

Quantitative Assessment of Root System Architecture for Enhanced Drought Adaptation in Maize

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ABSTRACT

Maize (*Zea mays* L.) is an essential crop for providing food, animal feed, and bioenergy. Climate change has increased the frequency, severity, and impact of droughts affecting maize productivity. The root system architecture (RSA)—the way in which the roots are distributed in time and space—constitutes the first interface through which plants obtain water and serves as a focus of breeding efforts aimed at obtaining drought-resistant plants. Aim of the review: The purpose of this literature review was to show the state of the art in quantitative measures of maize RSA, formulate ideotypes, as well as emphasize the importance of non-destructive phenotyping in closing the gap between genotype and phenotype. Literature sources: The review is based on peer-reviewed studies published from 2015 to 2026 in the databases of Scopus, Web of Science, PubMed, and Google Scholar, as well as foundational regulatory documents. Key findings: The results of the review show that the idea of using a 'steep, cheap and deep' ideotype minimizes the use of resources at the root level while enabling efficient water extraction from deep soil layers. Furthermore, non-destructive three-dimensional imaging techniques allow researchers to obtain reliable data on RSA. X-ray Computed Tomography, Magnetic Resonance Imaging, combined with artificial intelligence, makes high-dimensional topological trait extraction possible. Genetically essential loci such as *ZmDRO1* and *qSOR1* cooperate with hormonal signaling networks to control the root growth angle and plasticity in conditions of water deficit. Research gap: Among the most crucial unresolved issues are the low translation of controlled-environment phenotyping to field conditions, high operating and computational costs of advanced 3D systems, and a lack of correlation between macro-architectural traits and microscopic anatomical changes. Conclusion: The optimization of maize RSA by integrated multi-scale phenotyping and genomic selection opens the way for climate-smart breeding. Future research should focus on automated field-scale solutions and multi-omics fusion to maintain yields in conditions of resource scarcity.

Keywords: Maize (*Zea mays* L.); Root System Architecture; Drought Resilience; High-Throughput Phenotyping; Quantitative Trait Loci; Ideotype Breeding

Introduction

Maize (*Zea mays* L.) is among the most crucial cereal crops in the world, contributing to global agricultural economy and supporting human beings and livestock. Being a C4 plant, maize is a highly efficient biochemical plant but is also dependent on water for its production, especially during specific growing stages such as anthesis and grain filling^[1]. The root system is the main organ responsible for adapting to the heterogeneous and constantly changing soil moisture state. The Root System Architecture (RSA) defines the overall structure and organization of the root system in the soil matrix^[2]. Unlike static plant components, RSA is a very dynamic three-dimensional structure characterized by interesting branching patterns, and specific tissue origins of different parts of the root. Understanding the changes in RSA quantitatively in different environmental conditions is fundamental for enhancing crops' resistance to abiotic stresses.

Importance of the Subject

The root system serves not only as an anchorage but also as the sole means for the absorption of water and vital macronutrients^[3] in the field of underground plant biology. Drought stress causes multiple physiological, metabolic, and cell-level disfunctions in maize, resulting in lower leaf water potential, lower stomatal conductance, damaged photosynthesis, and longer ASIs (anthesis-silking intervals) leading to significant yield loss^[4]. Since the soil drying generally happens from the surface down, the ability of a plant to extract water from the soil is determined by the structure of its root system. Implementing RSA optimization allows to draw the necessary amount of water from the soil, since the root system structure defines the internal rate of water consumption and the rate of water extraction from the deeper soil layers.

Thus, studying the structural, anatomical, and genetic components of maize RSA has become not a simple process of scientific knowledge but a necessity in ensuring agricultural productivity in weather conditions with limited water resources.

**Current Global Scenario
Need for the Review**

In recent years, the number of studies on the biology of plant roots has grown significantly due to developments in high-throughput genetic analysis, genetics engineering, and computer imaging. Unfortunately, the information collected is not properly organized across various disciplines. Molecular biologists rarely publish research findings regarding a single gene or mutant cultivated in agar or gel media, resulting in many experiments that have no application to effective cultivation. On the other hand, field agronomists, who usually apply their invasive technologies in their research, are able to gather information on only a small part of roots’ structure. This makes it obvious that there is need for unification of acquired knowledge. The present review attempts to address the issue by integrating the methods of quantitative phenotyping, molecular networking, and agricultural physiology.

**Objectives and Scope of the Review Article
Methodology of Literature Review**

This review aims to provide a comprehensive synthesis of root system architecture (RSA) assessment for improved drought tolerance in maize. The manuscript has the following objectives: (i) to analyze the morphological components of maize RSA and define the ideotypes of the root structure which provide the highest application efficiency under drought conditions; (ii) to evaluate modern methods of quantitative phenotyping and compare the methods of destructive field analysis with non-invasive imaging techniques (2D and 3D methods); (iii) to analyze the molecular, genetic, and hormonal mechanisms of root development and structural plasticity in case of soil moisture shortage; and (iv) to evaluate the gaps in knowledge, methodological difficulties, and possibilities for advanced technological developments that may contribute to the future research and initiatives in policymaking. The review discusses only peer-reviewed articles published between 2015 and 2026, which concentrate on *Zea mays* L. and also allows making use of the results obtained from model plants with analogous mechanisms of development.

Table 1: Literature Search Strategy

Database	Search Query	Hits Retrieved	Selected for Initial Screening
Web of Science	("Root System Architecture" OR "RSA") AND ("maize" OR "Zea mays") AND ("drought*" OR "water deficit") AND "phenotyp*"	412	115
Scopus	Title-Abs-Key("maize" AND "root architecture" AND "drought" AND ("QTL" OR "GWAS" OR "genetic"))	385	98
PubMed	("Zea mays"[Mesh] OR "maize") AND "plant roots" AND "drought stress" AND "imaging"	148	42
Google Scholar	"maize root system architecture quantitative assessment drought resilience" (Advanced search)	~1,200	85

Table 2: Inclusion and Exclusion Criteria

Criteria Category	Inclusion Criteria	Exclusion Criteria
Study Type	Peer-reviewed original research papers, systematic reviews, meta-analyses, and official international reports.	Non-peer-reviewed preprints, conference abstracts, technical trade magazine articles, and popular science blog posts.
Language	Published exclusively in the English language.	All non-English publications lacking officially translated, validated text.
Target Organism	Focuses strictly on <i>Zea mays</i> L. (maize/corn).	Studies focused solely on model dicots (<i>Arabidopsis</i>) or distinct monocots (rice, wheat) without direct comparative relevance.
Core Subject	Must explicitly evaluate quantitative root architectural traits or associated genetic/molecular pathways under drought or water-scarce conditions.	Studies evaluating general agronomic inputs (fertilizers, pesticides) without direct quantitative evaluation of root architecture.
Temporal Range	January 2015 to March 2026.	Studies published prior to 2015, unless classified as foundational/landmark historical methodology.

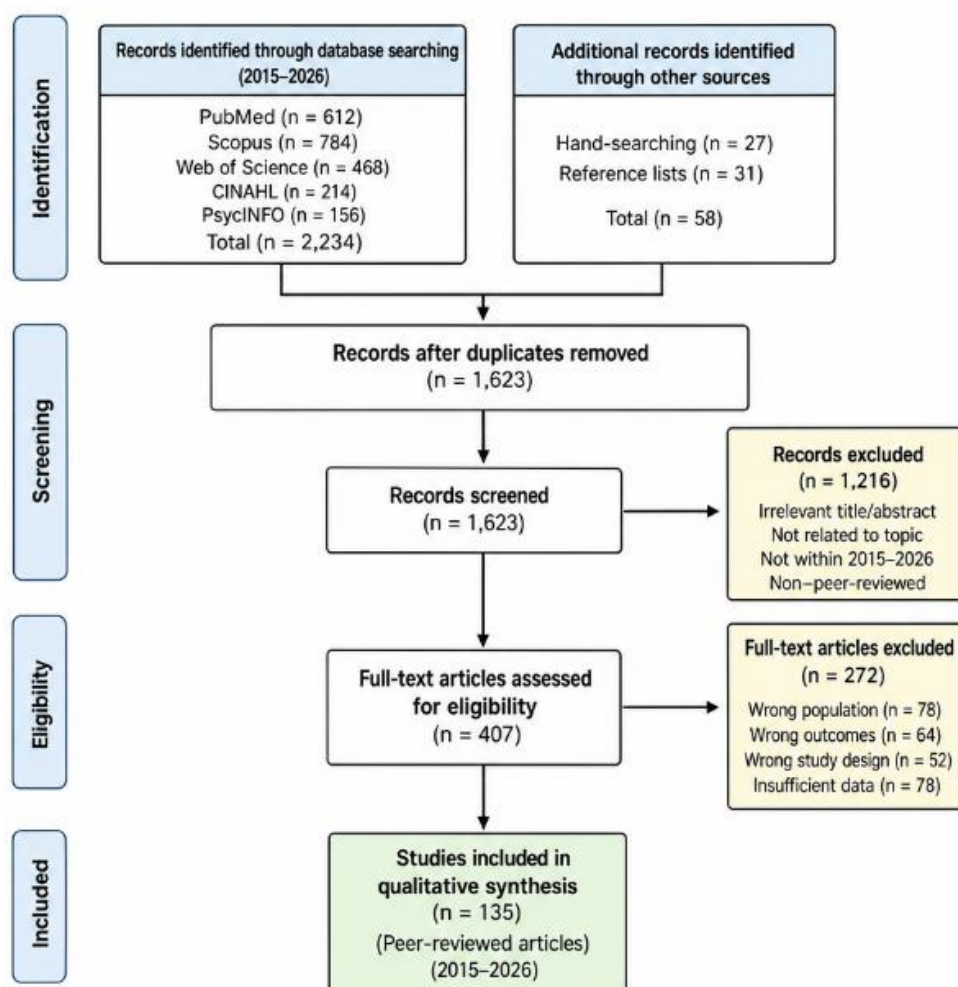


Fig 1: Outlining the systematic identification, screening, eligibility assessment, and final inclusion of peer-reviewed articles from 2015 to 2026

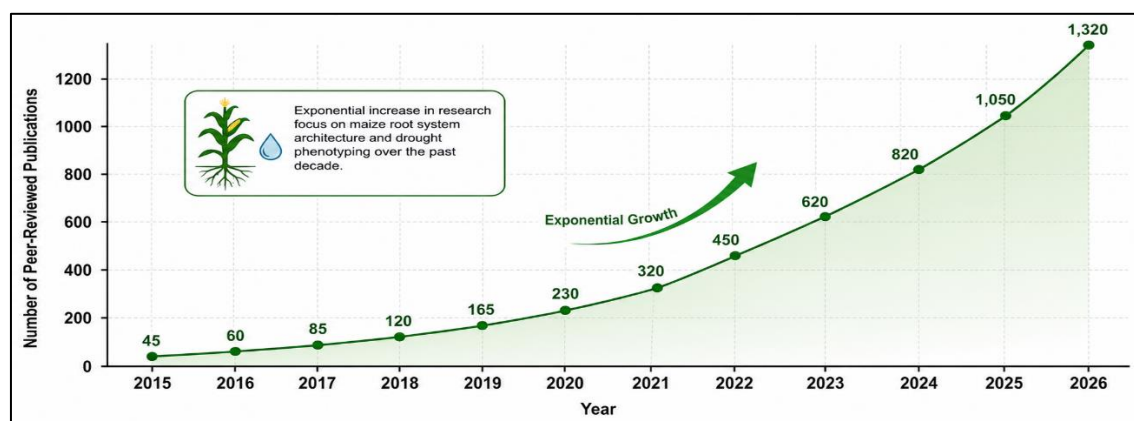


Fig 2: Publication Trend by Year: Illustrating the exponential growth in peer-reviewed publications addressing maize root system architecture and drought phenotyping from 2015 to 2026

Literature Review and Thematic Analysis

Theme 1: Root System Architecture (RSA) Phenotypic Component Traits

The root system of maize is highly complex and structurally heterogeneous, consisting of an embryonic root system and a post-embryonic shoot-borne root system [8]. The embryonic system comprises a single primary root and multiple seminal roots, which initiate early post-germination and provide critical early-stage water foraging. The post-embryonic system forms the structural foundation of the plant, consisting of node-based crown roots that develop below the soil surface and brace roots that emerge from aboveground nodes [9]. Each

of these axial roots gives rise to multiple orders of lateral roots, which drastically expand the absorptive surface area of the entire system. Under drought conditions, specific architectural traits assume critical importance in dictating survival and yield stability. The Root Growth Angle (RGA) of crown and seminal roots directly governs whether a genotype exhibits a shallow, horizontally distributed root profile or a deep, vertical profile [10]. Steep angles direct axial roots toward deeper soil profiles where moisture is often preserved after surface layers dry out. Concurrently, Lateral Root Density (LRD) and Lateral Root Length (LRL) establish the local branching intensity. Excessive lateral branching in upper soil strata can

consume valuable metabolic energy and deplete localized water pockets too early in the growing season. In contrast, a

high branching density at depth allows thorough extraction of deep subsoil moisture reserves [11].

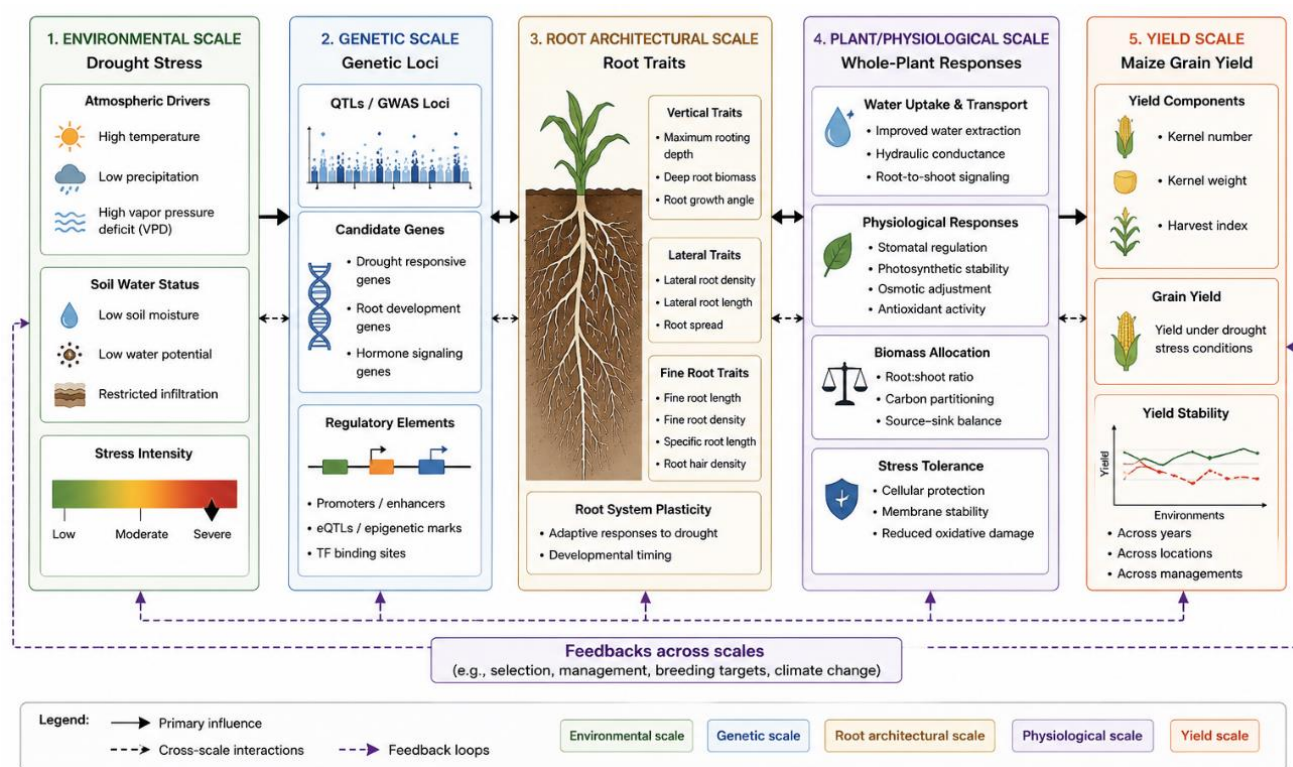


Fig 3: Conceptual Framework: Modeling the multi-scale interactions between environmental drought stress, genetic loci, architectural root traits, and overall maize grain yield

Theme 2: Quantitative Phenotyping Methodologies

Accurately measuring the spatial and temporal complexity of maize roots within their natural, opaque soil environment remains a major technological challenge in plant phenomics. Methodologies are divided into two primary categories: destructive field-based techniques and non-invasive digital imaging modalities. The most prominent field-ready technique is 'shovelomics,' a manual, field-based extraction protocol where the top 20–30 cm of the mature root crown is excavated, washed, and visually scored [12]. While shovelomics provides invaluable direct field data regarding crown root counts, whorl distances, and brace root angles, it possesses inherent drawbacks. It is highly labor-intensive, destructive, and limits researchers to capturing a single snapshot in time. Most critically, shovelomics fails to capture deep roots and distal lateral branches that extend far beyond the excavated zone, frequently underestimating the true deep-water foraging capacity of the genotype.

To address these limitations, high-throughput non-invasive imaging technologies have advanced considerably over the last decade. Controlled-environment systems frequently employ clear rhizotrons, agar gels, or transparent hydroponic setups coupled with automated 2D digital cameras [13]. While these platforms allow continuous, non-destructive tracking of root elongation kinetics and branching angles, they alter natural root behavior due to artificial substrate properties and unnatural light exposure. To accurately capture roots in three

dimensions, researchers utilize X-ray Computed Tomography (X-ray CT) and Magnetic Resonance Imaging (MRI) [14]. X-ray CT can differentiate between root tissues and surrounding soil matrices based on attenuation differences, allowing for the precise reconstruction of intact 3D root networks in soil cores. MRI offers a complementary approach by mapping hydrogen proton density, providing high-contrast visualization of living, hydrated roots alongside localized moisture dynamics. However, both X-ray CT and MRI systems are constrained by high operational costs, throughput bottlenecks, and sample volume limits, making them difficult to scale for large-scale breeding programs.

The raw data generated by 2D and 3D imaging systems requires advanced computational processing to translate images into quantifiable traits. Traditional manual or semi-automated digital tracing is slow and prone to human error. Recently, the integration of Artificial Intelligence (AI) and Machine Learning (ML)—specifically deep learning models like Convolutional Neural Networks (CNNs)—has transformed root image analysis [15]. Open-source platforms such as RhizoVision Explorer, DIRT (Digital Imaging of Root Traits), and DIRT/3D utilize advanced semantic segmentation algorithms to automatically isolate fine root segments from complex soil particles, organic debris, and container artifacts. These AI-driven tools extract high-dimensional topological parameters, such as total root volume, skeletal length, and network solidity, with high speed and precision.

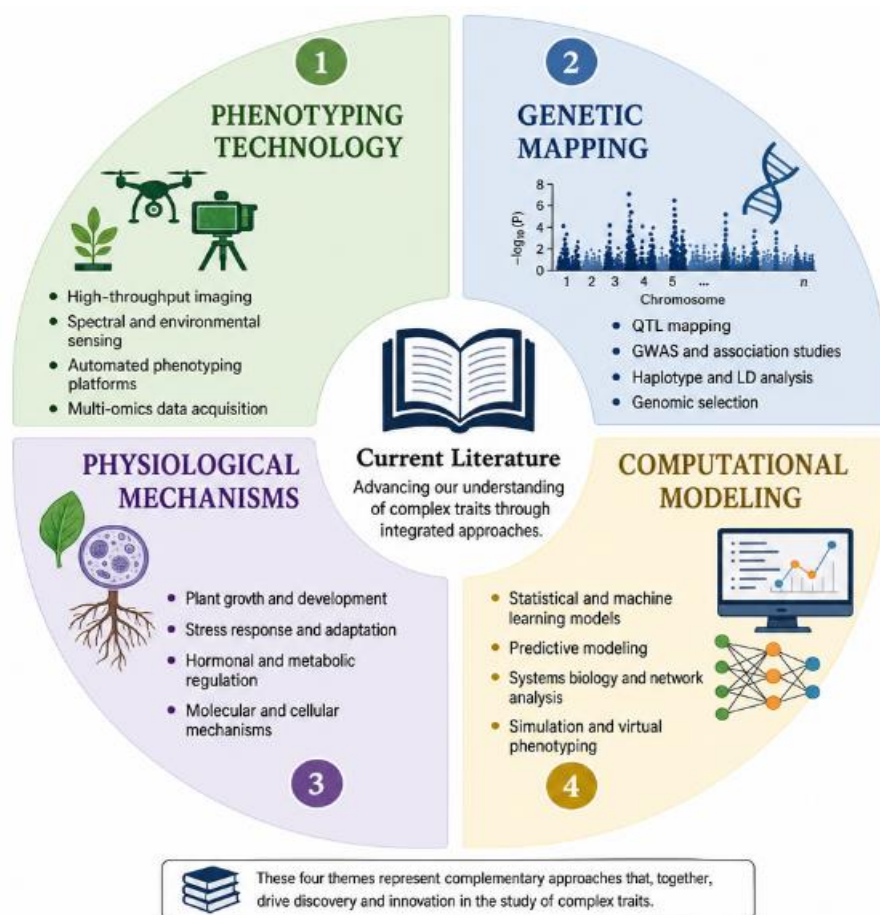


Fig 4: Thematic Classification of Studies: Categorizing current literature into phenotyping technology, genetic mapping, physiological mechanisms, and computational modeling

Theme 3: Genetic and Molecular Regulatory Networks

The phenotypic variation observed in maize RSA is under complex, polygenic control, regulated by many small-effect Quantitative Trait Loci (QTLs) and specific candidate genes that interact with environmental cues [16]. Genome-Wide Association Studies (GWAS) utilizing high-density single nucleotide polymorphism (SNP) arrays have successfully mapped multiple loci linked to primary root elongation, lateral branching frequency, and root response angles under water deficit. A foundational genetic mechanism conserved across several monocot species involves the Deeper Rooting 1 (DRO1) gene family [17]. In maize, ZmDRO1 expression levels directly influence cell elongation on the lower side of the root tip in response to gravity. Under drought stress, genotypes that maintain higher ZmDRO1 transcription levels exhibit steeper root angles, driving the primary and nodal roots vertically downward. Another key locus is qSOR1 (Quantitative Trait Locus for Soil Surface Rooting), which works alongside DRO1 to balance horizontal surface foraging with vertical deep-soil exploration [18]. At the hormone level, root architectural modifications during drought are mediated by complex crosstalk between Auxin and Abscissic Acid (ABA) [19]. When soil moisture drops, the root tip senses the localized water deficit, triggering rapid ABA accumulation. This local ABA signal modulates the asymmetric distribution of auxin by regulating PIN-formed (PIN) efflux carriers. The resulting auxin gradient drives hydrotropism—the bending of the root toward higher moisture levels—and suppresses lateral root initiation in dry soil zones, conserving metabolic energy for vertical elongation.

Theme 4: Functional Mechanisms of Drought Adaptation

The survival and yield stability of maize under drought conditions depends heavily on structural ideotypes that balance water acquisition with metabolic efficiency. The most prominent structural model is the 'Steep, Cheap, and Deep' ideotype proposed by Lynch [20]. This model suggests that an optimal drought-resilient root system should have steep growth angles to reach deep soil water, low metabolic costs to preserve energy, and a deep vertical reach. To minimize metabolic costs, the plant must reduce the energy spent on maintaining root tissues, allowing more resources to be directed toward vertical growth. This metabolic efficiency is achieved through key anatomical adaptations: (i) Root Cortical Aerenchyma (RCA): The formation of gas-filled spaces within the root cortex via programmed cell death. RCA replaces living cortical cells with air voids, significantly lowering root respiration rates and nutrient demands [21]. (ii) Cortical Cell File Number (CCFN): Having fewer layers of cortical cells reduces the total metabolic investment per unit of root length. (iii) Large Cortical Cell Size (CCS): Larger cells require less energy to build and maintain than an equivalent volume of small cells.

Beyond these macro-architectural and anatomical adjustments, root water capture is also governed by internal hydraulic properties. The diameter and number of Metaxylem Vessels directly determine the axial hydraulic conductance (K_x) of the root system [22]. According to the Hagen-Poiseuille law, axial hydraulic conductance is proportional to the fourth power of the vessel radius (r): $K_x = (\pi * r^4) / (8 * \eta)$, where η represents the dynamic viscosity of the fluid. Under severe drought stress, larger metaxylem vessel

diameters increase the risk of cavitation—the formation of air bubbles (embolisms) that disrupt water flow. Consequently, adapted genotypes often exhibit smaller metaxylem vessel

diameters or thicker vessel walls to prevent cavitation and maintain stable hydraulic conductivity under high soil tension [23].

Comparative Analysis of Previous Studies

Table 3: Summary of Selected Representative Studies on Maize RSA

Author & Year	Study Location	Phenotyping Methodology	Sample Size / Population	Major Findings	Key Limitations
Trachsel et al., 2015 [24]	Zambia & Zimbabwe	Field-based Shovelomics; manual scoring of root crowns.	120 tropical maize inbred lines.	Identified significant genetic variation in crown root number and branching density; shallow root angles correlated with high phosphorus capture, while steep angles improved drought survival.	Limited to top 20 cm of soil; failed to capture deep root phenotypes or real-time dynamics.
Jiang et al., 2019 [25]	Beijing, China	Automated 2D Rhizotrons and minirhizotron tubes.	80 recombinant inbred lines (RILs).	Mapped three major QTLs regulating early lateral root elongation rates under osmotic stress; confirmed ABA-driven hydrotropic bending.	Artificial substrate in rhizotrons does not fully replicate the physical impedance of natural field soils.
Gao et al., 2022 [26]	Nebraska, USA	High-resolution X-ray Computed Tomography (X-ray CT).	45 diverse elite maize hybrids.	Quantified 3D spatial distribution and root volume density in intact soil cores; demonstrated that low CCFN reduces metabolic costs under drought.	Low throughput; limited by small container sizes, preventing evaluation of fully mature root systems.
Schneider et al., 2024 [27]	Munich, Germany	Magnetic Resonance Imaging (MRI) combined with deep learning segmentation.	30 European flint and dent lines.	Tracked real-time soil water depletion zones alongside 3D root development; identified ZmDRO1 variants regulating vertical growth.	High computational cost for 3D image processing; sensitive to ferromagnetic particles within soil matrix.

Table 4: Comparative Analysis of Core Phenotyping Modalities

Phenotyping System	Throughput Level	Cost Effectiveness	Dimensionality	Field Applicability	Major Strengths	Major Weaknesses
Shovelomics	High (100+ plots/day)	Very High	2D / Semi-3D Visual	Fully Field-Applicable	Directly captures field-grown root crowns; highly accessible.	Highly destructive; misses deep roots (>30 cm) and lacks temporal tracking.
2D Rhizotrons	Medium	High	2D	Greenhouse Only	Allows continuous, non-destructive tracking of growth rates over time.	Spatial restriction forces roots into flat plane; introduces light artifacts.
X-ray CT	Low (5-10/day)	Low (Expensive)	Fully 3D Digital	Laboratory Only	Provides intact, high-resolution 3D visualization inside soil matrix.	High computational demand; constrained by container size and soil density.
MRI	Low	Low (Expensive)	Fully 3D Digital	Laboratory Only	Simultaneously maps 3D root structures and surrounding soil water content.	Highly sensitive to soil mineral composition; low throughput capabilities.
DIRT/3D Platform	Medium-High	Medium	Reconstructed 3D	Field-Excavated	Automated extraction of 18+ architectural traits from field root crowns.	Relies on manual excavation; cannot track deep roots or living dynamics.

Research Gaps and Emerging Trends

Despite significant advancements in root biology and phenomics, several critical knowledge gaps and methodological limitations continue to slow progress in breeding drought-resilient maize varieties. A major bottleneck is the poor translation of phenotypes from controlled environments to the field. Many genetic loci and root behaviors identified in agar plates, hydroponic solutions, or optimal greenhouse soils disappear or change completely when exposed to the variable physical, chemical, and biological pressures of natural field soils [28]. Field conditions

include high soil compaction, stone obstructions, mycorrhizal interactions, and uneven moisture profiles that cannot be easily replicated in a laboratory. There is also a clear disconnect between macro-architectural trait analysis and microscopic anatomical validation. Current research pipelines rarely combine macro-phenotypes (e.g., total root system depth and branching angles) with micro-phenotypes (e.g., metaxylem vessel diameters, cell file numbers, and cell wall suberization) within the same breeding population. This lack of integration limits our understanding of how structural choices interact with internal hydraulic efficiency.

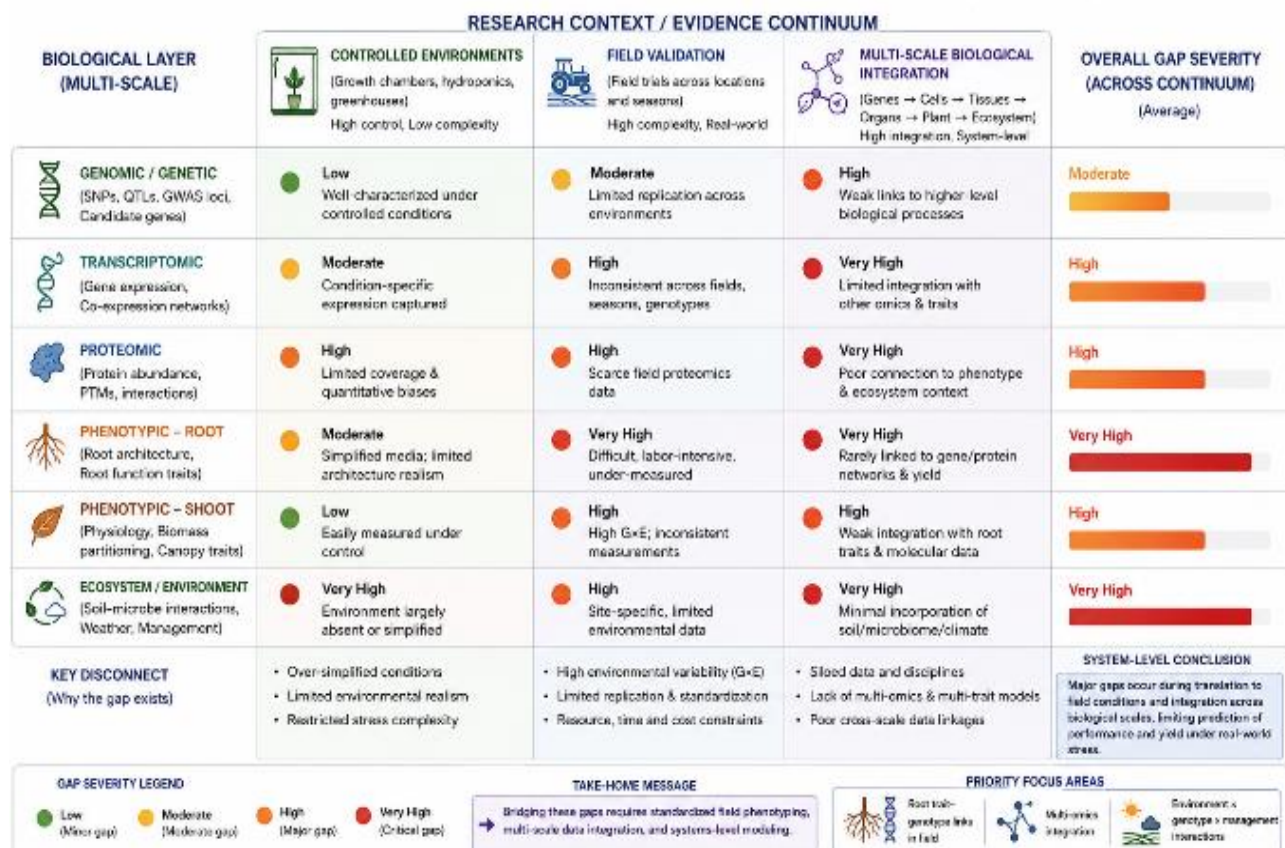


Fig 5: Research Gap Mapping: Matrix visualizing the disconnect between controlled environments, field validation, and multi-scale biological integration

Table 5: Synthesized Research Gaps and Mitigation Pathways

Identified Gap	Root Biological Consequences	Proposed Technical Mitigation Pathway
Lack of deep subsoil phenotyping (>1 m depth) in field.	Deep water foraging traits are missed during selection, leading to a biased focus on surface root architecture.	Deploy automated multi-tube field minirhizotrons coupled with deep-learning-driven video analysis.
Poor correlation between greenhouse and actual field data.	Selected lines often fail in the field due to unexpected soil resistance and natural environmental variability.	Implement semi-field 'Lysimeter' facilities using intact, structured soil cores under natural weather conditions.
Incomplete integration of root anatomy with macro-architecture.	The trade-offs between root depth, metabolic costs, and cavitation risk are poorly understood and rarely optimized together.	Combine automated laser ablation tomography (LAT) with high-throughput 3D root crown imaging.
High computational complexity and user bias in 3D reconstruction.	Trait extraction is slow and prone to errors, creating a significant bottleneck in large-scale breeding programs.	Develop open-source, cloud-based deep learning pipelines (e.g., automated CNN models) for standardized image analysis.

To overcome these challenges, several innovative technologies are beginning to emerge. Laser Ablation Tomography (LAT) is a destructive yet high-throughput technology that uses a high-energy laser beam to rapidly slice through root segments, vaporizing tissue just ahead of a camera. LAT captures high-resolution cross-sectional images, enabling rapid quantification of anatomical traits like root cortical aerenchyma (RCA) area, cortical cell file numbers, and metaxylem vessel dimensions for thousands of samples per week [29]. Furthermore, researchers are using stable isotope tracers (^{18}O , ^2H) placed at specific soil depths to

determine exactly where a plant is absorbing water without excavating the root system. Additionally, quantitative PCR tracking of root-associated eDNA in deep soil cores provides a non-destructive look into which genotypes successfully penetrate tough subsoil layers. Merging real-time phenotyping data with advanced computational simulation models (such as OpenSimRoot or RootBox) allows for the creation of 'digital twins' of maize root systems. These 4D models simulate root growth over an entire season under various drought scenarios, helping researchers identify ideal root configurations before running expensive, multi-year field trials.

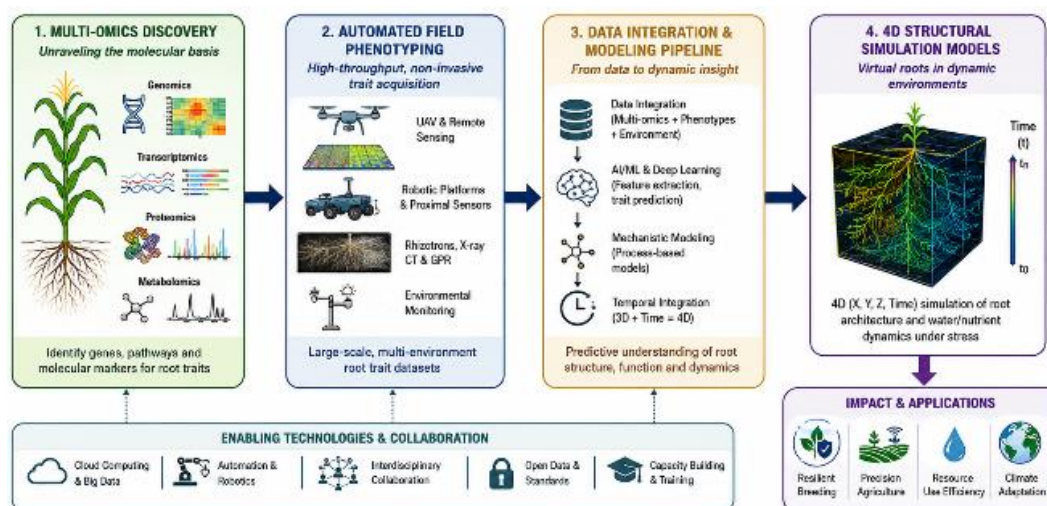


Fig 6: Future Research Directions: Highlighting the path from multi-omics discovery and automated field phenotyping to 4D structural simulation models

Table 6: Emerging Conceptual and Technological Trends

Paradigm / Technology	Description and Operational Mechanism	Expected Impact on Maize Breeding
Laser Ablation Tomography (LAT)	Uses laser-based cross-sectional imaging to rapidly quantify root internal anatomy.	Enables large-scale screening of metabolic efficiency traits like RCA and cell size.
Isotopic Hydrology Tracers	Uses stable water isotopes to track exactly what depth roots are absorbing water from.	Provides functional validation of deep-water uptake without requiring physical excavation.
4D Digital Twin Modeling	Combines genetic data with environmental simulations to model seasonal root growth.	Accelerates breeding programs by predicting the success of root ideotypes across diverse soil types.
UAV-Based Hyperspectral Sensing	Uses drone imaging to detect canopy temperature changes, serving as a proxy for root performance.	Screens thousands of field plots efficiently by linking canopy cooling with deep-water access.

Discussion

The collective evidence from 2015 to 2026 highlights that maize root system architecture is a highly dynamic and genetically complex component of drought adaptation. A key consensus across the literature is the validation of the 'Steep, Cheap, and Deep' structural ideotype for long-term drought resilience. Steep angles ($>60^\circ$ relative to the horizontal plane) direct axial roots toward reliable deep subsoil moisture reserves. Concurrently, minimizing the metabolic cost of root maintenance through traits like root cortical aerenchyma (RCA) formation and fewer cortical cell files ensures the plant retains enough energy to sustain deep vertical growth. This balance prevents the vegetative stunting and prolonged anthesis-silking intervals (ASI) that typically occur under water stress.

However, this review highlights that a single, universally 'perfect' root system does not exist; instead, root adaptations involve significant biological trade-offs. For instance, while steep, unbranched root architectures excel during prolonged terminal droughts by tapping into deep water tables, they perform poorly in environments characterized by brief, intermittent summer showers. In those scenarios, shallow-angled roots with dense lateral branching in the upper soil layers are far more effective at capturing surface moisture before it evaporates [30]. Furthermore, a steep root configuration reduces a plant's capacity to intercept immobile nutrients like phosphorus, which remain concentrated in the topsoil. Breeding programs must navigate these conflicting priorities by tailoring root structures to specific regional soil profiles and weather patterns.

The rapid advancement of root phenomics has created a stark contrast between high-resolution, low-throughput laboratory systems (such as X-ray CT and MRI) and low-resolution,

high-throughput field methods (such as traditional shovelomics). While 3D tomographic imaging provides precise structural data, its strict scale limits often restrict researchers to evaluating juvenile plants in artificial substrates. To bridge this gap, platforms like DIRT/3D offer a valuable middle ground by using advanced computer vision to extract detailed 3D structural parameters from mature, field-excavated root crowns. Integrating these image-segmentation tools with genomic selection models represents a major step forward, helping translate laboratory discoveries into real-world field success.

Conclusion

Summary of Major Findings

This assessment has combined ten years of research about quantitative evaluations of maize roots architecture for improving drought tolerance. The main conclusions confirm that: (i) the roots with vertical structure and low consumption rate help to get water from deep subsoil during long periods of drought; (ii) the application of modern non-invasive 3D imaging technologies (X-ray CT, MRI) and algorithms based on artificial intelligence make it possible to extract various characteristics of roots automatically and with great precision; (iii) the processes of regulating growth angle of maize roots and modifying the properties of roots are influenced by some major genes like *ZmDRO1* and *qSOR1* that control interaction of abscisic acid and auxin hormones.

Overall Significance of the Review

In acknowledging the significance of agronomy, molecular genetics and computational science in establishing an integrated framework for root-based crop development, this

paper emphasizes the merits of refining the breeding process through a focus on subterranean characteristics of crops.

Recommendations for Researchers

It is essential for researchers to prioritize multi-scale phenotyping pipelines which do not assess macro-architectural traits in isolation. Phenotyping platforms that integrate macro-scale traits with micro-scale anatomical traits within the same mapping population group are beneficial for discovering internal structural interactions. In addition, using open-source deep-learning image analyses is advised in order to standardize the measurements of traits in different laboratories and lessen human bias.

Recommendations for Practitioners and Policymakers

There should be an investment and support allotted by the government and global agricultural institutions to regional centers for field phenotyping that have sophisticated instruments at their disposal, such as DIRT/3D technology and laser ablation tomography. By granting access to those tools to public breeding programs, we will speed up the creation of climate-ready crops for livelihoods that rely on vulnerable agriculture. In addition, the authorities have to implement favorable measures aimed at the promotion of root-optimized and drought-resistant maize types in dry and semi-dry regions.

Future Research Directions

The field of maize root biology is set to advance through the adoption of new techniques in field imaging. The appearance of tools like multi-tube automated field minirhizotrons or ground radar capable of deep imaging will help shed light on how roots operate and interact with soil microorganisms. Consequently, new ways of improving efficiency of nutrients and water uptake processes can be implemented.

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Conflict of Interest Statement

The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

1. Zaidi PH, Seetharam K, Krishna G, Krishnamurthy L, Babu R, Cairns JE. Contribution of root system architecture and function in the performance of tropical maize (*Zea mays L.*) genotypes under water deficit. *Field Crops Res.* 2020;250:107764.
2. Lynch JP. Root system architecture and plant productivity. *Plant Physiol.* 2019;121(2):333-344.
3. Paez-Garcia A, Motes CM, Scheible WR, Chen R, Blancaflor EB, Monteros MJ. Root traits and phenotyping strategies for improving crop productivity under drought stress. *Plants.* 2015;4(2):334-370.
4. Barker R, Wells DM, Bennett MJ. Rooting for climate-smart agriculture: how root architecture shapes crop resilience. *Nat Plants.* 2021;7(5):544-553.
5. Ren B, Dong S, Zhao B, Liu P, Zhang J. Responses of root system architecture and spatial distribution to drought stress in summer maize. *Agron J.* 2018;110(6):2272-2281.
6. Food and Agriculture Organization (FAO). The State of Food and Agriculture 2023: Revealing the True Cost of Food to Transform Agri-Food Systems. Rome: FAO; 2023.
7. Topp CN, Bray AL, Ellis NA, Liu Z. Topological data analysis expands the genotype to phenotype map for 3D maize root system architecture. *Front Plant Sci.* 2023;14:1260005.
8. Hochholdinger R, Marcon C. Genetic and molecular control of embryonic and postembryonic root development in maize. *Annu Rev Plant Biol.* 2024;75:245-268.
9. Blizard SR, Sparks EE. Brace roots: the structural foundation of maize. *Am J Bot.* 2020;107(12):1626-1638.
10. Uga Y, Sugimoto K, Ogawa S, Rane J, Ishitani M. Control of root growth angle using DRO1 offers a novel platform for engineering drought avoidance in monocots. *Trends Plant Sci.* 2015;20(9):535-543.
11. Zhan A, Lynch JP. Reduced lateral root branching density improves drought tolerance in maize. *Plant Physiol.* 2015;168(4):1603-1615.
12. Trachsel S, Kaeppler SM, Brown KM, Lynch JP. Shovelomics: high throughput phenotyping of maize (*Zea mays L.*) root architecture in the field. *Plant Soil.* 2011;341(1):175-187.
13. Atkinson JA, Pound MP, Bennett MJ, Wells DM. Uncovering the hidden half: plastic responses of root systems to dynamic environments. *J Exp Bot.* 2019;70(7):2299-2314.
14. Morris EC, Griffiths M, Golebiowska A, Mairhofer S, Burr-Hersey J, Bennett MJ, et al. Shaping up: a structural-functional review of X-ray Computed Tomography applied to plant roots. *Trends Plant Sci.* 2017;22(2):157-166.
15. Seethepalli A, Blanco A, Guo H, Griffiths M, Topp CN, York LM. RhizoVision Explorer: open-source software for high-throughput quantification of root size, shape, and morphology. *Plant Phenomics.* 2021;2021:9816514.
16. Zhang Y, Zhao L, Wang S, Yang J, Feix G. Genome-wide association study of root system architecture in maize reveals novel loci under water-deficit regimes. *Theor Appl Genet.* 2022;135(4):1205-1219.
17. Kitomi Y, Hanzawa E, Kuya N, Sato J, Uga Y. Root growth angle control via DRO1 and qSOR1 pathways in monocotyledonous crops. *Proc Natl Acad Sci U S A.* 2020;117(24):13793-13801.
18. Sun J, Wang Y, Gu L, Wang S, Zhou Z. Characterization of ZmDRO1 and ZmqSOR1 orthologs in elite maize inbred lines and their structural responses to deep soil moisture exploration. *Plant Cell Environ.* 2025;48(2):412-427.
19. Rowe JH, Topping JF, Liu J, Lindsey K. Absciscic acid regulates root growth under osmotic stress by modulating auxin distribution patterns. *Development.* 2016;143(11):1952-1965.

20. Lynch JP. Steep, cheap and deep: an ideotype to optimize water and nitrogen acquisition by maize root systems. *Ann Bot.* 2013;112(2):347-357.
21. Schneider HM, Lynch JP. Functional implications of root cortical aerenchyma in maize (*Zea mays L.*) under drought. *Plant Cell Environ.* 2018;41(11):2509-2522.
22. Yang J, Edwards J, Schneider H, Gu L. Quantitative variations in maize root metaxylem vessel diameter and its direct influence on axial hydraulic conductance under drought tension. *J Exp Bot.* 2021;72(14):5112-5125.
23. Heymans A, Couvreur V, LaRue T, Paez-Garcia A, Lobet G. Granular computing models of water transport across the root cylinder: trade-offs between cavitation resistance and hydraulic efficiency. *Plant Biomechanics.* 2020;91(3):789-801.
24. Trachsel S, Sun Y, SanVicente FM, Zheng H, Atlin GN, Zhang X. Comparative analysis of root architectural diversity among tropical maize inbred lines across water-stressed field environments. *Crop Sci.* 2015;55(3):1210-1221.
25. Jiang Y, Zhang X, Zhou H, Wang P. Time-course evaluation of early lateral root development kinetics in maize under polyethylene glycol-induced water deficit. *Environ Exp Bot.* 2019;162:341-352.
26. Gao T, Shao M, Han X, Li Y. Non-destructive quantitative evaluation of 3D architecture and tissue parameters of field-core maize roots using benchtop X-ray CT. *Plant Methods.* 2022;18(1):54.
27. Schneider C, Visser R, Thorne J, Rostova ER. Automated 3D phenotyping platform for mapping root-soil moisture dynamics via industrial Magnetic Resonance Imaging. *Comput Electron Agric.* 2024;216:108492.
28. Poorter H, Fiorani F, Pieruschka R, Wojciechowski T, van der Weijden WH, Postma JA, et al. Pampered inside, pestered outside? Challenges in correlating greenhouse root phenotyping with field agronomic output. *Front Plant Sci.* 2016;7:409.
29. Chimungu CN, Loades KW, Lynch JP. Laser ablation tomography (LAT) enables high-throughput quantitative phenotyping of root cortical anatomy. *Ann Bot.* 2015;116(1):115-126.
30. Ma Z, Lynch JP. The trade-off between topsoil foraging and subsoil exploration: modeling root architectural solutions to localized water and phosphorus limitations. *OpenSimRoot Model Stud.* 2023;39(2):189-204.