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Review

Genetic regulation of the root angle in cereals

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The root angle plays a critical role in efficiently capturing nutrients and water from different soil layers. Steeper root angles enable access to mobile water and nitrogen from deeper soil layers, whereas shallow root angles facilitate the capture of immobile phosphorus from the topsoil. Thus, understanding the genetic regulation of the root angle is crucial for breeding crop varieties that can efficiently capture resources and enhance yield. Moreover, this understanding can contribute to developing varieties that effectively sequester carbon in deeper soil layers, supporting global carbon mitigation efforts. Here we review and consolidate significant recent discoveries regarding the molecular components controlling root angle in cereal crop species and outline the remaining research gaps in this field.

Highlights

The root angle in cereals determines soil resource capture, stress resilience, and yield, especially in suboptimal conditions.

Root angle regulation involves competing gravitropic and antigravitropic offset mechanisms.

Understanding the mechanisms underlying root angle regulation in cereals is important due to their complex root system made up of distinct root types, formed at different stages of development.

Recent studies in cereals revealed genes regulating the root angle. However, the precise mechanisms determining and maintaining root angle in distinct root types remain unclear.

Understanding the molecular mechanisms underlying root angle control is essential for incorporating the root angle trait into breeding programs.

Root types, their growth angles, and their roles in stress resilience

The primary functions of the root system are to acquire nutrients and water from the soil and provide anchorage. Typically, plants produce only one or a limited number of roots during embryogenesis, with the majority of the root system developing after germination as the plant establishes. Root system architecture varies widely among species, influenced by genetic and environmental factors. Although there is no simple classification scheme for root system architecture, it is widely accepted that two main root system morphologies are present in angiosperms. Dicotyledonous plants, such as arabidopsis (*Arabidopsis thaliana*) and tomato (*Solanum lycopersicum*), have an allorhizic tap root system with an embryo-borne primary root and lateral roots. Monocotyledonous plants, like cereal crops, have a homorhizic fibrous root system with primary, seminal, lateral, crown, and brace roots (Figure 1A).

These different root types emerge at different angles to reduce self-competition and maximize nutrient and water uptake from different soil layers (Figure 1A). The angle at which a root grows in relation to gravity or other stimuli is referred as the 'root angle', whereas the angle at which a plant aims to maintain the root in response to gravity is termed the 'gravitropic set-point angle' (GSA). The GSA was initially defined by Digby and Firn [1]. For example, primary roots grow vertically downward, aligning with the gravity to anchor the seedling in the soil after germination to access deeper layers for nutrients and water. By contrast, seminal roots exhibit a wide range of GSAs, which aids foraging by the root system for resource acquisition shortly after germination. Later in development, crown and brace roots grow at even shallower angles, enabling them to enhance topsoil foraging for acquisition of immobile nutrients such as phosphorous and provide stability to the plant [2,3]. Lateral roots emerge from all root types and grow at a more horizontal GSA to enhance soil foraging for water and nutrients.

The root angle, influenced by various soil and environmental factors, is considered a crucial determinant of root system architecture and, thus, agronomic productivity in challenging conditions [4,5]. Recent studies highlight the importance of the root angle, specifically steeper versus shallower root angles, in adapting to different soil environments. Steeper root angles promote deeper

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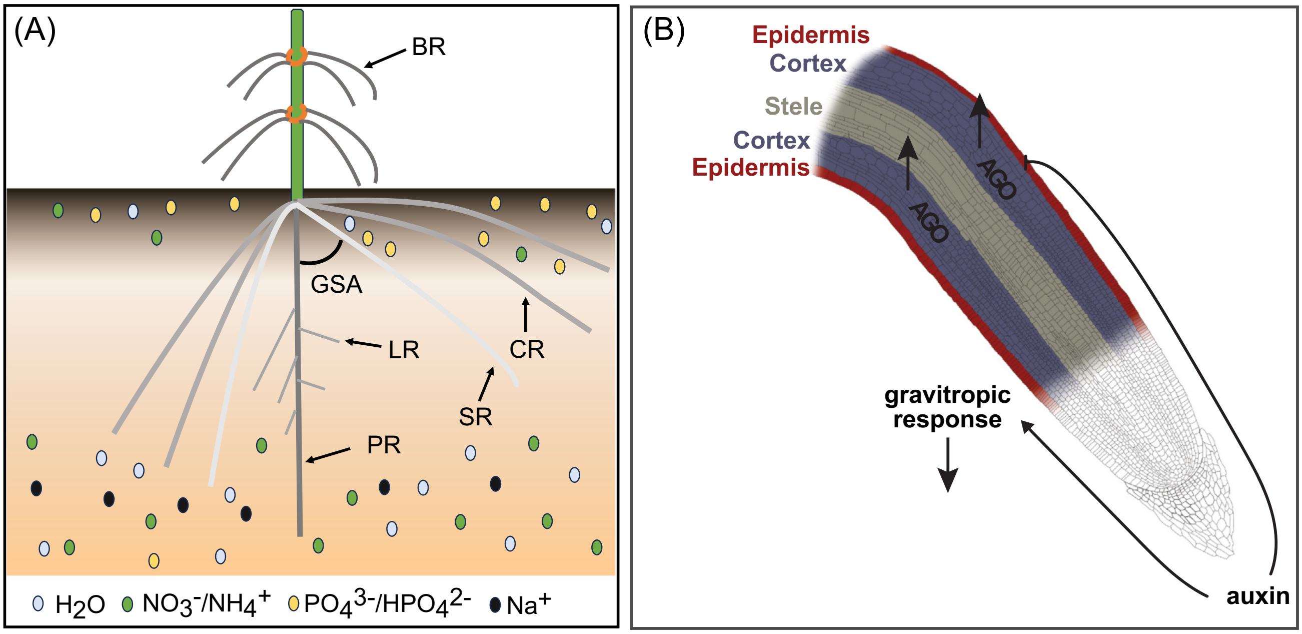

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Figure 1. Root angle of different root types is controlled by competing gravitropic and antigravitropic offset mechanisms. (A) The root system of cereals comprises the embryo-borne primary root (PR), characterized by a vertical growth angle, and a variable number of embryonic seminal roots (SRs) that emerge from the scutellar node during embryonic development with a shallower growth angle. Postembryonically, nodal roots emerge from the stem, including crown roots (CRs) that extend from the underground nodes and brace roots (BRs) from the aboveground nodes. Lateral roots (LRs) develop from all root types, enhancing soil coverage with their more horizontal growth. (B) The current model in cereal crops explains how gravitropic and antigravitropic offset (AGO) mechanisms determine the root's specific angle. Auxin-dependent gravitropic responses occur in the epidermal tissues, whereas auxin-independent antigravitropic offset responses function within the root cortical tissues in the basal meristem and the transition zone.

root growth, often associated with improved access to water and nitrogen in subsoil profiles during water-limiting [4,6] and low-nitrogen conditions [7]. Root angle also influences the rate and force of seedling emergence in sodic conditions [8] and may aid in responding to rising topsoil temperatures [9]. By contrast, shallower root angles are associated with better performance under phosphorus-starved conditions due to enhanced phosphorus acquisition from the topsoil [10], reduced salinity stress [11], and increased tolerance to flooding in paddy field conditions [12].

Gravitropic and antigravitropic components control root angle

Different root types exhibit different GSAs. The vertical GSA of primary roots is maintained by a positive gravitropic mechanism, whereas the nonvertical GSA in other root types (such as seminal, lateral, and crown roots) is determined by competing gravitropic and antigravitropic offset mechanisms (Figure 1B). Extensive research in the model plant arabidopsis has uncovered the underlying mechanisms of gravitropism in primary roots and antigravitropic offset pathways in lateral roots. By contrast, our understanding of both gravitropic and antigravitropic mechanisms in crop species remains limited.

Gravitropic machinery

The genetic regulation of root gravitropism involves a complex network of genes. The processes in which these genes are involved in regulating can be broadly categorized into three main groups: gravity perception, signal transduction, and response. Below, we discuss recent advances in understanding of genes involved in these processes in cereals (Table 1).

Table 1. Genes regulating root angle in crops

Gene name	Plant species and identifier	Function	Mechanism	Refs
Rice Morphology Determinant (RMD)	Rice (LOC_Os07g40510/ Os07g0596300)	Actin dynamics regulation	Antigravitropic offset	[16]
LAZY (LZY)/DEEPER ROOTING1 (DRO1)/quantitative trait locus for SOIL SURFACE ROOTING 1 (qSOR1)	Rice (DRO1: LOC_ Os09g26840, qSOR1: LOC_Os07g42290)	Gravity-sensing process	Gravitropic	[11,24]
VILLIN2 (VLN2)	Rice (LOC_Os03g24220)	Actin dynamics regulation	Antigravitropic offset	[31]
OsAUXIN RESISTANT 1 (OsAUX1)	Rice (LOC_Os01g63770)	Facilitates auxin transport to create asymmetric auxin distribution	Gravitropic	[36]
OsPINFORMED 2 (OsPIN2)	Rice (LOC_Os06g44970)	Auxin efflux carrier, facilitates auxin transport to create asymmetric auxin distribution	Gravitropic	[30]
SOIL-SURFACE ROOTING 1 (SOR1)	Rice (LOC_Os07g42290)	Ringlike E3 ligase	Gravitropic	[37]
ZmROOT SYSTEM ARCHITECTURE 3.1 (ZmRSA3.1)	Maize (GRMZM2G138268)	Aux/IAA protein	Gravitropic	[32]
ZmROOT SYSTEM ARCHITECTURE 3.2 (ZmRSA3.2)	Maize (GRMZM2G044055)	Formin homology protein	Gravitropic	[32]
ENHANCED GRAVITROPISM 1 (EGT1)	Barley (HORVU6Hr1G068970)	Tubby-like F-box protein	Antigravitropic offset	[41]
ENHANCED GRAVITROPISM 2 (EGT2)	Barley (HORVU.MOREX.r2.5HG0370880), arabidopsis (AtWEEP: At3G07760), wheat (TraesCS5A01G102000, TraesCS5B02G164200LC), peach (WEEP: Ppa013325)	Sterile alpha motif domain gene	Antigravitropic offset	[42]
CBL-Interacting serine/ threonine-protein kinase 15 (ZmCIPK15)	Maize (Zm00001d033316)	CBL-interacting serine/threonine-protein kinase	Antigravitropic offset	[33]

Gravitropic machinery: gravity perception

Gravity perception mainly occurs in the columella cells of the root cap (Figure 2). In these cells, specialized starch-containing plastids called amyloplasts sediment in the direction of gravity, triggering the gravity-sensing process [13]. The movement of amyloplasts has been suggested to involve actin filaments (AFs) [14,15]. In the case of rice, an AF-binding protein known as rice morphology determinant (RMD) has been shown to establish a direct link between AFs and statoliths [16]. RMD is localized on the surface of statoliths, and the seminal roots of knockout mutants of *RMD* show steeper angles and exhibit an enhanced gravitropism response after gravistimulation due to the faster sedimentation rate of the statoliths. RMD also plays a role in enabling roots to shape shallower angles during low-phosphate conditions, facilitating the acquisition of limited phosphate that accumulates in the topsoil. This adaptation occurs by upregulating the abundance of RMD, resulting in a greater presence of ring-like AFs surrounding the statoliths. This, in turn, reduces the sedimentation of statoliths during the gravity-sensing process, ultimately leading to a decreased overall gravity response and thereby a shallower angle [16].

Amyloplast displacement is thought to trigger the signal transduction, which, in turn, induces the asymmetrical distribution of auxin, leading to a root bending response in the elongation zone. Several hypotheses have been proposed to explain how the physical process of amyloplast displacement generates the biochemical signals in gravity-sensing cells: (i) the force-sensing model, in which the energy of the sedimenting amyloplasts activates calcium channels by exerting tension or pressure on the AF cytoskeleton lining the plasma membrane [17]; and (ii) the position-

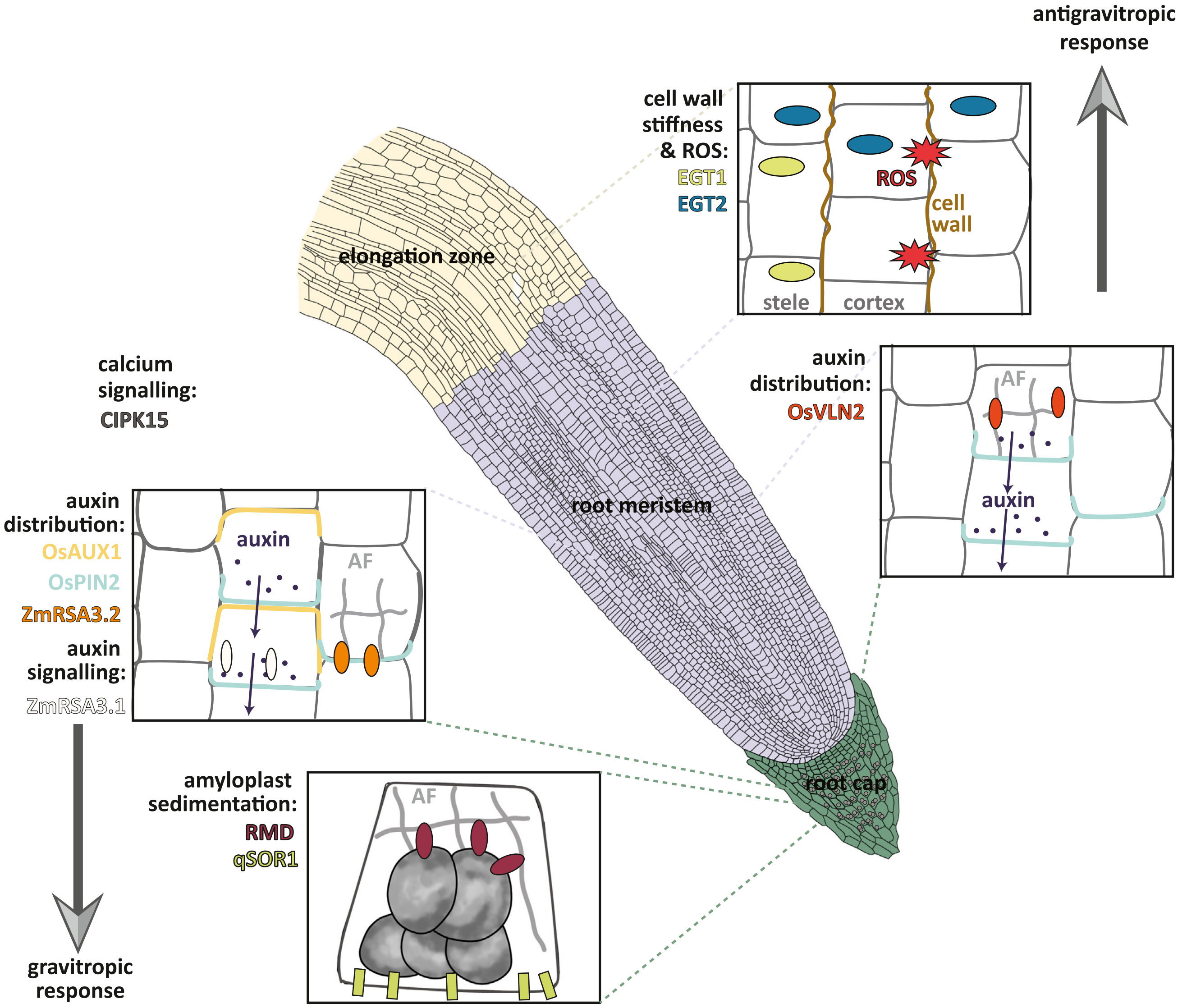

Figure 2. Model illustrating the functioning of gravitropic and antigravitropic components identified in cereal crops at the cellular level. Gravity is mainly perceived in the root cap, where amyloplast sedimentation triggers a signal that is transduced in the outer tissues through the meristematic zone. This signal leads to an asymmetric auxin distribution, which, in turn, causes asymmetric cell elongation in the elongation zone and, consequently, root bending as a gravitropic response. In cereal crops, several proteins have been identified that are involved in the amyloplast sedimentation and creation of the asymmetric auxin distribution. To date, only some components of the antigravitropic response are known: the regulation of the asymmetric auxin distribution and of ROS signaling and cell wall stiffness in the elongation zone. Abbreviation: AF, actin filament.

sensing hypothesis, in which the position of the statoliths rather than the exhibited force determines the downstream biochemical signals [18].

Recently, several studies have revealed that LAZY1-LIKE (LZY/LAZY1/LA1) family proteins serve as signaling molecules for transmitting the positional information of statoliths to the adjacent segment of plasma membrane. LAZY genes contain five regions with conserved sequences and belong to a larger gene family defined by a highly conserved 'IGT' amino acid motif in region II [19,20].

In arabidopsis, LAZY proteins translocate from the amyloplast to the plasma membrane located on the side of the statocytes facing the gravity vector. This translocation creates a polarity in the distribution of LAZY proteins on the plasma membrane, subsequently triggering signaling pathways to create an asymmetrical auxin distribution [21,22]. This process could happen through the interaction of LAZYs with the RCC1-like domain (RLD) proteins. The interaction of the conserved C terminus in LAZY1 family proteins (CCL) domain of LAZYs with the BREVIS RADIX (BRX) domain of RLD is important for the recruitment of RLD from the cytoplasm to the plasma membrane by LAZYs [23]. Subsequently, polarized localization RLD might recruit the PIN3 to the new position by regulating PIN3 trafficking, leading to asymmetric auxin flow.

In rice, *DEEPER ROOTING 1* (*DRO1*) and the *quantitative trait locus for SOIL SURFACE ROOTING 1* (*qSOR1*) share sequence homology to the *LAZY* genes and function in root gravitropism [11,24]. Mutants of *DRO1* and *qSOR1* exhibit reduced gravitropism and a shallower root angle. Although *DRO1* is expressed in the whole root meristem, *qSOR1* is specifically expressed in the columella cells of the root cap, with the protein localizing to the plasma membrane. This tissue specificity and protein localization pattern suggests that qSOR1 plays a role similar to LAZY homologues in arabidopsis within the columella cells. The control of root angle by *DRO1* and *qSOR1* has proved valuable in enhancing adaptation to environmental conditions. Higher expression levels of *DRO1* result in a steeper root angle, leading to improved performance under drought conditions [11]. Plants with loss-of-function *qSOR1* alleles exhibit a shallower root angle, resulting in soil surface roots, contributing to better performance in saline soils [11] and facilitating better uptake of topsoil phosphorous [25].

Gravitropic machinery: signal transduction

The activation of the gravity signal transduction pathway initiates the formation of a lateral auxin gradient. In arabidopsis, the relocalization of auxin efflux carriers, specifically PIN3 and PIN7, contributes to auxin gradient formation. Although PIN3 and PIN7 are normally present on the plasma membrane on all sides of the statocytes, upon gravistimulation, they are relocated to the lower side of the cells, leading to an asymmetric auxin distribution [26,27]. Once the auxin gradient forms across the root cap, auxin is transmitted to the elongation zone. Recent studies on Arabidopsis lateral roots indicate that PIN-mediated auxin transport maintains the nonvertical angle. The relative magnitude of upward gravitropic auxin fluxes that is mediated by phosphorylated PIN3 and PIN7 and downward antigravitropic auxin fluxes mediated by unphosphorylated PIN3 and PIN7 determines the root angle [28].

Several proteins that function in the signal transduction process have been identified in rice and maize, including auxin carriers, cytoskeleton-related proteins, and auxin-signaling components. Knockout mutants of the auxin influx carrier *Osaux1* and the auxin efflux carrier *Ospin2* (also named *large root angle1*, *lra1*) exhibit a shallower GSA due to reduced root gravitropic responses [29,30]. Both OsAUX1 and OsPIN2 facilitate the transport of auxin from the root cap to the elongation zone, which is required for the elevated auxin level and auxin response in the root epidermal cell within the elongation zone [29].

The asymmetric localization of PIN proteins through endocytosis and recycling back to the plasma membrane is regulated by microfilaments. Mutations in the actin-binding protein VILLIN2 (OsVLN2) cause altered microfilament dynamics, resulting in faster recycling of OsPIN2 and thereby altered auxin distribution, leading to a hypergravitropic phenotype [31]. In maize, the gene *ZmRSA3.2* is a homologue of the arabidopsis formin homology protein, which regulates AF and microtubule dynamics. Overexpression of *ZmRSA3.2* enhances the response to gravity.

ZmRSA3.2 is regulated by the AUXIN RESPONSE FACTOR 38 (ZmARF38) and is likely involved in the transport of auxin in root tips by mediating the rearrangement of the actin cytoskeleton [32].

Another gene that potentially plays a role in signal transduction is the *CBL-Interacting serine/threonine-Protein Kinase 15* (*ZmCIPK15*) in maize. Mutants of this gene exhibit an approximately 10° steeper root angle in nodal roots in specific positions [33]. CIPKs have been demonstrated to interact with calcineurin B–like Ca^{2+} binding protein (CBL) [34]. Calcium is believed to be involved in the transduction of the gravity sensing. In arabidopsis seedlings, a gravity stimulus is transduced into Ca^{2+} signals on a subsecond timescale [35]. Therefore, it is possible that ZmCIPK15 has a role in signal transduction through calcium signaling in response to gravity sensing.

Gravitropic machinery: gravity response

Auxin regulates plant growth and development through its effects on cell division, cell expansion, and organ patterning. After the activation of the gravity signal transduction pathway, auxin is transported laterally across the root tip, where it accumulates on the lower side. The accumulation of auxin in the lower side of the root inhibits cell elongation, and the root subsequently bends downward [36].

After the establishment of the asymmetric auxin distribution, auxin activates its downstream signaling pathways. Disruption of these downstream pathways results in a decreased gravity response, resulting in a shallower root system, like that observed in the *soil-surface rooting 1* (*sor1*) mutants in rice. The E3 ubiquitin ligase SOR1 plays a role by ubiquitinating a noncanonical Aux/IAA protein, OsIAA26, targeting it for degradation and thus facilitating auxin signaling [37]. Similarly, in maize, overexpression of the Aux/IAA protein-encoding gene *ZmRSA3.1* enhances the gravity response by increasing the accumulation of auxin in the root tips [32]. ZmRSA3.1 interacts with ZmARF4 and ZmARF29, and it may be targeted by the auxin receptor SCF^{TIR} for degradation through the ubiquitination pathway. This release of the ARFs allows the regulation of the transcription of auxin response genes.

Another factor that controls root angle in wheat and barley is the MADS-box transcription factor encoded by *VERNALIZATION1* (*VRN1*), which is best known for its role in regulating flowering in response to temperature. Plants carrying the *VRN1* winter allele require vernalization as a prerequisite for flowering, whereas those with spring alleles, characterized by a deletion in the first intron, can flower without vernalization. The presence of the winter allele leads to a steeper root GSA. At the level of whole-root system, it operates independently of DRO1 and auxin sensitivity, but the exact mode of action is unknown yet [38]. The example of VRN1's control of the root angle illustrates how genes that have been favored in breeding processes can exert effects on overall plant development.

Antigravitropic offset mechanism

Previous research on arabidopsis lateral roots has revealed that the regulation of antigravitropic offset mechanisms involves a complex interplay of cytokinin and auxin [39]. Additionally, it has been suggested that auxin transport and response also contribute to antigravitropic offset mechanisms [40], because exogenous application of auxin or auxin transport inhibitor influences the GSA. However, the exploration of these mechanisms in crops has been limited, and their relevance to other root types remains poorly understood.

Interestingly, recent studies in barley and wheat have revealed novel antigravitropic offset components that function in an auxin-independent manner. One such component is ENHANCED GRAVITROPISM1 (EGT1), an F-box and Tubby domain-containing protein highly conserved across plant species [41]. Mutations in barley and wheat *EGT1* genes result in a striking root phenotype, where every root class adopts a steeper angle. *HvEGT1* is highly expressed in elongation zone and primarily in stele tissues, which are distinct from the known root gravitropic perception and response tissues in columella and epidermis. Atomic force microscopy (AFM) measurements have revealed that the cell walls in the elongation zone of *Hvegt1* roots are significantly less stiff than wild-type roots. It appears that HvEGT1 controls root angle by functioning as an antigravitropic offset component in an auxin-independent pathway in elongating root tissues via regulation of cell wall stiffening and loosening, thereby counteracting gravitropic bending in the outermost tissues.

Similarly, mutants in the STERILE ALPHA MOTIF domain–containing protein-encoding gene *EGT2* show a steeper GSA in all root types and an enhanced gravitropic response to gravistimulation in both barley and wheat [42]. In barley, *EGT2* is expressed in the whole root tip, including the root cap, meristem, and elongation zone, and regulates cell wall and ROS-related gene expression in the elongation zone. It is hypothesized that EGT2 suppresses the expression of gravity-responsive genes that play a positive role in gravitropism while inducing the expression of genes with a negative role in gravitropism [43]. Like EGT1, EGT2 functions independently of auxin in the antigravitropic offset mechanism. However, both proteins regulate different sets of cell wall genes and do not regulate each other at the transcriptomic level [41,42]. Consequently, both pathways are likely to function as parallel antigravitropic offset mechanisms to control root angle.

Knowledge gaps in root angle research

GSA in different root types plays an important role in shaping overall root system architecture. The concept of GSA encompasses not only the immediate response to gravity but also the continuous response throughout a root’s lifespan during specific developmental stages or under certain environmental conditions. Given that roots readjust their growth to return to the GSA after being repositioned, for instance, to overcome obstacles, specific factors must be actively involved in consistently interpreting the gravity stimulus and translating it into the adaptive response of the root to adjust its angle. As of now, it remains unclear which genetic components govern this process and whether they are regulated at the transcriptional, translational, or post-translational level, or even at the level of metabolites and cellular structure. Further research is necessary to uncover these factors responsible for maintaining the GSA.

Additionally, it would be important to distinguish the genetic components responsible for GSA maintenance from those involved in the gravitropic response. This is challenging because mutants of these components are likely to be affected simultaneously in their gravitropic response. Moreover, the exact mechanisms governing the interplay between gravitropic and antigravitropic offsets and how they are fine-tuned to achieve the desired root angle in response to various environmental factors remain to be fully understood. These factors may include nutritional deficiencies, rhizosphere microbiomes, pathogens, or the changing soil conditions, such as moisture levels and temperature [16,41,42].

Research on gravitropic and antigravitropic offset mechanisms has been focused primarily on arabidopsis primary and lateral roots, respectively. Although these mechanisms might apply to their respective root types in cereals, they cannot be broadly generalized to other root types, such as seminal, crown, and brace roots. Thus, it is important to investigate such mechanisms directly in these root types. Additionally, the mechanisms governing GSA maintenance may differ between arabidopsis and cereals due to significant differences in the root system architecture.

Different types of roots are considered to share both common and specific genetic and hormonal regulatory networks. Recent discoveries indicate that the regulation of root angle involves a combination of shared and root-specific components. For instance, EGT1 and EGT2 consistently function across all analyzed root types, including seminal, laterals, and crown roots and likely in diverse plant species [41,42]. Conversely, certain genes, such as *CIPK15*, exclusively control the root angle of specific root types, and even within those root types, their effects are limited to specific node positions [33]. This suggests that root angle can be influenced by various factors, even within the same root type. In cereal crops, roots of the same type can even show diverse types. For example, in rice, lateral roots can be divided into L-type lateral roots, which are thick and long, and S-type lateral roots, which are thin and short [44]. Understanding root angle regulation within this diversity is both a challenge and an opportunity to target the root angle of different root classes for optimizing resource uptake.

Recent advances in developing genetic and genomic resources in crops, in combination with high-throughput phenotyping methods and artificial intelligence-enabled quantification approaches, have emerged as valuable tools for uncovering the underlying mechanisms of root angle regulation in cereal crops [45,46]. Root architecture and function are significantly influenced by specific soil characteristics, including texture and structure, pH, temperature, nutrients, and water availability and the presence of beneficial microbes. Therefore, in the coming years, understanding and leveraging genetic variation in root angle under specific soil and environmental stress conditions will be of paramount importance. This research will contribute to the selection or development of varieties with enhanced soil exploration capabilities, making them better suited to mitigate abiotic stress resulting from climate change. Additionally, it will reduce the reliance on fertilizer applications. In turn, this will guide and accelerate breeding efforts aimed at achieving sustainable agriculture.

Concluding remarks

In summary, the root angle plays a crucial role in determining root system architecture, exerting a great influence on the access of roots to soil resources. The regulation of root angle is coordinated by gravitropic and antigravitropic response mechanisms. Although the majority of studies have primarily concentrated on primary and lateral roots in arabidopsis, recent studies have revealed additional components within the root angle signaling network in other root types in cereal crops. These new findings provide valuable insights into understanding the intricate control mechanisms governing root angle in complex root systems and offer opportunities for optimizing root system architecture to enhance soil resource acquisition (see Outstanding questions).

Outstanding questions

What specific genetic components are responsible for interpreting gravity stimulus and maintaining GSA in different root types, and how are they regulated at the molecular level?

Is the regulation of GSA maintenance primarily at the transcriptional, translational, or post-translational level, and are there specific metabolites and cellular structures involved in this process?

How can researchers effectively distinguish genetic components responsible for GSA maintenance from those involved in gravitropic response, considering the challenge posed by simultaneous effects on mutants?

What are the precise mechanisms governing the interplay between gravitropic and antigravitropic offsets, and how are these mechanisms fine-tuned to achieve the desired root angle in response to environmental factors such as nutritional deficiencies, microbiomes, pathogens, moisture levels, and temperature?

How do the mechanisms governing GSA maintenance differ between arabidopsis and cereals, and what are the specific mechanisms involved in seminal, crown, and brace roots that cannot be generalized from primary and lateral roots?

What are the common genetic and hormonal regulatory networks shared among different root types, and how do root-specific components such as EGT1, EGT2, and CIPK15 contribute to root angle regulation across diverse plant species?

How does genetic variation in root angle respond to contrasting soil and environmental stress conditions in cereal crops, and how can this variation contribute to the selection or development of crop varieties with enhanced soil exploration capabilities?

In what ways have genetic and genomic resources in crops, combined with high-throughput phenotyping methods and artificial intelligence or machine learning, provided insights into the underlying mechanisms of RGA regulation

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Declaration of interests

The authors declare no competing interests.

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in cereal crops, and how can this knowledge guide sustainable agriculture practices and breeding efforts?