



REVIEW ARTICLE

Decoding the hidden half: Advances in root growth dynamics and functional architecture of maize (*Zea mays* L.)

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Abstract

Maize (*Zea mays* L.) is a major cereal crop whose productivity across diverse agro-ecological environments is strongly influenced by belowground traits. The root system functions as the primary plant-soil interface, regulating water and nutrient uptake, providing mechanical support and enabling adaptive responses to abiotic and biotic stresses. Despite its central importance, maize root biology has historically received less attention than aboveground characteristics. The maize root system comprises primary, seminal, nodal and lateral roots differing in developmental origin, growth behaviour and physiological role. Key architectural traits-such as rooting depth, root growth angle and branching density-play a crucial role in root system development. These traits, along with anatomical features like cortical aerenchyma and root hair development, are governed by complex genetic networks involving regulatory genes, quantitative trait loci and hormone-mediated signalling pathways. Root growth and spatial distribution are further shaped by soil properties and agronomic practices, including irrigation and nutrient management. Recent advances in high-throughput phenotyping, three-dimensional (3D) reconstruction and artificial intelligence (AI) based image analysis technologies have enhanced quantitative assessment of root traits. This review consolidates recent progress in maize root research with emphasis on root system architecture (RSA), developmental regulation and their functional relevance to crop productivity. Uniquely, it integrates structural, genetic and phenotyping advances in maize root research into a unified framework, while explicitly linking RSA with its functional significance, an aspect often treated separately in earlier reviews. Optimising maize root systems is therefore essential for improving productivity, resource-use efficiency and agricultural sustainability under changing climatic conditions.

Keywords: crop productivity; maize root architecture; nutrient acquisition; rhizosphere; root phenotyping; root system architecture (RSA); stress tolerance

Introduction

Maize (*Zea mays* L.) is among the most extensively cultivated cereal crops globally, ranking 3rd after rice and wheat, with annual production exceeding 1.2 billion tonnes (t) across approximately 197 million hectares (ha) globally (1). Maintaining stable productivity under increasing climatic variability and resource constraints has become a major challenge for sustainable agricultural systems (2).

The maize root system serves as the direct interface between plant and soil, enabling water and nutrient uptake, mechanical support and mediation of biotic and abiotic stress responses, including drought, nutrient deficiency and soil compaction (3). Despite strong evidence that root traits significantly influence crop performance under stress-prone conditions, root research has progressed more slowly than aboveground studies, leaving critical knowledge gaps regarding genetic control and environmental plasticity (4).

Recent advances in high-throughput phenotyping, X-ray computed tomography (CT), quantitative genetics and genome-editing technologies have substantially improved the

capacity to characterise RSA and its regulation (5). This review synthesises recent progress by integrating physiological and developmental mechanisms, root morphological diversity and agronomic practices influencing root performance, with emphasis on climate resilience and breeding implications, providing a framework for future crop improvement and sustainable maize production.

Root system architecture of maize

Overview of maize root system architecture

Maize develops a complex fibrous root system composed of several distinct root classes that function collectively to acquire soil resources. Root system architecture describes the three-dimensional (3D) spatial organisation and orientation of roots within the soil profile, which strongly influences plant performance under water and nutrient limitation (4). Root system architecture has therefore emerged as a critical target for improving maize adaptation to climate variability and soil-related constraints. A schematic representation of maize RSA is presented in Fig. 1.

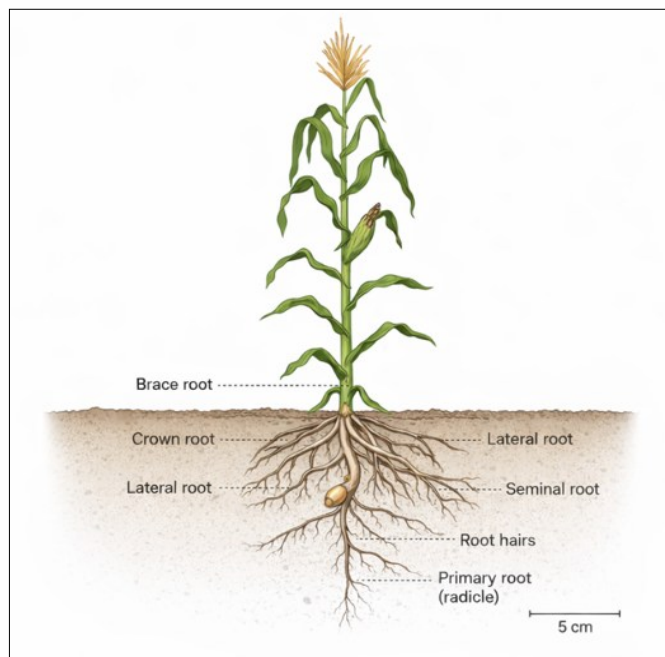


Fig. 1. Schematic representation of maize (*Zea mays* L.) root system architecture.

Root types in maize

Primary root

In maize, the radicle emerges as the primary root upon germination, penetrating the soil through positive gravitropism driven by auxin redistribution in the root cap (6). As the sole organ for water and nutrient uptake and anchorage until nodal roots develop, it dominates early seedling establishment (7). Despite its short functional lifespan, the primary root remains critical under moisture stress by elongating deeper into the soil profile before the nodal root system becomes functional (5).

Seminal roots

Seminal root primordia are initiated between 22 and 40 days after pollination at the scutellar node and together with the primary root form the entire early root framework of the maize seedling (8). Typically, 2–6 seminal roots develop at steep angles, directing biomass toward deeper nitrate-rich soil layers and contributing approximately 35 % of total nitrogen (N) and phosphorus (P) uptake during the first 25 days of growth (9). This early nutrient capture supports seedling vigour and establishes yield potential, making seminal root traits important targets in breeding for early-season resource efficiency and stress resilience. Under heterogeneous soil conditions, seminal roots support seedling vigour by proliferating preferentially in nutrient-rich patches before the nodal root system becomes functional, enhancing early adaptability under variable environments (10).

Nodal roots

Nodal roots, also referred to as crown or shoot-borne roots, constitute the predominant component of the mature maize root system. They emerge sequentially in acropetal whorls at each node from the V1 stage onward. Crown roots typically appear around 14 days after germination (DAG), while brace roots initiate at approximately 40 DAG (11). They provide mechanical support and lodging resistance, with above-ground brace root whorls contributing most to anchorage strength. This plasticity enhances nutrient acquisition, supports grain filling under stress, improves yield stability and represents a key target for breeding

climate-resilient maize (12). By the V6 stage, nodal roots become the dominant pathway for water and nutrient uptake, sustaining absorption through reproductive stages. Their architecture and persistence are critical for maintaining grain filling under stress, making them key targets for breeding climate-resilient and high-yielding maize cultivars (13).

Lateral roots

Lateral roots develop from primary, seminal and nodal roots, expanding absorptive surface area when auxin maxima at phloem pole pericycle cells trigger asymmetric divisions leading to primordium emergence through cortical tissues, they form mainly during early vegetative stages and reflects genotype $\times$ environment $\times$ management ($G \times E \times M$) interactions, where genetic potential is modulated by soil conditions and management to determine lateral root proliferation and distribution (14). Branching frequency and elongation are dynamically adjusted in response to local soil gradients. Auxin redistribution stimulates proliferation in nutrient-rich microsites, enhancing phosphatase activity and nutrient capture (15). The carbon (C) investment is optimised through fewer but longer laterals under N limitation, while dense branching is favoured under P deficiency (16).

Root depth, growth angle and branching patterns

Root depth

Rooting depth in maize can reach up to 2 m under favourable conditions and varies with genotype, soil texture and management practices. Depth is largely established by the R3 stage, with elongation driven by hydrotropic responses. Under drought, genotypes exhibit plasticity by reallocating root biomass to deeper soil layers. Greater rooting depth enhances water capture during reproductive stages, improving drought tolerance, stabilising yield and serving as a critical trait for breeding climate-resilient maize under water-limited conditions (17, 18).

Root growth angle

Root growth angle determines vertical versus horizontal root distribution, with steeper angles promoting subsoil moisture access and shallower angles enhancing surface nutrient exploration (19). The gene *EGT1* sets the gravitropic set-point angle by counteracting auxin-driven bending with moisture gradients, further modulating final angle during soil penetration (20). Steeper angles are optimal under drought, while increasing plant density reduces horizontal spread through decreased auxin content, inducing compensatory vertical extension (21).

Branching characteristics

Root branching regulates soil volume explored with hydro patterning directing lateral initiation toward moist zones via auxin while suppressing it in dry regions (22). Nitrogen-rich patches concentrate branching in topsoil while P deficiency drives denser branching throughout the profile and lateral root exudates selectively recruit beneficial rhizosphere microorganisms (23). Optimal branching is nutrient-dependent: sparse under N limitation to reduce metabolic costs, dense under P deficiency, where immobility demands high surface coverage (16).

Functional traits affecting water and nutrient uptake

Root anatomical traits

Cortical aerenchyma formation develops through programmed cell death, reducing living cortical tissue and lowering respiratory demand. Larger cortical cells further decrease metabolic cost per

unit root length, while xylem vessel size and density determine hydraulic conductivity and water transport efficiency. The concept of root cortical burden (RCB) the metabolic cost of maintaining cortical tissues has gained prominence, with reduced RCB associated with more efficient internal resource allocation (24).

Under drought and N-limited conditions, increased aerenchyma formation and reduced RCB enable greater C allocation to root elongation and deeper soil exploration, improving stress tolerance and nutrient acquisition (5).

Root hair development

Root hair development involves regulated cell differentiation and elongation processes, resulting in variation in root hair length and density among maize genotypes (25).

Root hair traits respond strongly to nutrient availability, particularly P deficiency, increasing soil contact area and enhancing uptake of immobile nutrients at low C cost. Under dry conditions, root shrinkage reduces root-soil contact, limiting the contribution of root hairs to water uptake (26).

Mycorrhizal associations

Maize forms symbiotic associations with arbuscular mycorrhizal fungi (AMF), initiated by plant-released strigolactones that stimulate fungal spore germination. Fungal mycorrhizal (Myc) factors trigger calcium signalling and transcriptional changes leading to arbuscule formation, facilitating nutrient exchange at the periarbuscular interface (27, 28).

Arbuscular mycorrhizal fungi extend the effective root system through extraradical hyphae, enhancing uptake of P, N and micronutrients beyond depletion zones. This symbiosis can increase P uptake efficiency by up to 80 %, improve water absorption under drought and enhance overall nutrient acquisition by expanding the soil volume explored (5, 29).

Factors influencing root growth dynamics

Genetic regulation of maize root growth

Major genes and quantitative trait loci (QTLs)

Maize root architectural traits are predominantly controlled by complex polygenic systems involving major and minor-effect loci (30). *RTCS*, a LOB-domain transcription factor on chromosome 1 (bin 1.02), is essential for seminal and crown root initiation. *RUM1*, an auxin/indole-3-acetic acid (AUX/IAA) regulator on chromosome 3 (bin 3.07), controls embryonic and post-embryonic root initiation. Both genes function within auxin-centred regulatory networks and correspond to major QTLs governing seminal root number (31).

Root hair development proceeds through bulge initiation, tip growth and elongation, regulated by bHLH transcription factors, including *ZmLRL5*, with auxin activating *RSL2* and *RSL4* to drive tip growth (32). Six RTH mutants have been characterised with *RTH1* mediating polar exocytosis, *RTH3* regulating cellulose organisation,

RTH5 generating reactive oxygen species (ROS) for cell wall loosening and *RTH6* controlling the bulge-to-tip transition (33). Additionally, *ZmTIP1* influences root hair length and drought tolerance networks, with defective root hair genotypes showing compromised P and water uptake. Root angle and depth are controlled by QTLs on chromosomes 1, 2, 4 and 7, affecting gravitropism and deep rooting, while lateral root density is governed by QTLs on chromosomes 3, 5 and 8, linked to branching, auxin regulation and nutrient foraging (34).

Hormonal regulation

Auxin, generated by the TAA/YUC pathway, defines root initiation sites and governs meristem activity and lateral root positioning through PIN-family efflux carriers, including *ZmPILS6*, *ZmPIN1B* and *ZmPIN9* (35). Cytokinins antagonise auxin by promoting PIN degradation and suppressing polar transport, limiting lateral root density, while elevated abscisic acid (ABA) under drought activates *PYR/PYL-SnRK2* signalling to direct root growth deeper into the soil via an ABA-auxin cascade (14). Ethylene inhibits primary root elongation but promotes root hair initiation and lateral root hydro-patterning toward moist soil zones, while brassinosteroids promote root elongation synergistically with auxin (36). Strigolactones act as negative regulators of lateral branching under P and N deficiency, while facilitating mycorrhizal associations. These hormonal pathways interact with genomic regions controlling root angle, depth and branching density, integrating genetic and environmental signals to shape overall RSA (37). Major genes controlling maize root architecture are given in Table 1.

Environmental factors affecting maize root growth

Soil physical properties

Soil texture and structure

Soil texture governs maize root architecture through its effects on water availability, aeration and mechanical resistance. Clay soils restrict depth and favour surface rooting, whereas sandy soils promote deeper systems despite low water retention. Loamy soils provide optimal conditions, supporting rooting depths of 1.8–2.2 m by flowering, with soil texture contributing substantially to variation in rooting depth, explaining approximately 20–40 % of phenotypic variance (PVE) across environments (41–43).

Soil compaction and Soil aggregation

Soil compaction markedly restricts maize root elongation when penetration resistance exceeds 2.0 MPa, limiting access to deeper soil layers and reducing effective rooting depth (41). This constrains water uptake under drought and reduces nutrient acquisition from subsoil layers. Well-aggregated soils containing stable macropores (> 50 µm) facilitate root elongation by providing preferential growth pathways that reduce the metabolic costs of soil penetration and enhance exploration of soil volume, improving water and nutrient uptake efficiency (44).

Table 1. Major genes controlling maize root architecture

Gene	Chromosome location	Root trait	Molecular function	References
<i>RTCS</i>	Chr 1, bin 1.02	Seminal and crown root initiation	LOB-domain transcription factor; auxin-responsive	(38)
<i>RUM1</i>	Chr 3, bin 3.07	Embryonic and post-embryonic root initiation	AUX/IAA auxin repressor; meristem regulation	(38)
<i>ZmCIPK15</i>	Chr 5	Root angle and depth	CBL-interacting serine/threonine-protein kinase	(39)
<i>ZmPILS6</i>	Chr 6	Root morphogenesis	Auxin efflux carrier; polar auxin transport	(35)
<i>ZmLRL5</i>	Chr 2	Root hair elongation	bHLH transcription factor; tip growth regulation	(32)
<i>ZmTIP1</i>	Chr 1	Root hair length and drought tolerance	S-acyltransferase; GWAS-identified	(34)
<i>RTH5</i>	Chr 2	Root hair cell wall loosening	Monocot-specific NADPH oxidase; ROS generation	(40)
<i>RTH6</i>	Chr 4	Root hair tip growth transition	D-type cellulose synthase (CSLD5)	(33)

Soil moisture

Maize root elongation is vigorous at matric potentials above -0.3 MPa, declining progressively as soils dry, while under moderate deficit (-0.25– -0.40 MPa) primary and seminal elongation is maintained with genotype-dependent lateral root responses (45). This supports continued soil exploration and water uptake under mild stress. Under severe drought below -1.5 MPa, primary and nodal roots continue elongating into deeper layers with hybrids showing stronger hydrotropic responses improving access to subsoil moisture, sustaining grain filling and enhancing drought adaptation and yield stability (46).

Soil temperature

Soil temperature strongly influences maize root growth, with optimal elongation occurring between 25 and 30 °C following Arrhenius-type metabolic response patterns (47). Low temperatures below 15 °C delay lateral root emergence and suppress root hair development, reducing early-season phosphorus uptake and limiting initial crop establishment (48). Conversely, temperatures exceeding 35 °C inhibit root elongation by disrupting cellular metabolism and reducing root biomass accumulation, thereby constraining water and nutrient uptake and negatively affecting overall crop performance (49).

Soil aeration

Adequate soil aeration is essential for maize root respiration and elongation; when air-filled porosity falls below 10 %, oxygen (O) deficiency shifts roots to anaerobic fermentation, accumulating ethylene that inhibits meristem activity and elongation (50). Hypoxic conditions additionally impair microbial nutrient cycling and promote the accumulation of toxic metabolites, including ethanol and lactic acid, suppressing nutrient uptake efficiency (51).

Soil porosity

Soil macro-porosity strongly regulates maize root penetration, with root length, surface area and angle correlating positively with pore sizes in the 0.10–0.5 mm range (52). Bio-pores created by decaying roots and soil fauna reduce penetration resistance and channel root growth into deeper layers with bio-pore walls enriched in nutrients and microbial activity relative to bulk soil (53). Under compaction, maize roots preferentially colonise existing bio-pores rather than penetrating the surrounding soil matrix (44).

Soil chemical properties

Soil pH and nutrient availability

Soil pH fundamentally influences maize root growth by regulating nutrient solubility, aluminium (Al) toxicity and microbial activity, with optimal root development occurring between pH 6.0–7.0 (54). In acidic soils below pH 5.5, Al toxicity severely restricts root elongation and lateral root formation by disrupting cell division and altering root cell patterning in the transition zone (55). Alkaline soils above pH 7.5 induce iron (Fe), zinc (Zn) and manganese (Mn) deficiencies through precipitation as insoluble hydroxides, impairing root growth by disrupting enzymatic functions and hormonal signalling essential for root morphogenesis (56).

Soil electrical conductivity

Soil electrical conductivity (EC) reflects dissolved ion concentration and serves as the primary salinity stress indicator, with maize root elongation and meristematic cell division inhibited above 1.7 dS m⁻¹ as osmotic stress and Na⁺/Cl⁻ toxicity disrupt membrane integrity and nutrient transporter function (57). As EC increases further, root

architecture shifts toward shorter, thicker roots with fewer lateral branches, reducing absorptive surface area and compromising nutrient and water uptake efficiency. At the rhizosphere level, elevated EC alters ion exchange dynamics, disrupts microbial activity and modifies root exudation patterns, collectively influencing nutrient availability and root-soil interactions under saline conditions (58).

Soil organic matter content

Soil organic matter (SOM) positively influences maize root development through enzyme-mediated mineralisation of N, P and sulphur (S), directly increasing rhizosphere nutrient availability (59). Soil organic matter additionally improves aggregate stability, reduces bulk density and increases water-holding capacity, while supporting diverse microbial communities that enhance nutrient cycling, IAA production and pathogen suppression in the root zone (60). It also contributes to rhizosphere buffering by stabilising pH, moderating nutrient fluctuations and reducing toxicity effects, thereby maintaining a favourable environment for root growth. In the absence of adequate SOM, maize roots experience increased mechanical impedance, reduced nutrient and water availability, diminished microbial support and greater susceptibility to soil-borne pathogens, collectively limiting root elongation, lateral branching and overall root system functionality (61).

Soil cation exchange capacity

Soil cation exchange capacity (CEC) determines the capacity to adsorb and supply plant-available cations, including Ca²⁺, Mg²⁺, K⁺ and NH₄⁺ by retaining them on negatively charged clay and organic matter surfaces, preventing leaching while replenishing root-zone concentrations during uptake (62). Higher CEC soils provide a more stable cation supply buffering against nutrient deficiency, while low CEC sandy soils require more frequent fertilisation; CEC increases with SOM and pH, making organic matter management critical for sustaining maize root nutrition (63).

Soil sodicity

Soil sodicity (ESP > 15 %) restricts maize root development through excess Na⁺ displacing Ca²⁺ and Mg²⁺ causing clay dispersion, collapse of macroporosity and increased mechanical impedance that restricts root penetration depth (58). Sodium toxicity additionally inhibits meristem activity and cell elongation, with maize water absorption decreasing approximately 1 per 1 % increase in ESP, reducing leaf area index and grain yield (64). Gypsum application reclaims sodic soils by displacing Na⁺ with Ca²⁺, restoring soil structure and root penetrability; additionally, Ca²⁺ mitigates Al toxicity by reducing Al³⁺ activity in the rhizosphere and stabilising root cell membranes, thereby protecting root growth and function. (65).

Agronomic management practices

Irrigation management

Irrigation practices determine soil moisture distribution patterns and wetting front depth, directly shaping maize root architecture. Conventional furrow irrigation concentrates roots in the 0–40 cm layer, while alternate furrow irrigation promotes deeper penetration through ABA-mediated hydrotropic elongation toward deeper moist layers (66).

Flood irrigation creates hypoxic conditions, producing shallow root systems vulnerable to drought, whereas subsurface drip irrigation with emitters at 30–45 cm depth encourages deep rooting

and reduces water use by 35–55 % (67). Rain hose irrigation produces shallower root profiles than drip systems but improves distribution uniformity over furrow irrigation with 20–30 % water savings, thereby influencing RSA by promoting a more surface-oriented root distribution compared with the deeper and more vertically extensive rooting patterns observed under drip irrigation (68).

Nutrient management

Split N application supports sustained root growth and deeper rooting compared with single basal applications, while deep N placement at 15–25 cm stimulates lateral root proliferation and enhances N uptake efficiency and grain yield (69). Banded P application creates localised concentration zones that stimulate dense lateral root proliferation and root hair elongation through auxin-mediated signalling, improving early P uptake efficiency over broadcast application (70). Potassium (K) availability primarily regulates nodal root elongation rate and diameter rather than localised proliferation, with deficiency triggering increased root length-to-mass ratios to maximise soil volume explored per unit C invested, while nutrient imbalances among major ions (e.g., N, P and K) can disrupt root growth patterns and physiological processes, ultimately limiting nutrient uptake efficiency and overall plant performance (71).

Organic amendments and biofertilisers

Organic amendments improve soil structure, water-holding capacity and nutrient availability, promoting deeper maize root systems; Humic substances stimulate H⁺-ATPase activity to loosen cell walls, while auxin-like IAA groups trigger lateral root primordium initiation and upregulate high-affinity nutrient transporter expression (72). Arbuscular mycorrhizal fungi extend root system reach through extraradical hyphal networks, absorbing P, Zn and water beyond the depletion zone (27). Plant growth-promoting rhizobacteria (PGPR) promote root development through IAA production, N fixation, P solubilisation and ACC deaminase synthesis that relieves abiotic stress-induced growth inhibition (73). *Trichoderma* stimulates lateral root initiation via secreted IAA and volatile compounds while solubilising P and inducing systemic resistance through jasmonic and salicylic acid pathways and also promotes rhizosphere priming, enhancing microbial activity and nutrient mineralisation in the root zone (74).

Tillage and residue management

Conventional tillage promotes rapid early root growth by reducing surface compaction, but may generate dense subsurface layers restricting deep rooting. Long-term no-tillage enhances root penetration through stable biopore networks - formed by decaying root channels, earthworm activity and fungal hyphal networks and improved soil aggregation, thereby improving drought tolerance and water-use efficiency (75).

Crop residues

Residue retention moderates soil temperature, conserves moisture and stimulates biological activity, supporting sustained root growth with wheat straw and maize stover decomposition, improving soil organic C, aggregate stability and pore continuity to promote deeper root penetration (76). Legume residues accelerate N mineralisation and stimulate lateral root proliferation, though high C: N residues may temporarily immobilise N, requiring appropriate nutrient management (77).

Crop and plant geometry

Higher planting density restricts horizontal and vertical root growth, while narrower row spacing improves resource distribution and promotes vertical elongation and fine root development (78). Modern maize breeding has shifted root angles toward steeper configurations to accommodate high-density planting, reducing intraspecific root competition under crowded conditions (21).

Crop rotation

Continuous maize monoculture leads to soil degradation, pathogen accumulation and simplified rhizosphere microbiomes that reduce root health and elongation (79). Preceding legume crops enrich the rhizosphere with IAA-producing bacteria, stimulating lateral root development, while diversified rotations increase soil organic C by 8 % and microbial activity by 45 % relative to monoculture (80).

Intercropping

Maize-soybean strip intercropping promotes lateral root expansion and increases root dry weight in the 0–20 cm layer through reduced intraspecific competition (81). Legume intercrops increase N use efficiency by 25–30 % through mycorrhizal hyphal networks, while intercropping increases rhizosphere metabolite diversity, recruiting microbiomes that enhance N mineralisation and P cycling (82).

Agronomic practices enhance rhizosphere biology by enriching PGPR and promoting mycorrhizal colonisation, improving nutrient cycling and root-microbe interactions. This supports enhanced nutrient uptake, root growth and stress resilience, contributing to improved maize productivity (83).

Advances in root phenotyping and measurement techniques in maize

Laboratory and greenhouse-based root phenotyping systems

Hydroponic and semi-hydroponic systems

Hydroponic culture systems provide controlled environments for investigating maize root development under precisely regulated nutrient conditions, enabling non-destructive visualisation and repeated measurements (84). The paper roll method remains widely adopted for rapid screening of early root traits with automated imaging and machine-learning pipelines enabling high-throughput extraction of architectural traits across hundreds of genotypes (85). Gel-based systems using gellan gum provide 3D mechanical support with optical transparency, permitting time-lapse monitoring of root development and gravitropic responses with improved aeration over traditional agar systems (86). Deep hydroponic platforms enable characterisation of crown and nodal root development at later growth stages with automated nutrient delivery supporting extended growth durations across diverse maize genotypes. Despite these advantages, such systems are constrained by high setup and maintenance costs, limited scalability for large field-representative populations and reduced realism due to the absence of soil physical and biological complexity (87).

Growth pouches and rhizotron systems

Growth pouch systems combine hydroponic advantages with enhanced aeration and simplified handling with blue germination paper enclosed in transparent pouches, providing superior contrast for automated image analysis while maintaining healthy root growth (88). Greenhouse-adapted minirhizotron systems allow repeated non-destructive observation of maize roots over

time with automated image acquisition enabling high-resolution monitoring of root proliferation in response to localised nutrient patches at 2 day intervals throughout the growing period. However both systems are constrained by limited representation of soil conditions, relatively high installation and imaging costs (particularly for minirhizotrons) and scalability challenges due to labour, infrastructure and data processing requirements (89).

Soil-filled container systems

Transparent soil substitutes composed of Nafion particles closely mimic the hydraulic and mechanical properties of natural soils while permitting optical imaging of maize roots and rhizosphere processes (90). Soil column systems allow controlled root growth under realistic conditions with depth-resolved destructive sampling with cylindrical columns equipped with moisture sensors and tensiometers enabling simultaneous monitoring of root traits and soil water dynamics under varying nutrient treatments. These systems are constrained by high material and instrumentation costs, limited scalability for large populations and partial representation of field heterogeneity due to restricted soil volume and boundary effects (91). These systems exhibit clear trade-offs between resolution, throughput and scalability. Imaging-based approaches provide high-resolution data but are constrained in throughput, whereas hydroponic and paper-based systems enable higher-throughput screening (92). Laboratory methods ensure strong precision and control, but their ability to predict field performance remains limited due to environmental complexity (93).

Field-based root phenotyping methods

Shovelomics

Shovelomics involves excavating a 40 cm diameter, 25 cm deep soil cylinder, rinsing root crowns and visually scoring up to 10 architectural traits - including crown root number, angle and branching pattern within 2 min per sample (94). The protocol was refined using REST software for lateral root density estimation and further automated by the DIRT/3D platform using 10 synchronised cameras to compute 18 traits, including whorl spacing and nodal root diameter (95). Shovelomics-derived traits exhibit moderate to high heritability, enabling rapid phenotyping of hundreds of genotypes per day, with root crown traits significantly associated with drought resilience across multiple environments (5).

Soil coring and core break methods

Soil coring with multi-distance and multi-depth schemes accurately captures spatial heterogeneity in root length density, with the core break method providing additional insight into vertical root distribution by splitting intact cores longitudinally, these methods lack representation of soil mechanical impedance, alter root-microbe interactions and may overestimate root elongation due to sampling disturbance (96). Extracted roots are quantified using image analysis platforms, including WinRHIZO and RhizoVision Explorer, enabling fast and reliable root trait quantification from scanned images (97). Lab-based rhizotrons allow controlled observation of root growth under simplified conditions, whereas field minirhizotrons enable in situ monitoring of root dynamics under natural soil environments; however, scalability is constrained by installation costs, imaging frequency and data processing requirements (98).

Trench profile methods

Trench profile techniques expose roots along vertical soil faces for direct assessment of root distribution patterns with standardised protocols for maize involving excavation perpendicular to crop rows, followed by careful soil removal (19). High-resolution imaging of trench walls using calibrated grids enables quantitative analysis of root distribution across growth stages and N environments (99).

Minirhizotron systems

Minirhizotron technology employs transparent tubes installed in soil to enable repeated non-destructive monitoring of maize root dynamics with optimised installation protocols (100). Continuous observations reveal seasonal root growth patterns, root production rates, mortality and lifespan under contrasting irrigation and N management regimes (101). Strategic tube placement relative to plant rows improves capture efficiency of large-diameter crown and brace roots with arrays of tubes at varying distances better representing spatial heterogeneity within the maize root system. This approach primarily enables phenotyping of root distribution patterns and growth dynamics in situ, but may underrepresent fine roots and deeper architectural complexity (102).

Techniques such as trench profiling and minirhizotrons provide higher spatial and temporal resolution but are limited in throughput, whereas shovelomics enables rapid, large-scale phenotyping with moderate detail (94). These approaches offer strong field applicability under realistic soil conditions, though measurement precision is generally lower than in controlled laboratory systems (93).

Advanced imaging technologies

X-ray computed tomography

X-ray computerised tomography (CT) enables 3D non-invasive visualisation of maize root systems with high-resolution imaging at 10–20 μm quantifying anatomical traits including cortical aerenchyma, cortex thickness and xylem vessel dimensions for parameterising functional-structural models (103). Time-resolved CT captures gravitropic behaviour and lateral root initiation at 4-hour intervals, while synchrotron-based CT reveals micrometre (μm) scale rhizosphere modifications in soil porosity adjacent to growing roots. A key trade-off exists between resolution and sample size, with high-resolution imaging typically restricted to smaller soil volumes or younger plants (104). The large size of mature root systems restricts high-resolution imaging to representative subsamples, though deep learning-based segmentation tools substantially reduce manual annotation effort, in addition, high cost, limited accessibility, low throughput and challenges in imaging under field conditions constrain its broader application (105).

Magnetic resonance imaging

Magnetic resonance imaging (MRI) offers non-destructive visualisation of maize roots and water dynamics without ionising radiation, with applications focused on water uptake patterns and root hydraulic functioning (106). High-field MRI systems resolve internal root structures, including cortical tissues and xylem vessels, in intact soil-grown maize, while MRI-based flow techniques quantify xylem flow velocities and relate xylem structure to whole-plant water use efficiency (107).

X-ray CT provides ultra-high spatial resolution but is limited in throughput and sample size, whereas MRI enables functional imaging of water dynamics with moderate resolution and scalability (108). These approaches deliver exceptional laboratory precision but have limited field applicability due to high cost, infrastructure requirements and constraints on imaging large root systems (103).

Root anatomical and physiological phenotyping

Root anatomical trait measurement

Root anatomical traits are quantified using cross-sectional imaging and automated analysis tools, enabling high-throughput assessment of cortical and vascular structures (109, 110).

Deep learning approaches have further automated anatomical trait extraction, achieving expert-level annotation accuracy while substantially reducing processing time. Despite these advances, their field relevance remains limited due to controlled or destructive sampling conditions and they primarily focus on individual roots or sections, which may not fully represent the whole RSA and in situ functional interactions (85).

Root exudate collection and analysis

Root exudate collection employs sterile hydroponic systems with continuous trapping mechanisms under axenic conditions to preserve exudate integrity while minimising microbial interference (111). Zymography-based spatial sampling has further enabled visualisation of enzyme activity hotspots along maize root axes, revealing localised distributions of phosphatase, β -glucosidase and peptidase activities in the rhizosphere. In addition, studies have demonstrated that maize root exudates, particularly benzoxazinoids, play a significant role in regulating the composition and metabolic activity of the rhizobiome, highlighting the importance of root-derived compounds in shaping rhizosphere processes (112). However, field relevance remains limited due to simplified experimental conditions and measurements are often restricted to individual roots or segments, which may not fully represent whole root system exudation patterns and rhizosphere interactions under natural conditions (113).

Root hydraulic measurements

Root hydraulic conductivity is measured using pressure chamber techniques and high-pressure flow meters, with variation across maize genotypes linked to cortical permeability and aquaporin expression (114). *In vivo* water potential measurements using thermocouple psychrometers enable continuous monitoring of leaf water potential in field-grown maize across contrasting soil textures, facilitating assessment of root-mediated water uptake and root hair contributions to drought responses. These measurements are typically conducted under simplified or controlled conditions and their focus on individual roots or segments may not fully capture whole root system hydraulic behaviour under field conditions (115).

These approaches differ in their balance of detail, speed and scalability. Anatomical imaging and hydraulic measurements provide high-resolution, mechanistic insights but are constrained in throughput, whereas exudate analysis methods allow moderate scalability with targeted functional resolution (116). Quantitative analysis using high-performance liquid chromatography (HPLC) based methods has linked specific compounds such as benzoxazinoids to rhizosphere microbial community composition (117). While these techniques offer strong analytical precision

under controlled conditions, their direct applicability in field environments remains limited due to methodological complexity and sensitivity to environmental variability (117).

Computational tools and image analysis software

Root architecture analysis software

Software tools such as WinRHIZO, SmartRoot and RhizoVision enable automated quantification of root architectural traits from image datasets (118).

RhizoVision analyses excavated root crown images with strong agreement to manual measurements and DIRT provides automated trait extraction incorporating machine learning classifiers trained on maize root datasets (97).

Three-dimensional root reconstruction software

RooTrak and structure-from-motion photogrammetry reconstruct 3D maize root architectures from CT image stacks and multi-angle photographs, respectively, enabling accurate estimation of root angles and spatial arrangement (85). Point cloud processing via CloudCompare supports quantitative assessment of reconstruction quality for field phenotyping applications (118).

Machine learning and artificial intelligence

Deep convolutional neural networks enable accurate root segmentation and tissue classification, with RootNav 2.0 demonstrating automated root tracing validated on maize seedling images (119). Random forest models have been applied to predict maize root anatomical traits from external morphology, enabling indirect phenotyping without destructive sampling (85). Generative adversarial networks augment training datasets through synthetic image generation, improving model performance under limited data availability (120). Emerging approaches also integrate machine learning with functional trait prediction, including estimation of root hydraulic conductivity (L_p) and the expression patterns of aquaporins (PIP genes), enabling high-throughput assessment of water transport capacity alongside structural traits (121).

Computational tools differ in their balance between analytical detail, throughput and scalability. Image analysis and artificial intelligence (AI) based methods enable high-throughput and scalable phenotyping with reasonable accuracy, whereas 3D reconstruction approaches provide greater structural detail but are computationally intensive (122). These techniques enhance analytical precision in controlled datasets, though their field applicability depends on image quality and robustness under variable environmental conditions (123). Major root phenotyping techniques used in maize are given in Table 2.

Functional role of root growth in maize productivity

Root growth plays a central role in determining maize productivity by regulating the acquisition of water and nutrients and coordinating C allocation. Root system architecture, anatomical adaptations and temporal dynamics collectively influence resource capture efficiency, particularly under stress-prone environments.

Root architecture and its association with yield

Yield improvement under resource-limited conditions is closely tied to RSA, with crown root number, lateral branching intensity and rooting depth directly determining the capacity to acquire water and nutrients critical for grain filling and biomass accumulation (131). Genetic variation in RSA traits influences yield outcomes. The “steep, cheap and deep” ideotype improves yield

Table 2. Major root phenotyping techniques used in maize

Technique	Category	Key traits measured	Advantages	Limitations	References
Shovelomics	Field	Crown root number, angle, branching density, brace root traits	Rapid, high-throughput (100s/day), low cost	Destructive, surface roots only	(124)
Soil coring	Field	Root length density, biomass distribution across soil depths	Captures deep root distribution quantitatively	Destructive, labour-intensive	(13)
Minirhizotron	Field / Greenhouse	Root production, mortality, lifespan, seasonal root dynamics	Non-destructive, repeated observations over time	Installation disturbance, limited spatial coverage	(125)
X-ray CT	Lab/Field	3D root architecture, aerenchyma, xylem vessel dimensions	Non-destructive, high resolution, 3D visualisation	High cost, limited to small soil volumes	(126)
MRI	Lab	Water uptake patterns, xylem flow velocity, root hydraulics	Non-destructive, no ionising radiation	Low resolution for large mature roots	(127)
WinRHIZO	Software	Root length, diameter distribution, surface area, root topology	Widely validated, user-friendly, rapid quantification	Commercial license, 2D scanned images only	(13)
Gel-based systems	Lab	Root growth dynamics, gravitropism, lateral root branching	3D mechanical support, optically transparent medium	Not field-relevant, limited to early growth stages	(128)
Cross-sectional analysis	Lab	Cortical aerenchyma, cell file number, xylem vessel traits	Precise anatomical quantification across genotypes	Destructive, low throughput	(129)
Laser ablation tomography	Lab	3D aerenchyma connectivity, volumetric cellular organisation	Volumetric 3D anatomical reconstruction without sectioning	Destructive, specialised equipment required	(112)
AI / Deep learning	Software/AI	Automated root segmentation, trait extraction, root system tracing	High accuracy, scalable, reduces manual annotation by > 98 %	Requires large labelled training datasets	(130)

under drought and nutrient stress by maximising deep resource capture at lower C cost (132).

Water uptake and drought adaptation

Deep root system enables subsoil water during moisture-sensitive reproductive stages. Genotypes with greater rooting depth maintain higher stomatal conductance and photosynthetic activity, supporting sustained grain filling under drought (133). This contributes directly to yield by maintaining assimilate supply and reducing kernel abortion under water deficit conditions. Reduced cortical cell file number and increased aerenchyma formation lower respiratory demands while preserving water transport capacity, thereby improving carbon-use efficiency and sustaining biomass allocation to developing grains, representing key anatomical adaptations under prolonged water stress (134).

Efficiency of nutrient acquisition

Root foraging precision enhances nutrient capture under heterogeneous soil conditions with dense lateral branching in surface layers, improving interception and reducing leaching losses. This enhances nutrient availability during early growth, promoting canopy development and ultimately increasing yield potential (135). Deep axial root growth recovers leached nitrate from subsoil while regulated nitrate transporter expression reduces fertiliser dependence and contributing to improved grain filling and yield stability, whereas regulated nitrate transporter expression reduces fertiliser dependence. Phosphorus acquisition is enhanced by root hair density, shallow root angles and AMF symbiosis, which collectively maximise exploitable soil volume and improve nutrient-use efficiency, leading to better biomass production and grain yield (136).

Root-shoot coordination and carbon allocation

Carbon allocation between roots and shoots regulates nutrient acquisition and yield with greater belowground investment under stress, enhancing resource capture, while excessive allocation under optimal conditions limits reproductive sink strength (137). Root-shoot coordination operates through bidirectional signalling with root-derived CLE and CEP peptides regulating shoot responses via xylem transport while shoot-derived auxins, cytokinins and carbohydrates modulate root elongation and lateral root formation (14).

Root system longevity and seasonal dynamics

Fine root lifespan balances carbon investment against nutrient acquisition with targeted proliferation in nutrient-rich microsites, enhancing capture efficiency (138). Sustained root activity from early establishment through grain filling ensures continuous resource supply to developing kernels, making root growth timing and persistence key targets for improving yield stability (139). In addition, root hydraulic conductivity and aquaporin-mediated water transport are critical for maintaining plant water status across growth stages, highlighting the importance of integrating structural and hydraulic traits for efficient resource uptake (121). Collectively, maize productivity is governed by the integration of root architectural, anatomical and physiological traits that regulate water uptake, nutrient acquisition and C allocation across developmental stages.

Future prospects

Advances in AI and machine learning are increasingly applied to model root growth dynamics and root-soil interactions, while multi-omics integration with computational modelling will enable precision breeding of cultivars adapted to specific soil and climatic conditions. Climate-resilient breeding programs emphasise root traits conferring drought, waterlogging and nutrient stress tolerance, supported by genomic selection and clustered regularly interspaced short palindromic repeats (CRISPR)-Cas technologies. In parallel, Internet of things (IoT) based real-time sensing and digital agriculture tools, including AI-based analytics, may enable site-specific irrigation and nutrient management aligned with root developmental stages. Advances in breeding technologies are expected to accelerate the development of root trait-optimised cultivars. Improved understanding of root microbiome interactions offers opportunities for microbiome engineering, including targeted microbial inoculants and rhizosphere engineering to enhance nutrient uptake and stress tolerance. Coordinated efforts emphasising standardised phenotyping protocols, shared databases and open-access germplasm resources will accelerate translation of maize root research into field-level applications, improving productivity and long-term agricultural sustainability. Future progress in maize root research will depend on integrating high-resolution phenotyping, predictive modelling and functional genomics with field-based validation to develop resilient and resource-efficient cropping systems.

Conclusion

Integration of root system architecture (RSA), functional traits and advanced phenotyping approaches provides a framework for linking root biology with crop performance. Recent advances in phenotyping, imaging and computational approaches have revealed the remarkable plasticity of maize root systems and their sensitivity to genetic variation, environment and management, transforming roots into central targets for crop improvement. Key traits, including cortical aerenchyma formation, steeper root angles, reduced cortical cell file number and enhanced lateral branching, provide actionable breeding targets for climate resilience and resource-use efficiency. Addressing remaining challenges in root-soil microbiome interactions and field-level translation will require interdisciplinary research supported by standardised phenotyping protocols and shared data platforms, along with the integration of genetics, environment and management, positioning root biology as a cornerstone of future agricultural sustainability. Harnessing root system diversity through integrated phenotyping, genomics and agronomic strategies will be central to developing resilient and resource-efficient maize production systems.

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Authors' contributions

NB wrote the manuscript draft and TS revised it. NS, KRVS and KP verified the contents. All authors read and approved the final manuscript.

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