



REVIEW ARTICLE

Root architecture in crops: Functions and implications for efficient water mining

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Abstract

Root system architecture (RSA) plays a fundamental role in determining crop performance under water-limited conditions by regulating soil water uptake efficiency and plant adaptation. Key traits, such as root depth, growth angle, branching patterns and hydraulic characteristics, influence the spatial distribution and functional capacity of roots to access moisture within heterogeneous soil environments. This review integrates recent developments in root structural organisation and RSA, highlighting their functional and mechanistic contribution to effective water mining in plants in general and in drought conditions in particular. This highlights the integration of anatomical traits with physiological processes, including root hydraulic conductance and aquaporin-assisted water movement, as well as genetic control governed by key regulators and associated transcription factors. Despite significant advances, challenges remain in translating RSA traits into effective field-level water uptake and in improving crop productivity. Efficient water mining requires integrated root architectural, physiological and genetic traits to improve crop performance under drought conditions.

Keywords: aquaporins; drought adaptation; genetic regulation; hydraulic conductivity; root system architecture; water mining

Introduction

Water scarcity is one of the most critical constraints limiting agricultural productivity worldwide, particularly in rain-fed and drought-prone regions (1). As climate change intensifies the frequency and severity of drought events, improving crop water acquisition efficiency has become a major objective of sustainable agriculture and crop improvement programs (2). Plant roots represent the primary interface between plants and soil and play a fundamental role in the acquisition of water and mineral nutrients required for plant growth and development (3). The root system originates from the embryonic radicle during seed germination and subsequently develops into a complex network of primary, lateral and fine roots that collectively determine the plant's ability to explore soil resources (4). In addition to anchoring plants in the soil, roots perform essential physiological functions, including water uptake, nutrient absorption, storage of assimilates and interactions with soil microorganisms in the rhizosphere (5). The efficiency with which plants capture soil resources is largely determined by the spatial organisation and structural complexity of their root systems (6).

The term root system architecture (RSA) describes the three-dimensional (3D) configuration of roots in the soil, including their

length, branching pattern, angle of growth and spatial distribution (7). Root system architecture is governed by multiple traits, including root depth, growth angle, branching pattern, root length density and root hair development, which collectively influence the ability of plants to exploit heterogeneous soil water distributions (8). Deep and well-distributed root systems allow plants to access moisture stored in deeper soil layers, thereby enhancing their resilience to water deficit conditions (9). Root system architecture varies considerably among plant species and cropping systems, reflecting the evolutionary adaptations to diverse environmental conditions (10). In general, crop root systems are categorised into taproot systems, which penetrate deeply into the soil and fibrous root systems, which form dense networks in the upper soil layers (11). This structural diversity enables plants to optimise their water acquisition strategies under varying soil moisture conditions (12). Water mining refers to the capacity of plant roots to extract water from different soil depths and locations, particularly under conditions of limited water availability (13). Root system architecture traits that promote deeper rooting, efficient soil exploration and improved hydraulic conductivity enhance a plant's ability to mine water from soil profiles and maintain its physiological activity during drought stress (14). Consequently, optimising the RSA has emerged as a promising strategy for

improving crop performance and yield stability in water-limited environments (15).

Recent advances in plant physiology, phenotyping technologies and molecular genetics have significantly improved our understanding of the mechanisms regulating root development and architecture (16). Several genes controlling root growth patterns and rooting depth have been identified, including DEEPER ROOTING 1 (DRO1) in rice (*Oryza sativa* L.), which modifies the root growth angle and improves water uptake from deeper soil layers (17). In addition, hormonal regulation and tropic responses, such as gravitropism and hydrotropism, play critical roles in guiding root growth toward zones of higher water availability (18).

Therefore, understanding the structural, physiological and genetic determinants of root architecture is essential for developing crops with improved water acquisition efficiency and drought tolerance (19). This review examines the structure and functional traits of crop roots, the principles governing RSA and the mechanisms through which RSA contributes to efficient water mining and drought adaptation in agricultural systems (20).

Root structure and function

Plant roots form the primary interface between plants and the soil environment and play a crucial role in determining plant water acquisition and drought resilience (3). Beyond their traditional roles in anchorage and nutrient uptake, roots regulate plant water relations through structural, anatomical and physiological traits that influence the efficiency of water extraction from the soil profile (6). The organisation of root tissues and developmental zones not only supports resource acquisition but also determines the effectiveness of plant access to deeper soil moisture during periods of water deficit (14).

Root growth zones and their significance

Root growth occurs in the apical region, where several developmental zones coordinate root elongation and soil exploration (11). The root cap protects the root apex and functions as a sensory structure that detects gravity and moisture gradients, enabling directional growth toward zones of higher water availability through gravitropic and hydrotropic responses (18). Behind the root cap lies the meristematic zone, where continuous cell division generates new cells that contribute to root growth (4). These cells subsequently enter the elongation zone, where rapid expansion

drives root penetration into deeper soil layers, thereby increasing access to subsoil water reserves during drought conditions (12).

Further away from the root tip lies the maturation zone, where cells differentiate into specialised tissues and root hairs develop (21). Root hairs substantially increase the absorptive surface area and improve contact with soil particles, thereby enhancing the efficiency of water and nutrient uptake (9). The distribution and activity of these growth zones influence root elongation rates and determine the ability of plants to explore soil layers that contain available moisture under water-limited conditions (15) (Fig. 1).

Root tissues and hydraulic regulation

The internal organisation of root tissues plays a key role in regulating water movement from the soil to the vascular system (22). The epidermis, often bearing root hairs, serves as the primary site for water absorption from soil solutions (23). Beneath the epidermis lies the cortex, which facilitates radial water transport toward the central vascular tissues while also acting as a storage region for carbohydrates (24). Structural modifications within the cortex, such as the formation of cortical aerenchyma, can reduce the metabolic cost of root growth and allow plants to allocate resources to deeper soil exploration (25).

The endodermis forms a critical regulatory barrier through the presence of casparian strips composed of suberin and lignin, which restrict uncontrolled apoplastic water flow and enforce the selective transport of water and ions into the vascular cylinder (26). Inside the endodermis lies the stele, which contains xylem vessels responsible for the long-distance transport of water from the roots to the shoots (27). Variations in xylem anatomy, including vessel diameter and density, influence root hydraulic conductivity and determine the efficiency of water transport under drought conditions (28).

Recent research has highlighted the importance of aquaporins, membrane-bound water channel proteins that regulate the movement of water across root cell membranes (13). Aquaporins modulate root hydraulic conductivity and enable plants to rapidly adjust their water uptake capacity in response to soil drying or osmotic stress (23). Through the coordinated regulation of anatomical barriers and membrane transport proteins, roots can dynamically control water movement and maintain plant water

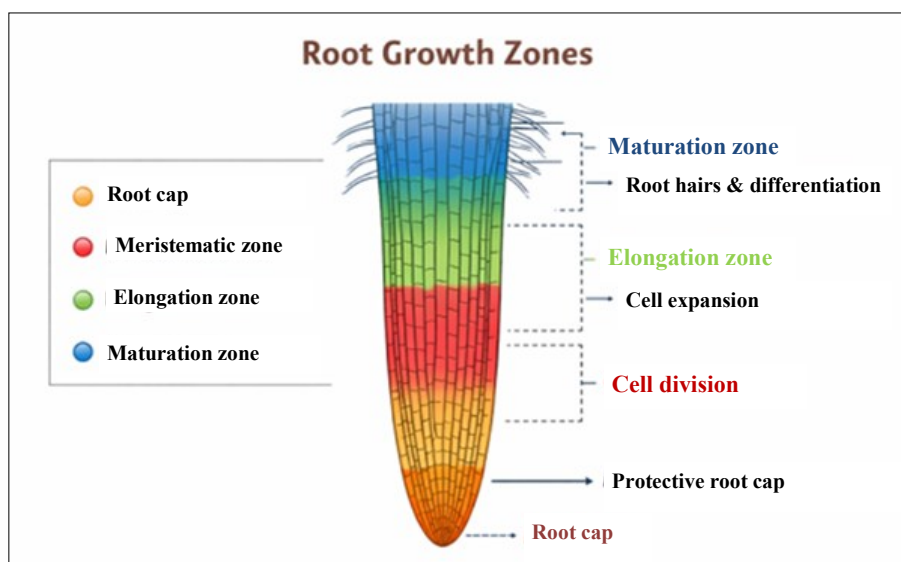


Fig. 1. Diagrammatic representation of root growth zones.

balance under fluctuating environmental conditions (8).

Root structural traits and water mining

Root structural traits strongly influence the ability of plants to extract water from different soil depths, a process commonly referred to as water mining. Traits such as deeper rooting depth, steeper root growth angles and increased root length density allow plants to access moisture stored in deeper soil layers that remain unavailable to shallow-rooted species. These traits are particularly important in drought-prone environments, where surface soil layers dry rapidly, whereas deeper soil horizons retain residual moisture.

Furthermore, increased lateral root branching and root hair development enhance the soil volume explored by roots, improving the efficiency of water capture in heterogeneous soil environments. Structural plasticity in root systems enables plants to adjust their root distribution and biomass allocation in response to soil moisture gradients, thereby optimising water acquisition under drought stress. In addition to structural organisation, root tissues exhibit adaptive modifications that regulate water movement under stressful conditions. The endodermis plays a critical role in controlling radial water transport by forming apoplastic barriers, such as the casparian strip and suberin lamellae. Suberin, a hydrophobic polymer deposited in the endodermal cell walls, restricts uncontrolled water loss and enhances selective permeability. Under drought stress, increased suberisation strengthens these barriers, reducing the backflow of water into dry soil and improving water-use efficiency (28–31). Overall, the structural organisation of root tissues and growth zones provides a physiological foundation for efficient water uptake and drought adaptation. Therefore, understanding how root structure interacts with hydraulic function and environmental signals is essential for improving crop performance in water-limited agricultural systems

Types of root system

Root systems show substantial variation in structure and spatial distribution, which strongly influences the acquisition of water and nutrients by plants. In higher plants, root systems are generally categorised into taproot systems, commonly found in dicotyledonous species and fibrous root systems, typical of monocot species. In addition, adventitious roots can develop from non-root tissues and contribute to architectural plasticity under varying environmental conditions (3, 19).

Taproot systems

In dicotyledonous crops, such as soybean and tomato, the root architecture is characterised by a dominant primary root, known as the taproot, which grows vertically into the soil profile. The main axis produces secondary and tertiary lateral roots that expand horizontally to explore the surrounding soil volumes (19). The deeper penetration of the taproot allows plants to access subsoil moisture reserves, which is particularly advantageous during periods of limited rainfall or during drought stress (14). Furthermore, lateral branches enhance soil exploration by facilitating the uptake of nutrients distributed at various soil depths (8).

Fibrous root systems

Monocotyledonous crops, such as rice and maize, develop fibrous root systems consisting of numerous adventitious roots originating from the stem base rather than a single dominant root. These roots form a dense network of fine roots that spread extensively in the upper layers of the soil. Due to their high surface area and shallow

distribution, fibrous roots are particularly effective at capturing nutrients concentrated in the topsoil, such as phosphorus (P) and nitrogen (N). However, their relatively shallow penetration may restrict water acquisition from deeper soil layers during prolonged droughts unless deeper adventitious roots are formed

Adventitious and specialised roots

Adventitious roots develop from non-root tissues, such as stems, nodes or leaves, often forming during later developmental stages or in response to environmental stress. For instance, in maize, brace roots emerge from aboveground stem nodes and provide additional mechanical support while also contributing to water and nutrient absorption. Other specialised root structures include prop roots, which enhance plant stability and aerial roots, which are observed in certain species and can absorb atmospheric moisture and gases (3).

Advantages of different root systems in stressed environments

Different root architectures confer specific advantages in response to environmental stress. Taproot systems enable plants to exploit deeper soil layers for water, thereby improving their drought tolerance (14). In contrast, fibrous root systems maximise nutrient uptake from nutrient-rich upper soil layers because of their extensive surface area and branching patterns. Adventitious roots further increase root system flexibility, allowing plants to modify their architecture in response to environmental challenges, such as flooding, soil compaction and nutrient heterogeneity (8). Collectively, the diversity of root system types plays a crucial role in plant adaptation and survival in fluctuating soil conditions

Root system architecture

Root system architecture refers to the 3D spatial configuration of roots in the soil, including root length, branching pattern, growth angle and distribution across soil layers. Root system architecture determines how effectively plants explore soil resources and is therefore a key determinant of water and nutrient acquisition, particularly under drought conditions (8, 12).

Efficient water mining depends on the ability of root systems to penetrate deeper soil layers, adjust branching density and regulate hydraulic conductivity to access water that remains unavailable to shallow-rooted plants (14). In water-limited environments, plants often modify their RSA by increasing root depth, altering root angles or reallocating biomass to deeper roots, thereby improving access to residual soil moisture.

Modern crop physiology research emphasises that root architectural traits are plastic and responsive to environmental signals, allowing plants to dynamically adjust their root growth patterns in response to soil moisture gradients, nutrient availability and mechanical impedance (15). Consequently, RSA has become a major target in crop breeding programs aimed at enhancing drought resilience and improving water use efficiency.

Root morphology, topology and spatial distribution

Root morphology includes measurable parameters such as root length density, root diameter, root surface area and root hair development, all of which influence the absorptive capacity of roots and their ability to exploit soil resources under stress conditions (14, 32).

Recent studies on crops have indicated that morphological root traits strongly influence drought adaptation and water acquisition efficiency. For example, maize (*Zea mays* L.) root systems show significant plasticity under water deficit conditions by

increasing axial root elongation and deeper soil penetration, thereby enhancing access to subsoil moisture (12, 33).

Similarly, research in wheat (*Triticum aestivum* L.) has demonstrated that genotypes possessing greater root length density and steeper root angles can maintain higher water uptake and sustain yield under drought stress conditions (34, 35).

Root topology describes the branching pattern and connectivity between primary and lateral roots, which influence the efficiency of soil exploration in spatially heterogeneous environments (10). Studies on common beans (*Phaseolus vulgaris* L.) have shown that genotypes with modified lateral root branching patterns can improve water and nutrient acquisition by optimising root distribution within the soil profile (36).

Root geometry, particularly the root growth angle, plays a crucial role in determining the depth of soil exploration. The identification of the DRO1 gene in rice (*O. sativa* L.) demonstrated that steeper root growth angles enable plants to penetrate deeper soil layers and access water during drought conditions (17). The spatial distribution of roots across soil horizons further determines a plant's ability to utilise stored soil moisture. Crops with deep and vertically distributed root systems are better able to extract water from deeper soil layers than shallow-rooted genotypes (37).

Advances in high-throughput root phenotyping technologies, including rhizotrons, X-ray computed tomography (CT) and imaging-based root analysis, have improved the ability to quantify RSA traits and identify crop genotypes with superior water-acquisition capacity (16, 38). Collectively, these studies highlight that variation in root morphology, topology and spatial distribution plays a critical role in determining crop adaptation to drought stress and represents a key target trait in breeding programs aimed at improving water-use efficiency and climate resilience in agricultural systems (15, 33, 37).

Root plasticity and environmental responses

Root system architecture is highly dynamic and responsive to environmental signals, such as soil moisture gradients, nutrient heterogeneity, soil compaction and temperature fluctuations. This adaptive capacity, commonly referred to as root plasticity, allows plants to modify root growth patterns to optimise water and nutrient acquisition under changing environmental conditions (7, 8).

Root plasticity also involves the modification of lateral root formation and branching patterns. Under heterogeneous soil moisture conditions, plants often reduce lateral root proliferation in dry soil regions while enhancing root growth toward zones with higher water availability through hydrotropic responses (39). Physiological adjustments within the roots also contribute to plastic responses. For example, the regulation of aquaporin proteins, which control membrane water permeability, plays a key role in maintaining root hydraulic conductivity and regulating water transport from soil to shoots during water stress (26).

Recent studies have indicated that the expression of plasma membrane intrinsic proteins (PIPs), a class of aquaporins, increases under drought conditions in crops such as maize and barley, enhancing root water uptake capacity and maintaining plant water status (40). Advances in root phenotyping and molecular genetics have further revealed that root plasticity is controlled by complex signalling pathways involving plant hormones, such as auxin, abscisic acid (ABA) and ethylene, which regulate root elongation,

branching and directional growth responses to environmental stimuli (41).

Root phenotyping technologies for studying root system architecture

Understanding the RSA in crops has historically been challenging because roots develop below the soil surface and are difficult to observe without disturbing the plant. Advances in root phenotyping technologies have greatly improved the ability of researchers to visualise, quantify and analyse root traits associated with water and nutrient acquisition (42).

Traditional approaches, such as soil excavation and root washing, have long been used to study root morphology; however, these techniques are labour-intensive and often disrupt the natural structure of root systems (15). To overcome these limitations, several modern imaging and sensing technologies have been developed that allow the non-destructive observation of root growth and architecture.

One widely used technique is rhizotron and mini-rhizotron imaging, in which transparent observation windows or tubes are installed in the soil to allow continuous monitoring of root growth and branching patterns over time (43). These systems have been extensively used in crops such as wheat and maize to study root elongation rates and distribution under drought conditions.

Another important advancement is X-ray CT, which allows three-dimensional visualisation of root systems growing in soil without disturbing the plant (44). This technology enables researchers to quantify root traits, such as root length density, root volume and root angle, providing detailed insights into how root architecture influences water uptake.

High-throughput phenotyping platforms have also been developed to efficiently analyse large numbers of plants. For example, automated imaging systems combined with specialised software can measure root traits, such as root length, branching patterns and root surface area, in controlled environments (45).

In addition, shovelomics, a field-based phenotyping method, has emerged as a rapid and cost-effective approach for evaluating root architecture in crop-breeding programs (46). This method involves the partial excavation of the root crown to assess traits such as root angle, number and biomass directly in field-grown plants.

The integration of these phenotyping technologies with genomic tools has accelerated the identification of the genetic determinants of root architectural traits. Such advances enable plant breeders to select crop varieties with improved root systems that enhance water acquisition and drought resilience (16) (Table 1).

Mechanisms of water uptake and transport

Root hydraulic conductivity

Root hydraulic conductivity describes the efficiency with which roots absorb water from the soil and transport it toward the vascular tissues for distribution throughout the plant (22). Water movement through roots occurs via multiple pathways, including the apoplastic route through cell walls, the symplastic pathway via plasmodesmata and the transcellular pathway across cell membranes and the relative contribution of these pathways determines the overall hydraulic conductivity (3).

Root anatomical characteristics, particularly xylem vessel diameter, vessel density and membrane permeability, strongly

Table 1. Root phenotyping technologies used to study root system architecture in crops

Phenotyping technology	Principle/ description	Crops studied	Key root traits measured	Reference
Rhizotron / Minirhizotron imaging	Transparent observation tubes or soil windows allow non-destructive monitoring of root growth and dynamics in soil over time	Wheat, maize, barley	Root length density, root growth rate, root distribution, branching patterns	9, 43
X-ray computed tomography (CT)	Non-destructive 3D imaging technique that reconstructs root architecture within intact soil columns	Wheat, maize, barley	Root volume, root angle, root depth, spatial distribution	12, 42
Magnetic resonance imaging (MRI)	Uses magnetic signals to visualise roots and water distribution inside soil without disturbing the plant	Maize, bean, rice	Root structure, water uptake dynamics, root–soil interactions	47
Ground-penetrating radar (GPR)	Electromagnetic waves detect underground root biomass and structure in field conditions	Maize, cassava, tree crops	Root biomass, root depth distribution	48, 49
Shovelomics	Field-based root excavation method for rapid phenotyping of root crown traits in breeding programs	Maize, wheat, sorghum	Root angle, root number, root crown architecture	46, 50
Hydroponic root imaging systems	Plants grown in nutrient solutions with transparent containers for direct observation and imaging of root development	Rice, maize, Arabidopsis	Root length, lateral root density, root hair formation	45
Gel-based growth systems (GLO-Roots / Transparent media)	Roots grow in transparent gel matrices enabling real-time imaging of root growth and branching	Arabidopsis, rice	Root architecture dynamics, root angle, branching patterns	51
Automated high-throughput phenotyping platforms	Integrated imaging systems combined with software for large-scale root trait analysis	Rice, maize, wheat	Root length, root surface area, root diameter, branching density	16

influence hydraulic conductivity and therefore, regulate the capacity of plants to maintain water uptake under drought conditions (14). Variations in these traits among crop genotypes can significantly affect drought adaptation and water-use efficiency (52). Recent experimental studies in maize (*Z. mays*) have shown that root pruning and architectural modification can alter root hydraulic conductivity, leading to improved water uptake efficiency and enhanced drought tolerance under field conditions (53). Similarly, investigations in bread wheat (*T. aestivum*) have demonstrated that environmental stress can induce physiological adjustments in root tissues that modify hydraulic conductivity through changes in aquaporin activity and root membrane permeability (54).

Recent research in plant hydraulics has also indicated that plants face a trade-off between hydraulic efficiency and hydraulic safety, where wider xylem vessels improve water transport capacity but increase susceptibility to embolism formation during drought (55). Consequently, modern crop breeding programs are increasingly targeting optimised xylem architecture, aiming to balance efficient water transport with greater resistance to hydraulic failure in water-limited environments (56).

Aquaporin-mediated water transport

Aquaporins are specialised membrane channel proteins that facilitate rapid water movement across biological membranes and play a central role in regulating root hydraulic conductivity (57). Among the different aquaporin families, PIPs are the most important for controlling water transport across root cell membranes (58).

Recent molecular studies have demonstrated that aquaporin expression is highly responsive to environmental stress, particularly drought (59). In maize, drought stress induces dynamic changes in the expression and localization of PIP aquaporins in root tissues, allowing plants to adjust their water transport capacity during both the stress and recovery phases (60).

Research has identified specific aquaporin genes involved in drought tolerance. For instance, the maize gene *ZmTIP2;3* has been shown to contribute to improved water uptake and physiological performance when plants establish symbiotic associations with arbuscular mycorrhizal fungi, indicating that aquaporins also interact with rhizosphere processes (61). Similarly, studies on pearl

millet (*Pennisetum glaucum* (L.) R.Br.) have revealed that the aquaporin gene *PgPIP2;6* plays an important role in maintaining water transport and transpiration efficiency under progressive drought stress (62). These findings highlight the significance of aquaporins as key molecular regulators of water movement in crop roots and as potential targets for breeding drought-resilient crop varieties (63).

Apoplastic barriers and suberisation

In addition to physiological regulation, the movement of water across root tissues is controlled by structural barriers that regulate radial transport toward the vascular cylinder (33). The casparian strip and suberin lamellae, located in the endodermal cell walls, act as selective barriers that prevent uncontrolled apoplastic flow and ensure the regulated uptake of water and solutes (64). Recent studies have demonstrated that environmental stress, particularly drought, can trigger structural modifications in these apoplastic barriers (28). Under water-deficit conditions, plants often increase suberin deposition in the endodermis, which reduces water leakage from the vascular tissues and improves water retention within the root system (30). Experimental research in rice (*O. sativa*) has shown that drought stress can stimulate the ABA-dependent regulation of aquaporin activity and suberization processes, thereby enhancing the ability of roots to maintain hydraulic function under low soil water potential (65). This structural plasticity of the endodermis enables plants to dynamically regulate root permeability, allowing efficient water uptake while minimising excessive water loss during periods of drought stress (66).

Hormonal regulation of root water uptake

Plant hormones play a fundamental role in coordinating root development, hydraulic regulation and water transport under environmental stress (67). Among these hormones, ABA is widely recognised as the central regulator of plant responses to drought stress (68). Water deficit commonly leads to increased ABA accumulation in roots, which triggers a range of physiological responses, including stomatal closure, enhanced root elongation and modulation of root hydraulic conductivity (69). Absciscic acid also interacts with other plant hormones, such as auxin, cytokinin and ethylene, forming complex signalling networks that regulate

root growth and adaptation to stress (70). Recent studies on several crop species have shown that ABA signalling pathways can simultaneously regulate aquaporin activity and endodermal suberisation, thereby linking hormonal signalling with the structural and physiological mechanisms that control water uptake in roots (71). Through this intricate hormonal crosstalk, plants coordinate root architecture, hydraulic conductivity and water transport capacity, enabling them to maintain water balance and sustain growth under drought limited (Fig. 2 and 3).

Genetic regulation of root architecture in water mining

Root system architecture is governed by complex genetic networks that regulate the root growth angle, depth distribution, branching patterns and overall spatial configuration of roots within the soil environment. These genetic controls determine the capacity of crops to access water from deeper soil layers and are therefore central to plant adaptation under drought stress. An improved understanding of the genetic mechanisms underlying RSA has become an important focus in crop breeding programs aimed at enhancing drought resilience and water-use efficiency.

Recent advances in plant genomics and molecular breeding have enabled the identification of numerous genes and quantitative trait loci (QTLs) associated with root architecture in crops. These genetic components regulate traits such as root elongation, root

angle, branching density and hydraulic properties, which collectively influence the efficiency of water uptake from the soil.

The major genetic mechanisms regulating root architecture under drought can be broadly categorised into (i) root growth angle regulators, (ii) branching and biomass regulators, (iii) anatomical modification regulators and (iv) hormonal and tropic response pathways (Fig. 4).

Root system architecture as a quantitative trait

Root system architecture is a complex quantitative trait controlled by multiple genes that is strongly influenced by environmental conditions. Unlike aboveground plant traits, RSA is difficult to measure directly because of its underground growth, making phenotyping challenging (72). Consequently, root traits, such as root angle, root biomass, lateral root density and root depth, are typically governed by several genetic loci rather than single genes.

Quantitative trait loci mapping and GWAS have revealed numerous genomic regions associated with RSA traits in major crops. These loci influence traits such as root length density, root penetration ability and root distribution within soil profiles, all of which are essential for effective water acquisition during drought (73–75). The polygenic nature of RSA suggests that breeding strategies must integrate multiple root traits, rather than targeting individual genes.

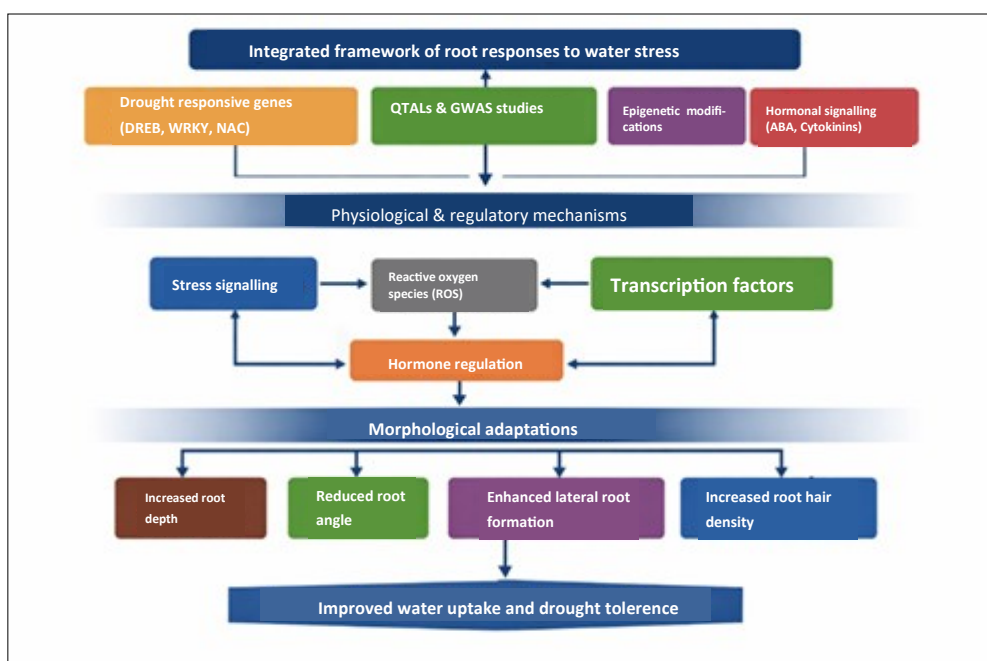


Fig. 2. Multilevel regulatory framework of root adaptation to drought stress.

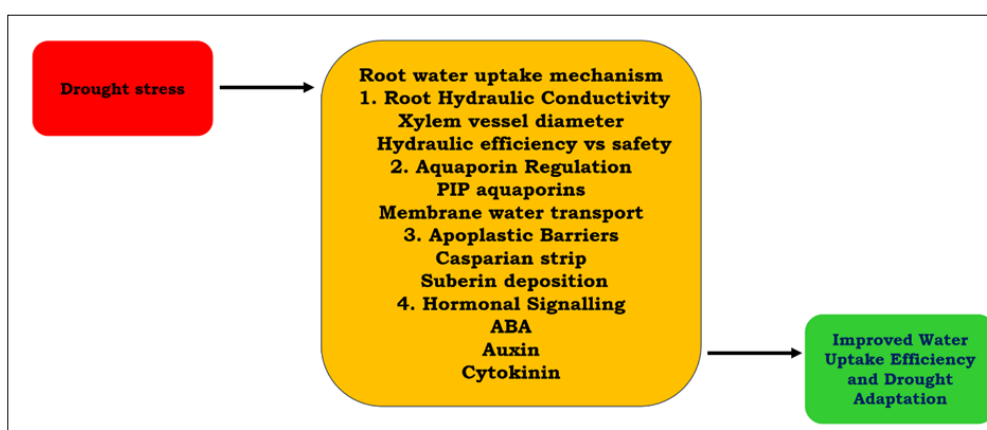


Fig. 3. Schematic representation of mechanisms regulating water uptake in crop roots.

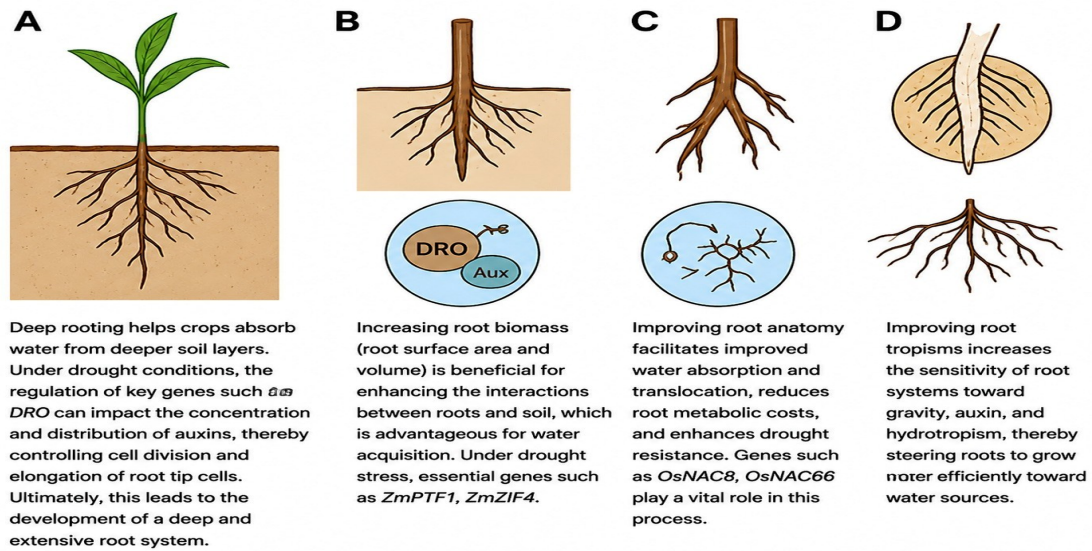


Fig. 4. Genetic regulation of crop root structure architecture under drought stress.

Root angle and deep rooting regulators

Among the genetic determinants of RSA, genes controlling root growth angle play a critical role in determining rooting depth and water-mining capacity. One of the most well-characterised genes is *DRO1* in rice, which regulates the gravitropic response of roots. Functional *DRO1* alleles promote steeper root growth angles, allowing roots to penetrate deeper soil layers where moisture availability is often higher during drought conditions (76). The mechanism underlying *DRO1*-mediated root angle control involves the regulation of auxin distribution at root tips, which influences gravitropic bending and directional root growth (76). Field experiments have demonstrated that rice varieties carrying functional *DRO1* alleles develop deeper root systems and exhibit improved drought resistance and yield stability. Homologs of *DRO1* have also been identified in other cereal crops. In maize, *ZmDRO1* contributes to steeper nodal root angles, enhancing subsoil water acquisition under drought conditions (77). Similar root-angle QTLs have been identified in wheat, indicating that this mechanism is conserved across cereals and represents a promising target for breeding programs aimed at improving drought adaptation.

Additional loci such as *DRO2*, *DRO3* and *qSOR1* further modulate root angle responses, enabling plants to exhibit diverse rooting patterns ranging from shallow to deep root systems depending on environmental conditions (78–79).

Regulators of root biomass and branching

Root biomass and branching patterns determine the volume of soil explored by plant roots. Increased root length, density and lateral branching enhance the plant's ability to extract water from soil, particularly under water-limited environments (80). Several transcription factors have been identified as key regulators of root branching and biomass accumulation. In maize, *ZmPTF1* promotes lateral root development and activates ABA signalling pathways that enhance drought tolerance (81). Similarly, *ZmZIF4* regulates ABA biosynthesis and increases both primary root length and lateral root number, contributing to improved root system expansion (82). In rice, genes such as *OsERF48* and *RRS1*, an MYB transcription factor, regulate lateral root density and primary root elongation. These genes increase the effective root surface area, thereby improving water uptake efficiency during drought stress (83–85). These findings

suggest that improving root branching patterns represents a viable strategy for enhancing soil exploration capacity and increasing plant access to deep soil water resources.

Anatomical trait regulators

In addition to root growth patterns, internal root anatomical features play a significant role in regulating water transport efficiency and metabolic costs associated with root growth. Several NAC transcription factors have been shown to influence root anatomical traits in rice. Overexpression of *OsNAC5*, *OsNAC9* and *OsNAC10* increases root diameter and strengthens vascular tissues, enabling more efficient water transport under drought conditions (85–87). Similarly, *OsERF71* regulates lignin biosynthesis and cell wall modification, leading to thicker roots with enhanced structural strength and larger aerenchyma formation. These anatomical changes improve root penetration ability and maintain root growth under drought stress (88). In maize, genes such as *ZmTIP1* regulate root hair elongation, increasing the absorptive surface area of roots, while *ZmVPP1* enhances lateral root formation and root biomass accumulation, contributing to improved water-mining efficiency (89, 90). These anatomical modifications allow plants to optimise water uptake while minimising the metabolic cost associated with root development (Fig. 5).

Tropism and hormonal control of root architecture

Root architecture is highly dynamic and responds to environmental stimuli through tropic responses mediated by plant hormones. Hormonal signalling pathways integrate external signals such as soil moisture gradients to guide root growth toward favourable conditions.

For instance, *qSOR1* in rice modifies gravitropic sensitivity, resulting in shallower root growth patterns that may be advantageous in flooded or surface-moist soils (91). In contrast, deeper rooting responses are typically associated with enhanced drought tolerance. In *Arabidopsis*, *EXOCYST70A3* regulates auxin transport and root curvature, thereby influencing root growth direction and depth (92). Hydrotropism, the directional growth of roots toward moisture gradients, is mediated through ABA signalling components such as *SnRK2.2* and *MIZ1*, which redirect root growth toward wetter soil regions (93). Other hormonal regulators also contribute to RSA plasticity. Cytokinin oxidase genes *CKX1* and *CKX3* regulate cytokinin levels and influence root growth dynamics, while

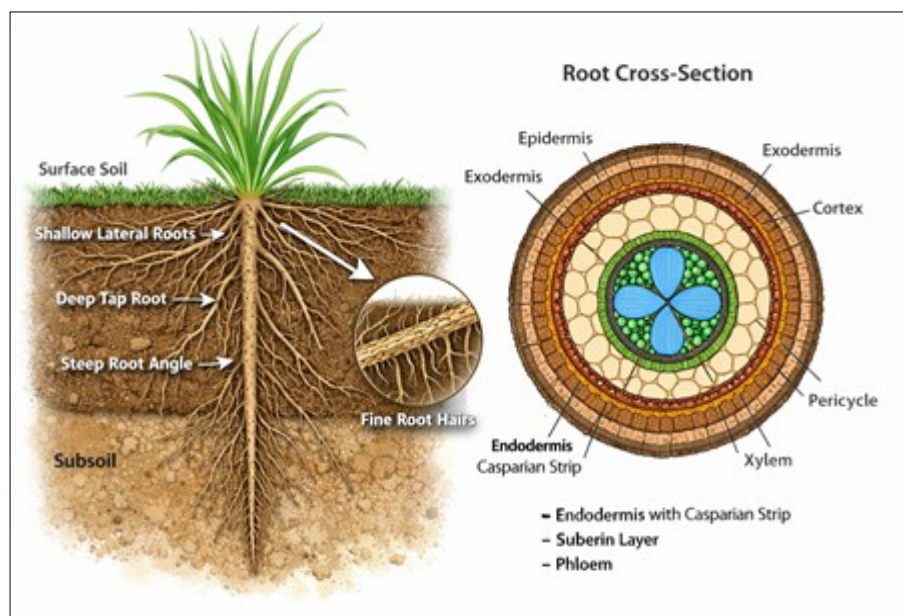


Fig. 5. Diagrammatic representation of root cross section.

the brassinosteroid receptor BRL3 enhances root growth and drought resilience through hormone-mediated signalling pathways (94). Together, these hormonal networks provide plants with the ability to dynamically adjust root architecture in response to environmental conditions, optimising water acquisition during drought stress. A summary of key genes involved in these mechanisms are presented in Tables 2 and 3.

Rhizosphere and root-soil interactions

The rhizosphere plays a critical role in regulating plant responses to drought through complex interactions among roots, soil and microbial communities. Recent studies indicate that the root-associated microbiome enhances drought tolerance by improving water uptake, modulating phytohormone signalling and sustaining root growth under stress conditions (104–106). Beneficial microorganisms, particularly plant growth-promoting rhizobacteria (PGPR), influence RSA and increase access to soil moisture. In addition, rhizosheath formation characterised by the adhesion of soil particles to root surfaces mediated by mucilage and microbial exudates, improves soil aggregation and water retention in the root

zone, thereby enhancing water availability during drought (107–109). Emerging research highlights that these rhizosphere processes interact dynamically with root architectural traits, suggesting that integrating microbiome function with RSA can significantly improve water-use efficiency and crop resilience under water-limited environments.

Translational implications for crop breeding

Understanding the genetic regulation of root architecture provides valuable opportunities for developing drought-resilient crops. While individual genes contribute to specific root traits, breeding programs increasingly focus on integrating multiple favourable root characteristics such as deep rooting angles, enhanced branching and optimised anatomical structures to improve water-mining efficiency. Modern breeding strategies, including marker-assisted selection, genomic selection and genome editing technologies such as CRISPR/Cas systems, enable the targeted manipulation of RSA-related genes. By combining genetic insights with high-throughput root phenotyping technologies, breeders can develop crop varieties with optimised root systems capable of sustaining productivity

Table 2. Genetic and physiological mechanisms regulating root water mining

Gene / QTL	Crop species	Root trait affected	Mechanism of action	Contribution to water mining	Reference
DRO1 (Deeper Rooting 1)	Rice	Root growth angle	Regulates gravitropic response through auxin redistribution	Promotes deeper root penetration enabling access to subsoil moisture	17
ZmDRO1	Maize	Nodal root angle	Controls gravitropic root growth	Enhances deeper soil exploration under drought	95
DRO2 / DRO3	Rice	Root angle variation	QTLs regulating root gravitropism	Modulates root depth distribution	17
qSOR1	Rice	Root orientation	Alters gravitropic sensitivity	Promotes shallow or deep rooting depending on environmental signals	96
ZmPTF1	Maize	Lateral root formation	Transcription factor regulating root growth under nutrient stress	Increases root surface area and soil exploration	97
ZmZIP4	Maize	Root length and branching	Regulates ABA biosynthesis	Enhances drought tolerance through increased root proliferation	98
OsERF48	Rice	Lateral root density	Ethylene-responsive transcription factor regulating root development	Improves root surface area for water uptake	99
RRS1	Rice	Primary and lateral root growth	MYB transcription factor controlling root elongation	Improves root penetration and water uptake efficiency	100
ZmVPP1	Maize	Root biomass	Vacuole proton pump influencing root growth	Increases lateral root number and drought tolerance	89
ZmTIP1	Maize	Root hair elongation	Aquaporin regulating water transport and root hair growth	Enhances water absorption surface	101

Table 3. Hormonal regulation of root architecture in relation to water mining

Hormone / Gene	Crop species	Root trait regulated	Mechanism	Role in drought adaptation	Reference
ABA (Absciscic Acid)	Rice, Maize, Wheat	Root elongation and hydraulic conductivity	Regulates stomatal signaling and root hydraulic properties	Enhances root growth toward deeper moisture zones	35
Auxin (IAA)	Rice, Arabidopsis	Root angle and branching	Controls gravitropism and lateral root initiation	Determines root architecture and soil exploration	8
CKX1 / CKX3 (Cytokinin oxidase)	Arabidopsis, Rice	Root growth regulation	Degrades cytokinin to promote root elongation	Enhances deeper root systems under drought	102
BRL3 (Brassinosteroid receptor)	Arabidopsis	Root growth and stress tolerance	Brassinosteroid signaling regulating root development	Improves drought tolerance through root plasticity	94
SnRK2.2	Arabidopsis	Hydrotropism	ABA-dependent signaling controlling root orientation	Directs root growth toward moist soil	53
MIZ1	Arabidopsis	Hydrotropic response	Mediates root bending toward water gradients	Enhances water foraging efficiency	103

under water-limited conditions.

Challenges and Future prospects in root-based water mining

Challenges

Despite major progress in understanding RSA, several limitations still restrict the practical use of root traits in crop improvement programs. One of the main challenges is that roots grow below the soil surface, which makes them difficult to observe and measure accurately under natural field conditions. Conventional methods such as soil excavation or root washing are destructive and often fail to represent the complete 3D structure of the root system within the soil.

Modern technologies including X-ray imaging, magnetic resonance imaging and rhizotron systems allow non-destructive observation of roots. However, these techniques are expensive, technically demanding and difficult to apply in large breeding programs. As a result, large-scale phenotyping of root traits under real field environments remains a major challenge.

Another important limitation is the complex genetic and environmental control of root traits. Characteristics such as root depth, branching pattern, root angle, root length density and root biomass are regulated by multiple genes and are strongly influenced by soil moisture, nutrient availability, soil texture and mechanical resistance. Because of this strong interaction between genetics and environment, root traits may vary across different locations and climatic conditions, making it difficult to identify stable root characteristics for crop breeding.

Increasing root biomass to improve water uptake can also create physiological trade-offs. Developing and maintaining a larger root system requires additional energy and carbon resources. In some cases, this increased investment in roots may reduce the resources available for shoot growth and grain production, especially under non-stress conditions.

Another challenge is that traditional crop breeding programs have mainly focused on above-ground traits such as plant height, grain yield and disease resistance. Due to the difficulty in measuring roots, root traits have often been overlooked in breeding strategies. Consequently, many modern crop varieties may not possess root systems that are optimised for efficient water extraction during drought. In addition, climate change exposes crops to multiple stresses simultaneously, including drought, heat, salinity and soil degradation. Root architectures designed only for deep water uptake may not function efficiently under such combined stress conditions. Therefore, a more integrated understanding of root development, soil conditions and environmental stresses is required

for improving crop resilience.

Future prospects

Future research on RSA is expected to play a crucial role in developing crops that can efficiently acquire water under drought conditions. One important direction is the development of high-throughput root phenotyping technologies that allow rapid and accurate measurement of root traits under field conditions. Advances in digital imaging, automated sensors and data analysis tools are improving the ability to monitor root growth, depth, branching patterns and soil-root interactions in real time.

Key genes controlling root architecture such as root angle, depth, lateral branching and biomass play a critical role in enhancing water acquisition under drought conditions. Advances in genome editing, particularly CRISPR-based tools, enable precise modification of these traits with minimal off-target effects, accelerating the development of drought-resilient cultivars. Future breeding strategies should prioritise optimised RSA rather than increased root size alone, focusing on deeper rooting, efficient branching patterns and lower metabolic cost. Improvements in root anatomical features, including xylem efficiency and aerenchyma formation, can further enhance water transport and resource use efficiency. Additionally, root tropic responses like gravitropism and hydrotropism are emerging as key determinants of soil water exploration. The role of rhizosphere microorganisms in improving soil structure, nutrient availability and moisture retention also warrants greater attention. Integrating these root traits with sustainable soil and water management practices will be essential for improving water use efficiency and ensuring long-term agricultural productivity under climate stress conditions (Fig. 6).

Conclusion

Root system architecture (RSA) plays a fundamental role in determining the ability of plants to access and utilise water from different soil depths, particularly under drought conditions. The spatial distribution, growth angle, branching pattern and anatomical characteristics of roots collectively influence the efficiency of water acquisition and the overall resilience of crops to water-limited environments. Advances in plant physiology, molecular genetics and imaging technologies have significantly improved the understanding of how root traits contribute to water mining and drought adaptation in major crops. Recent studies have identified several genes, transcription factors and quantitative trait loci that regulate key root architectural traits such as root angle, root elongation, lateral root formation and vascular development. These genetic regulators interact with hormonal signalling

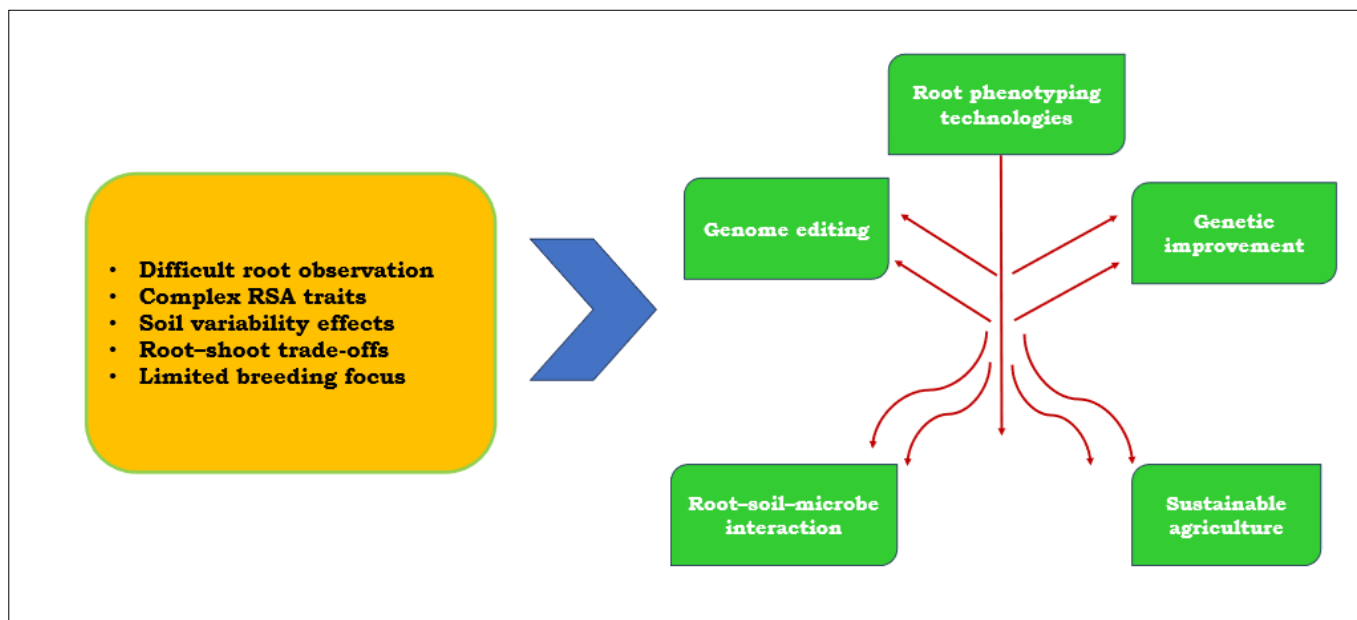


Fig. 6. Challenges and future strategies for enhancing drought resilience in crops.

pathways and environmental cues to shape root growth and plasticity. Such insights provide valuable opportunities for developing crop varieties with optimised root systems capable of extracting water more efficiently from deeper soil layers.

Despite these advances, important challenges remain. Root phenotyping under field conditions continues to be technically demanding and the complex interaction between genetic factors and environmental variability often limits the consistent expression of desirable root traits. In addition, the energetic costs associated with increased root growth and the trade-offs between root and shoot development must be carefully considered when designing crops with improved root systems.

Future research should therefore focus on integrating high-throughput phenotyping, genomic tools and advanced breeding strategies to better characterise and utilise beneficial root traits. Combining genetic improvement of RSA with sustainable soil and water management practices, as well as improved understanding of root-soil-microbe interactions, will be essential for enhancing crop water-use efficiency. A multidisciplinary approach that links plant physiology, genetics, agronomy and digital agriculture will be critical for translating root biology research into practical crop improvement strategies.

Overall, optimising RSA represents a promising pathway for improving crop productivity and resilience under increasing water scarcity and climate variability, making root-based strategies an important component of future climate-resilient agriculture.

Limitations

Despite considerable progress in understanding RSA and its role in water acquisition, several limitations restrict the broader applicability of current knowledge. A large proportion of available studies has been conducted under controlled or semi-controlled conditions, which do not fully capture the complexity and variability of field environments, including soil heterogeneity, dynamic moisture distribution and multiple interacting stresses. This limits the direct translation of experimental findings to real-world agricultural systems.

In addition, the characterisation of root traits and their relationship with actual water uptake under field conditions remains challenging due to the hidden nature of root systems and the limited scalability of high-throughput phenotyping approaches. Although advanced imaging technologies have improved root visualisation, their application in large-scale breeding programs is still constrained.

The genetic regulation of RSA is inherently complex, involving multiple interacting genes and strong genotype $\times$ environment interactions, which complicates the identification and deployment of stable traits across diverse agroecological conditions. Furthermore, there is a lack of integrative understanding linking root anatomical features, such as suberin deposition and endodermal barriers, with physiological processes including hydraulic conductivity and aquaporin-mediated water transport.

Finally, the rapidly evolving nature of root biology research suggests that emerging insights may not yet be fully captured. Addressing these gaps will require integrated, field-based and multidisciplinary approaches to improve the translation of RSA traits into crop improvement strategies for enhanced drought resilience and water-use efficiency.

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Authors' contributions

KAJ and KMK conceptualised and designed the review. KAJ prepared the manuscript and synthesised the literature. GH, TK and DM contributed to literature review and interpretation. APK, LMI and AJPR assisted in organisation and presentation of content. SN and RP critically revised the manuscript. All authors read and approved the final manuscript.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used ChatGPT solely for the purpose of generating a conceptual image to aid in visualisation of scientific content. The generated image was reviewed and validated by the authors for scientific accuracy and relevance. The authors take full responsibility for the integrity, originality and scientific content of the work.

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