zhang *et al.* 2001), root growth and lateral root development (Joo *et al.* 2001), and the lignification of cell walls (Potikha *et al.* 1999). By applying H_2O_2 to cucumber and mung bean, Li *et al.* (2009, 2018) discovered that H_2O_2 interacts with auxin and promotes adventitious root growth. Following the application of different concentrations of H_2O_2, the primary roots of pea bent in a non-geotropic manner; the degree of bending increased with increasing concentrations of H_2O_2. Further analysis revealed an asymmetric distribution of auxin on the inside and outside of the curved primary root. The lateral cells of primary roots that were horizontally curved following H_2O_2 application were columnar and densely arranged, whereas the inner cells were loosely arranged in filaments and were significantly shorter than the lateral cells. These findings suggest that H_2O_2 functions downstream of the auxin-induced root geotropism response (Joo *et al.* 2001).

Arabidopsis AtCRK5 protein kinase is involved in the establishment of appropriate auxin gradients during many developmental processes and the At*crk5-1* mutant exhibited a delayed gravitation response through impaired PIN2 mediated apical auxin transport. This phenotype was associated with lower content of superoxide anion ($O_2^{\bullet}$-) and H_2O_2 compared with wild type, but higher content of nitric oxide (NO) in the mutant root tip. Paraquat (PQ), an oxidative stress inducer, triggers the formation of $O_2^{\bullet}$- and H_2O_2 and can rescue the gravity response of At*crk5-1* roots. Direct application of H_2O_2 had the same effect. Under gravity simulation, auxin distribution in the mutant root tip was restored (at least partially restored) by PQ or H_2O_2 treatment. The redistribution of the PIN2 auxin efflux vector in the heavily simulated PQ treated mutant and untreated wild-type roots was similar. PQ treatment reduced endogenous NO content in the root tip to normal level. The mutant phenotype can be restored by directly manipulating endogenous NO content using NO scavenger (cPTIQ). AtCRK5 protein kinase plays an important role in the control of auxin-ROS-NO-PIN2-auxin regulatory loop (Cséplő *et al.* 2021).

Regulation of gravitropism by ubiquitin E3 ligases: SGR9 (shoot gravitropism9) is a $C_3H_2C_3$-type ring finger protein in *Arabidopsis*. This protein has ubiquitin E3 ligase activity and is located in amyloplasts, where it regulates amyloplast dynamics (Nakamura *et al.* 2011). The *sgr9* mutant shows a weakened gravity response of the stem and a slight weakening in the roots. The *sgr9* amyloplasts do not sediment, instead, they exhibit enhanced mobility. Following site-directed mutagenesis of the conserved RING domain of SGR9, both $SGR9^{W244A}$ and $SGR9^{C232A}$ showed significant decreases in ubiquitin E3 ligase activity, suggesting that the ubiquitin E3 ligase activity of SGR9 *in vitro* depends on its RING finger domain (Nakamura *et al.* 2011). *Arabidopsis* WAV3 is another RING-H2 ubiquitin E3 ligase. When wild-type *Arabidopsis* plants were grown on hard agarose medium in tilted plates, the roots showed curved growth owing to the simultaneous action of their own growth driving force, gravity, and resistance to the agar medium. In the *wav3* mutant, the root bending angle was larger and showed a smaller half-wavelength distance. WAV3 affect apical PIN sorting decisions (Sakai *et al.* 2012, Konstantinova *et al.* 2022). The bending angle of *wav3* in response to gravity was larger than that in response to irradiance, indicating that the *wav3* mutation enhances the root gravity response. *WAV3* belongs to a small gene family that also includes *EDA40*, *WAVH1*, and *WAVH2*, and a*wav3wavh1wavh2* triple mutant showed a strongly altered gravitropic response (Sakai *et al.* 2012).

Other signals influencing gravitational responses: Other signals affecting root gravitropism include pH (Scott and Allen 1999, Fasano *et al.* 2001), calcium content (Lee *et al.* 1984, Urbina *et al.* 2006), potassium ions (Desbrosses *et al.* 2003, Vicente-Agullo *et al.* 2004), ABA (Han *et al.* 2009), and reactive oxygen species (ROS) (Joo *et al.* 2001, Hu *et al.* 2005).

When a plant is placed horizontally, the aggregation of auxin on the lower side of the root open channels in the cell membrane. This leads to increased content of intracellular Ca^{2+}, which act as a second messenger to activate the H^+/OH^- pump in the membrane. OH^- is then pumped out of the cell, resulting in an increase in pH at the cell surface on the lower side of the root (Monshausen *et al.* 2011). The alkaline environment on this side of the root inhibits the extensibility of the cell wall, thereby inhibiting cellular expansion. The imbalance between the expansion of the cells at the top and their inhibited expansion at the bottom ultimately leads to bending of the root.

In contrast to auxin, ABA is a negative regulator of the gravity response. Treatment with 0.5 μM ABA significantly reduced gravitropism of the polar auxin transport carrier-related mutants *auxl-7* and *eirl-l*, but the same concentration of ABA had no effect on wild-type plants (Han *et al.* 2009). The inhibitory effect on the gravity response of naphthyl-1-carbamylbenzoate (NPA), an inhibitor of polar auxin transport, was reduced in the ABA biosynthesis mutants *abal-l*, *aba2-4*, and *aba3-2*, suggesting that the role of ABA in inhibiting the gravity response involves the auxin pathway. However, the specific mechanism underlying the role of ABA in the gravity response requires further study.

Studies in maize and soybean demonstrated that changes in the direction of gravity caused the accumulation of auxin at the bottom of the root, leading to the accumulation of ROS (Joo *et al.* 2001) and NO (Hu *et al.* 2005) in this region. The application of H_2O_2 on one side of the root caused the root tip to bend in the direction of the H_2O_2, and the application of sodium nitroprusside, the precursor of NO, to the bottom of the horizontally placed root also promoted the gravitational response of the root. NPA treatment inhibits the synthesis of ROS and NO mediated by auxin, but the exact role of auxin in these processes is unclear.

The input and output vectors of auxin are important in the auxin transport pathway in *Arabidopsis* roots, but they are not the only carriers controlling auxin distribution. The *KT/KUP/HAK* polygene family is also inextricably related to auxin transport. *TRH1* (*TINY ROOT HAIR1*), a member of this family, encodes a potassium ion transport carrier that affects the formation and growth of plant root hairs. There is a relationship between TRH1 activity and the polar transport of auxin, along with the redistribution of auxin, which directly affects the gravitropism of plant root tips. Therefore, TRH1 is essential for the occurrence and elongation of root hairs and the gravitational growth of roots in *Arabidopsis*. The transport of auxin from bud growth points to root tips and the efflux of ^3H-labeled IAA were significantly inhibited in *trh1* roots, whereas in yeast cells overexpressing *TRH1*, the efflux of this radioisotope-labeled auxin was promoted. In *trh1*, the flow rate of auxin from the root tip columnar cells to the epidermis was significantly inhibited by isotope labeling, which affected the formation and gravitropism of root hairs. This inhibition was relieved by auxin treatment. The gravity sensing, growth, and occurrence and extension of root hairs in the *trh1* restorer line *trh1/TRH1* were similar to those of the wild type. TRH1-GUS was localized to the columnar cells of the root and the cells on both sides of the root cap, that is the sensing site of gravity stimulation and the redistribution site of auxin. When the K^+ concentration in the medium decreased from 20 to 0.1 mM, the gravitropism of the roots disappeared (Desbrosses *et al.* 2003, Vicente-Agullo *et al.* 2004).

Plant architecture refers to the spatial distribution and morphological characteristics of the aboveground and underground parts of a plant. A plant constantly adjusts its growth direction according to the direction of gravity, ultimately reaching a fixed angle with the gravity direction (Digby and Firn 1995). An abnormal gravity response of the aboveground parts of a plant will lead to a change in this fixed angle, which is important in shaping plant type (Firn *et al.* 2000). Plant type is one of the most important factors determining crop yields. Therefore, it is important to study the mechanisms underlying the gravity responses of plants to facilitate crop improvement.

Due to the increasingly serious pollution caused by industrial activities, burning fossil fuels, improper treatment of sewage sludge, excessive application of fertilizers and pesticides, and heavy metal are major environmental problems. Excessive Ni can cause leaf chlorosis and inhibit plant growth, but its potential growth inhibition mechanism is still unclear. Detailed analysis of root development of *Arabidopsis* in the presence of Ni showed that this heavy metal induced gravitation defects and locally inhibited root growth by inhibiting cell elongation without significantly damaging the stem. Analysis of auxin reactivity reports showed that excessive Ni inhibited the targeted distribution of auxin. PIN2 is very sensitive to Ni because the presence of this heavy metal rapidly reduces PIN2 content in roots. Ni affects the expression of many genes associated with plant cell walls, and Ni induced transcriptional changes are largely independent of iron. Excessive Ni increases the accumulation of ROS and interferes with the integrity and direction of microtubules (Lešková *et al.* 2020).

In *Arabidopsis* gravitropism is affected by two antagonistically interacting proteins, AGD12 (ADP-ribosylation factor GTPase-activating protein) and EHB1 (enhanced bending 1). While AGD12 enhances gravitropic bending, EHB1 functions as a negative regulator (Rath *et al.* 2020).

The effect of light and dark on the interaction between tropisms is not clear. It has been reported that, in contrast to seedlings fully exposed to irradiance, wild type *Arabidopsis* seedlings exhibit enhanced hydrotropism; specifically, their buds are exposed to light, while their roots grow in darkness. Due to the reduction of amyloid content in root tip and the reduction of *PGM1* (a key starch biosynthesis gene) expression, the gravitropism of root system is significantly reduced, potentially contributing to an enhanced gravitropic response under dark conditions. In addition, the *pgm1-1* mutant showed greater hydrophilicity compared with the wild type. The amyloplast reaction and starch reduction in *Arabidopsis* roots are regulated both in the presence and absence of light, followed by a decrease in gravitropism and an increase in hydrotropism (Li *et al.* 2020).

The gravitropism of root system is very important for soil anchoring and water and nutrient exploration. It affects the root structure, which is one of the factors affecting crop yield. The mechanism of gravitropism of primary roots has been widely studied, but the regulation mechanism of lateral root gravitropism is still unclear. Topoisomerase 1α (TOP1α) inhibited lateral root gravitation, contrary to previous reports (Zhang *et al.* 2022b). TOP1α maintain the gravity of the primary root, revealing a dual function of TOP1α in root gravitropism regulation. The TOR (target of rapamycin) is inhibited in lateral root columnar cells, thus inhibiting the development of columnar cells, especially the development of amyloplasts. The study of Zhang *et al.* (2022c) revealed a new mechanism of lateral root adjustment to gravity, which may provide theoretical support for improving agricultural production.

The emerging role of asymmetric cytokinin signaling was found as a central anti-gravitropic signal. Differential cytokinin signaling is coopted in gravitropic lateral roots and hydrotropic primary roots to counterbalance gravitropic root growth (Waidmann and Kleine-Vehn 2020).

Light and gravity are two key environmental factors controlling plant growth and structure. However, the molecular basis for the coordination of radiation and gravity signals in plants remains unclear. Phytochrome interacting factors (PIFs) and elongated hypocotyl5 (HY5), can directly bind and activate the expression of *LAZY4*, a positive regulator of gravitropism in both shoots and roots in *Arabidopsis*. In the hypocotyl, radiation promotes the degradation of PIF to reduce the expression of *LAZY4*, thereby inhibiting the negative gravitropism of the hypocotyl. *LAZY4* overexpression can partially rescue the negative gravity phenotype of *pifq* in the dark without affecting the development of amyloplasts. The identification of PIF-LAZY4 regulatory module indicates that PIF protein has another role in gravitropism, and PIF positively regulates amyloid development to promote the negative gravitropism of hypocotyl. In the root, irradiance promotes the accumulation of HY5 protein to activate the expression of *LAZY4*, thereby promoting the positive gravity in the root. By regulating the proteins PIFs and HY5, radiation exerts an opposite regulation on *LAZY4* expression in shoots and roots to inhibit the negative gravitropism of *Arabidopsis* shoots and promote the positive gravitropism of roots (Yang *et al.* 2020).

Arabidopsis NPF7.3 (nitrate transporter 1/peptide transporter family7.3) proteins function as transporters of indole-3-butyric acid (IBA), a precursor of the major endogenous auxin indole-3-acetic acid (IAA). When expressed in yeast, NPF7.3 mediated cellular IBA uptake. Loss-of-function *npf7.3* mutants showed defective root gravitropism with reduced IBA content and auxin responses (Watanabe *et al.* 2020).

Conclusions and prospect

Plant roots can be roughly divided into three types: shallow roots, intermediate roots, and deep roots. Under traditional fertilization schemes, nutrient elements are layered in the soil. On the one hand, shallow roots have advantages in absorbing local nutrients (Ge *et al.* 2000). On the other hand, the distribution area of shallow roots in the soil space is large, reducing the competition among a plant's own roots for nutrients. Gravitropism allows plants to relocate their growth following stimulation by gravity to maintain the optimal angle of each organ and gravity direction (Firn and Digby 1997). Gravity is important in regulating the growth, development, and morphogenesis of plants.

Auxin IAA is essential in regulating plant growth and development, as well as the root gravity response. The asymmetric distribution of auxin transport carriers leads to the asymmetric distribution of auxin, which in

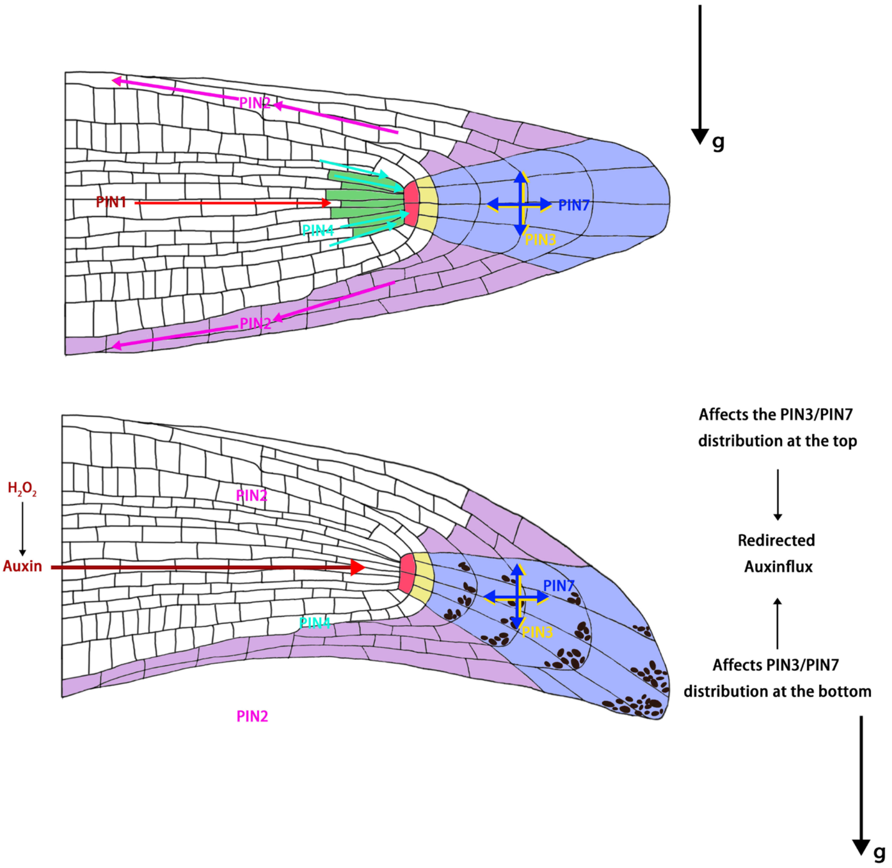

Fig. 1. Effects of auxin transport on the gravity response. PIN proteins involved in regulating the gravity response of roots.

turn leads to curved root growth (Leyser 2003, Gallavotti 2013). Placing *Arabidopsis* plants horizontally as a means of gravity stimulation results in root bending. The bent root experiences an asymmetric distribution of auxin, with the auxin concentration increasing at the near side of the root bend (leading to less elongation) while decreasing at the far side (leading to more elongation) (Ottenschläger *et al.* 2003, Paciorek *et al.* 2005). The asymmetric distribution of auxin leads to the differential growth of cells on the two sides of the root, resulting in curved root growth (Leyser 2003, Gallavotti 2013). Auxin is thus critical in the gravity response (Fig. 1).

The most widely accepted hypothesis explaining the gravitational mechanism of plants is that starch grains in plants act as balance stones. The sedimentation of most starch granules in root cap cells causes the root CCs to send signals of directional movement (Sack 1997, Kiss 2000). Therefore, in some mutants with abnormal starch grain distribution, defects in starch grain synthesis, or inability of starch grains to undergo sedimentation cause the plants to show reduced responses to gravity stimulation (Kato *et al.* 2002, Vitha *et al.* 2007, Wolverton *et al.* 2011).

Root CCs are the main sites for sensing gravity in roots. Under gravity stimulation, the root bends in the elongation zone (Holland *et al.* 2009). This bending to gravity is caused by the asymmetric flow of auxin from gravity-sensitive cells to the lateral region of the root and then to the elongation zone (Holland *et al.* 2009). The auxin efflux carrier PIN3 is expressed in root CCs and relocates to the sides of the root pillar cells after gravity stimulation to mediate lateral auxin transport (Friml *et al.* 2002). Although mechanisms for the roles of auxin transporters in the gravity response have been proposed in recent years, important unresolved issues remain. Since *aux1* and *pin2* are functional mutants with reduced gravity responses, studies of these mutants have clarified the roles of AUX1 and PIN2 in gravitational bending. However, the functions of some auxin transport carriers are unclear owing to the weak phenotypes of their functional mutants, such as *pin3* mutants.

In addition to answering basic questions in plant biology, further elucidating the root gravitational regulatory network could lay the foundation for improving the root configuration of crops, thereby increasing crop yields.

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