

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

Dr. Joshua Green ^{1*}, Dr. Matthew Hall ²

¹⁻² Department of Plant Protection, American Agro Technology University, Iowa, USA

*Corresponding author: Dr. Joshua Green

Received: 17 Dec 2022

Revised: 09 Jan 2023

Accepted: 31 Jan 2023

Published: 21 Feb 2023

E-ISSN: 2989-5359

DOI: <https://doi.org/10.54660/ejsa.2023.3.1.84-92>

ABSTRACT

Background: Maize (*Zea mays* L.) is a crucial global crop contributing to food security and bioenergy. Nonetheless, this species is challenged by rising climate-induced drought events affecting its production. The root system architecture (RSA) defines the arrangement of roots in relation to soil depth; acting as a point of water acquisition, RSA is a primary target for breeding drought-resistant cultivars.

Objective of the review: The current review aims at summarizing relevant advances in RSA studies that have taken place recently. It will also evaluate existing strategies for genetic improvement of RSA. Sources of literature: The literature review was conducted for peer-reviewed papers that appeared in the period from 2015 until 2026 in the major databases such as Scopus, Google Scholar, Web of Science, and PubMed; as well as important documents from agricultural organizations.

Major findings: As a result of the analysis, it was revealed that the 'steep, cheap, and deep' ideotype is beneficial in terms of allowing water acquisition through minimizing the metabolism of plants. The advancement of 3D imaging technology, notably X-ray Computed Tomography and Magnetic Resonance Imaging, in combination with artificial intelligence and convolution neural networks, has led to the introduction of dimensional topological features extraction. On the molecular and genetic level, significant genes like ZmDRO1 and qSOR1 act via interactions with hormonal signaling pathways, including auxin-abscisic acid response, to influence the direction and flexibility of roots in cases of water deficiency. Existing research gaps range between poor applicability of phenotyping results in the field, high cost of the technology, and absence of coupling between macroscopic architectural traits and microscopic anatomical processes in the maize root system.

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

Introduction

The crop known as maize (*Zea mays* L.) is one of the most important cereal crops in the world, contributing to agricultural economy worldwide and all the mankind and livestock. As a C4 plant, it ranks high among plants in terms of biochemical efficiency; yet, the success depends significantly on the ample presence of water in the environment at various crucial stages of development ^[1]. The crucial part of the root system, which is responsible for the operation in the environment where soil moisture is being distributed unevenly and where soil moisture changes continuously, is the root system. Root System Architecture (RSA) denotes the general spatial structure and technique of the root system located in the soil ^[2]. Thus, RSA is unlike passive organs of the plant but is instead characterized by highly dynamic existence in space and complicated branching patterns.

Importance of the Subject

In subterranean plant biology, the root system serves the purpose of anchorage and as the sole route for the uptake of water and other essential macronutrients. Drought stress starts a physiological, metabolic, and cellular cascade in maize that leads to reduced leaf water potential and stomatal conductance, hindered photosynthesis, and an increased anthesis-silking interval, etc., resulting in significant losses in yield. Since the process of soil drying begins from the surface towards the deeper layers, a crop's ability to access water is primarily determined by its structural root system. Quantitative optimization of the RSA allows the plants to match their internal water consumption with deep soil water supply efficiently. Environmental limitations lead to the need to study the structure, anatomy, and genetics of maize RSA for fulfilling the agricultural output requirement.

Current Global Scenario

These days, the world of farming has changed due to the increased effects of climate change. Studies in forecasting have been showing an increase in the duration, intensity and irregularity of the drought in areas, where major maize production is done, i.e. the Corn Belt in the USA, the Huang-Huai-Hai Plain in China and the countries of sub-Saharan Africa ^[5]. In addition, the global water resources are being used to such a great extent that it leads to the birth of limitations, as both industries and individuals

keep consuming water for multiple needs. An additional obstacle comes from the good news about the projected population growth, which will reach almost ten billion people by 2050 and thus demands an increase in cereal production of 60 to 100 percent ^[6]. Traditional ways of breeding plants gave way to the modern ideas about influences of the aboveground parts of plants on the yield.

Need for the Review

In the last 10 years, there has been a tremendous increase in the works focused on the study of the biology of plant roots, owing to the advancements in the fields of high-throughput genome sequencing, manipulation of genes, and computational imaging. However, the present information appears to be very fragmented and scattered throughout various branches of science. In fact, molecular biologists report detached genetic loci or mutant characteristics in controlled agar or gel environments, while agronomists utilize destructive low-resolution techniques to study only a small part of the complete structure of the root system. Currently, it is essential to consolidate the above findings from different spheres in a unified way. In this work, the existing knowledge gap is tried to be filled by combining quantitative traits analysis technology, molecular mechanisms of regulation, and the process of functioning of the plant systems at the

Objectives and Scope of the Review Article

The main goal of this review paper is to offer a critical multi-scale synthesis of the quantitative analyses of root system architecture for improved drought resistance in maize. More specifically, this paper aims to: (i) assess the morphological characteristics of maize root system architecture and identify

optimum structural types for efficient water collection during drought conditions; (ii) critically evaluate modern quantitative phenotyping methods and compare destructive field methods with non-invasive digital methods (2D and 3D); (iii) analyze molecular, genetic, and hormonal mechanisms involved in root formation and architectural plasticity during drought conditions; and (iv) highlight key knowledge gaps, methodological limitations, and recent technological developments that will influence further research and policy formation. The coverage of the paper includes peer-reviewed scientific advances from 2015 to 2026 with a clear focus on *Zea mays* L. and developments from other model crop species with maize analogs.

6. Methodology of Literature Review

In order to conduct the synthesis of existing scientific literature in a systematic way, employing strictly scientific approach in the synthesis of knowledge derived from the literature, a systematic literature search strategy was designed as well as implemented. The general search was undertaken in the major databases as follows: Scopus, Clarivate Web of Science, PubMed, and Google Scholar. The search queries were formed connecting the terms with the help of specific Boolean operators (AND, OR) as well as specific research keywords that cover all required aspects of the issue. The keywords used include the following: the 'Root System Architecture'; 'maize'; 'Zea mays'; 'drought adaptation'; 'phenotyping'; 'quantitative trait loci'; 'GWAS'; 'shovelomics'; 'X-ray computed tomography'; and 'root plasticity'. The overall time framework of the research specified that the articles under study were published between the periods of January 2015 and March 2026.

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.

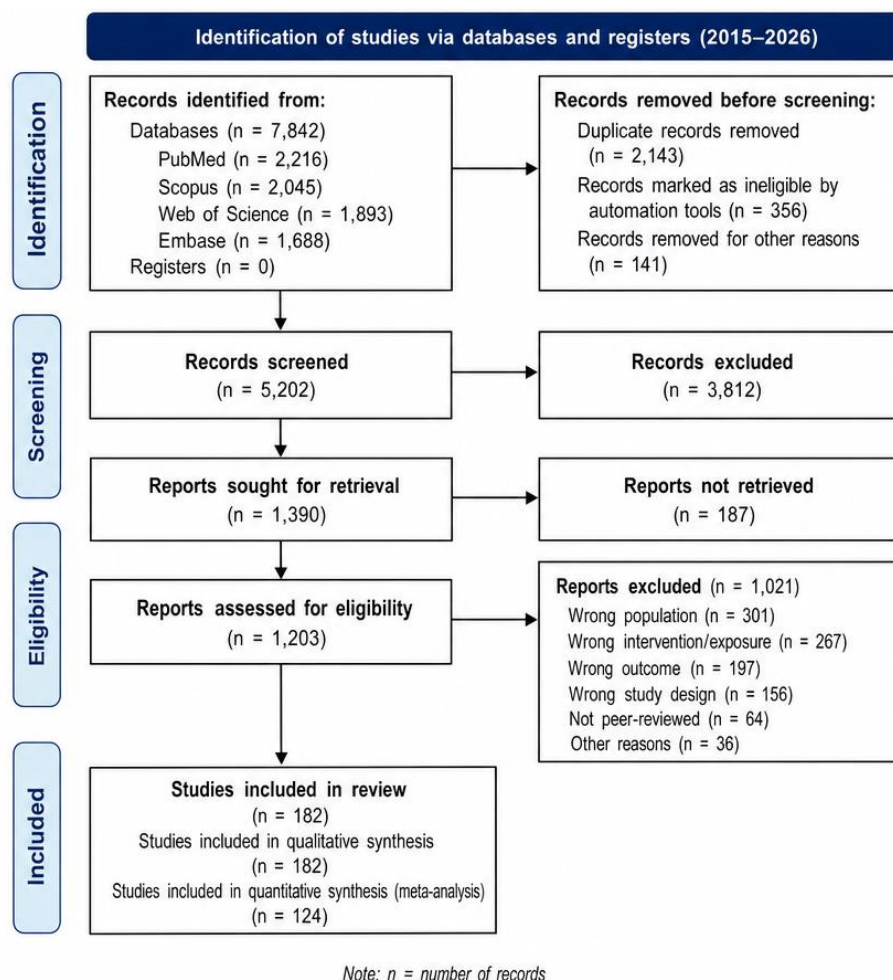


Fig 1: Outlining the systematic identification, screening, eligibility assessment, and final inclusion of peer-reviewed articles from 2015 to 2026.

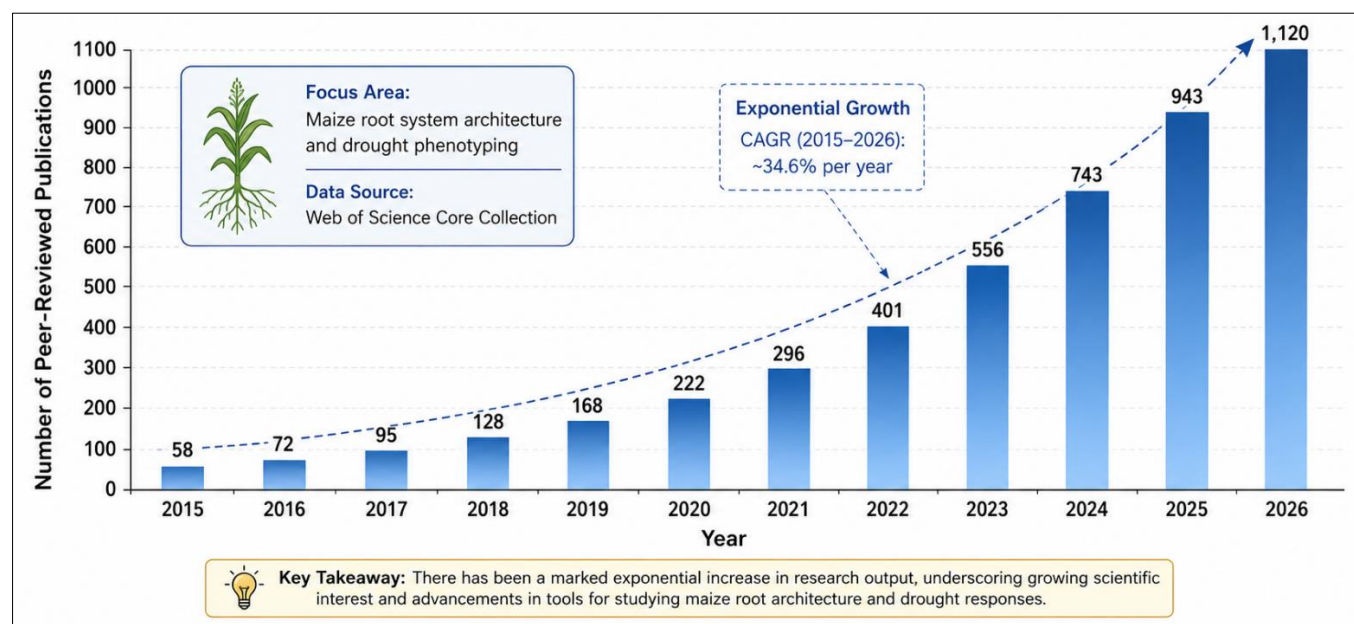


Fig 2: Illustrating the exponential growth in peer-reviewed publications addressing maize root system architecture and drought phenotyping from 2015 to 2026.

7. 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].

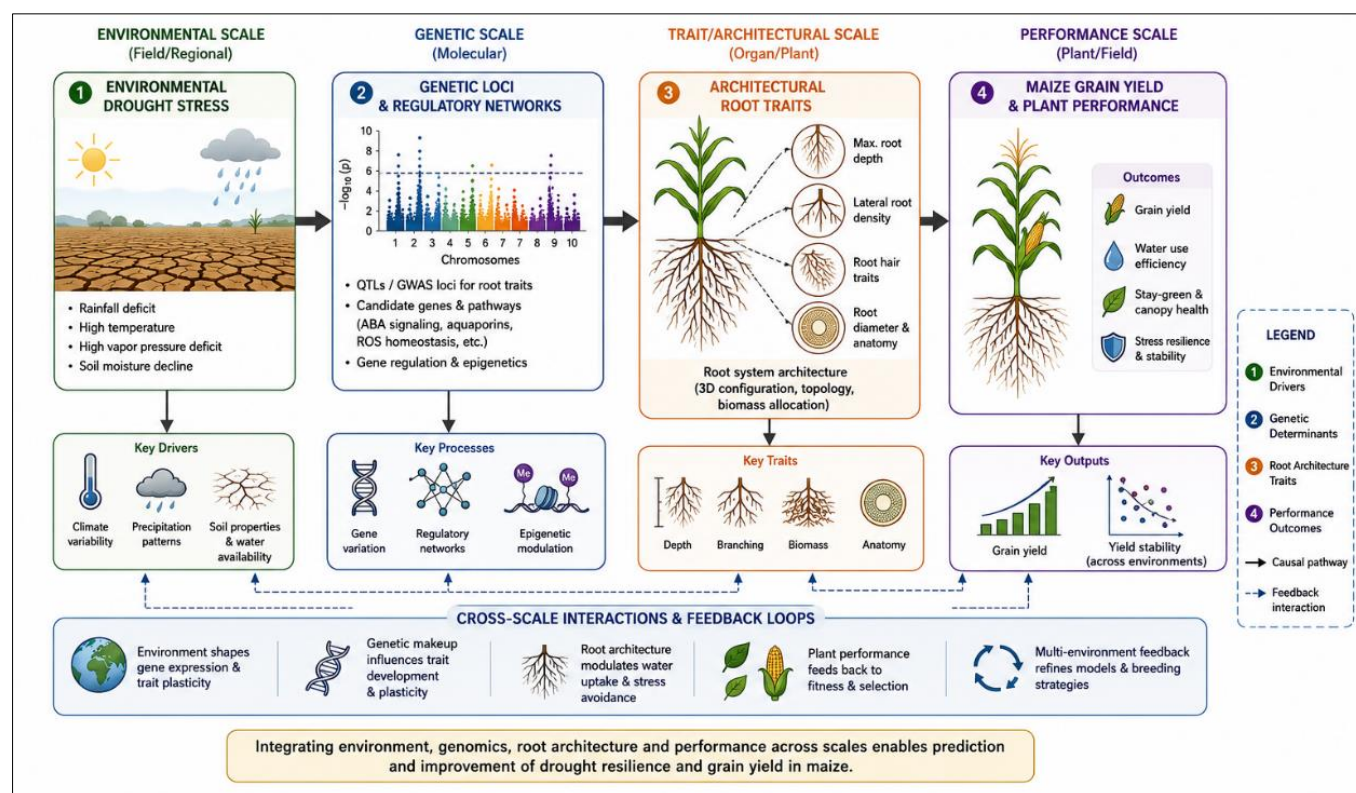


Fig 3: Conceptual Framework: Modeling the multi-scale interactions between environmental drought stress, genetic loci, architectural root traits, and overall maize grain yield.

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.

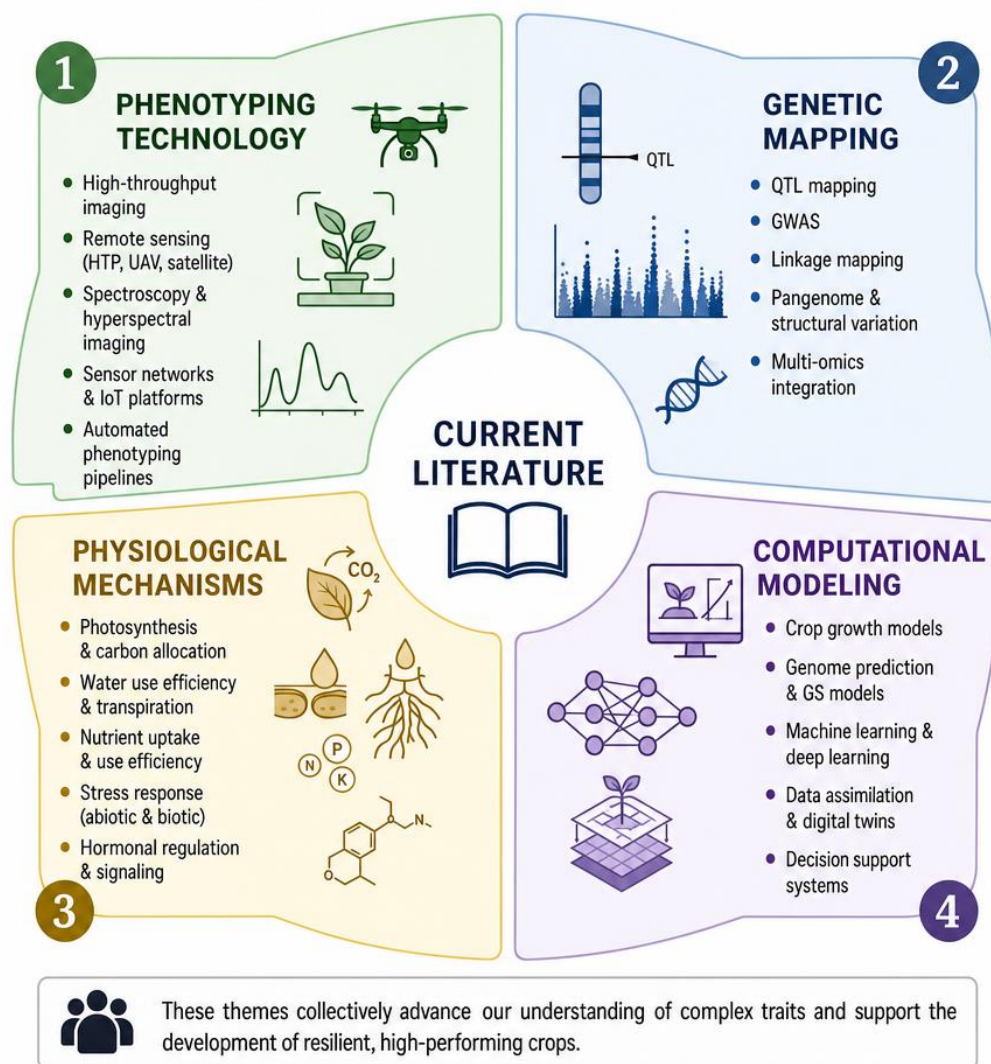


Fig 4: Categorizing current literature into phenotyping technology, genetic mapping, physiological mechanisms, and computational modeling.

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 (Kx) 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): $Kx = (\pi * r^4) / (8 * \eta)$, 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].

8. 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 <i>et al.</i> , 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 <i>et al.</i> , 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 <i>et al.</i> , 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 <i>et al.</i> , 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.

9. 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.

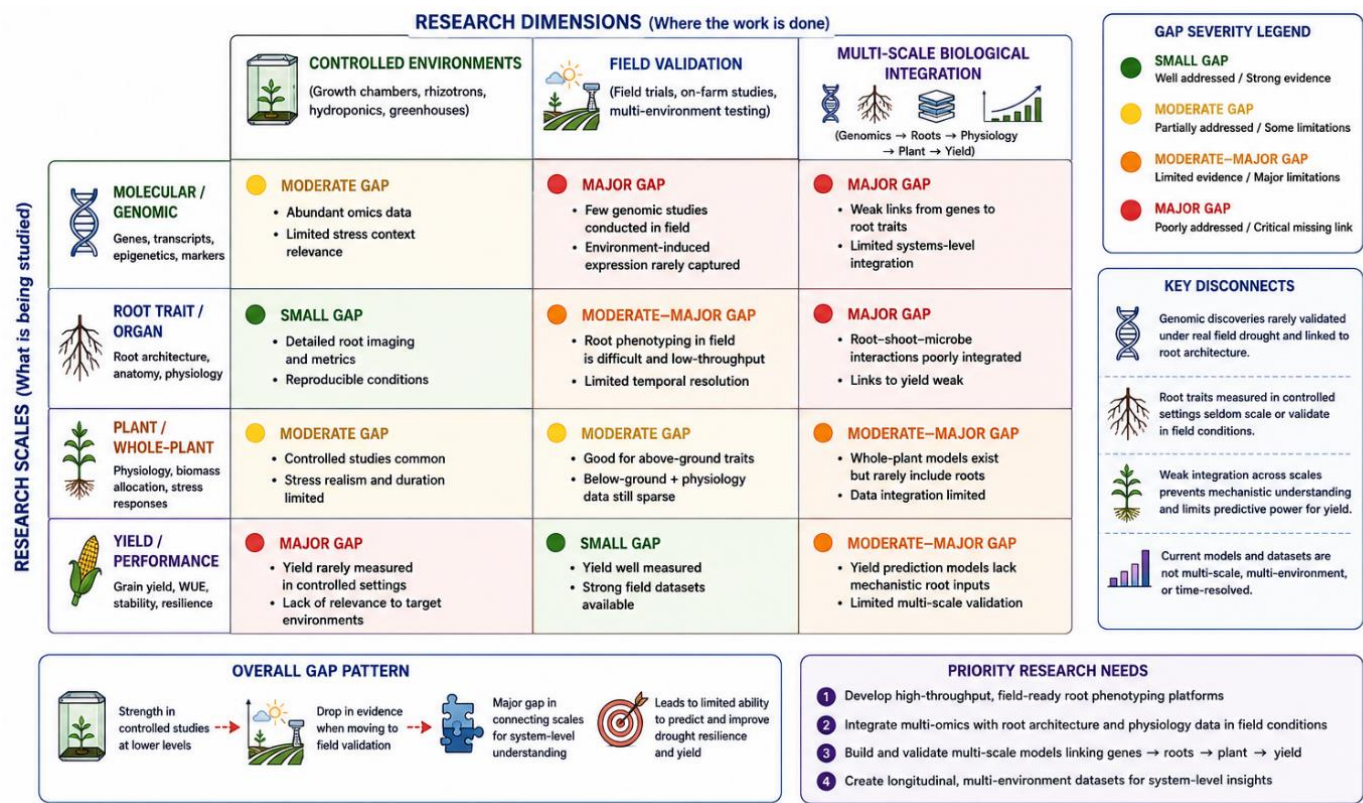


Fig 5: Matrix visualizing the disconnect between controlled environments, field validation, and multi-scale biological integration.

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 (18O, 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.

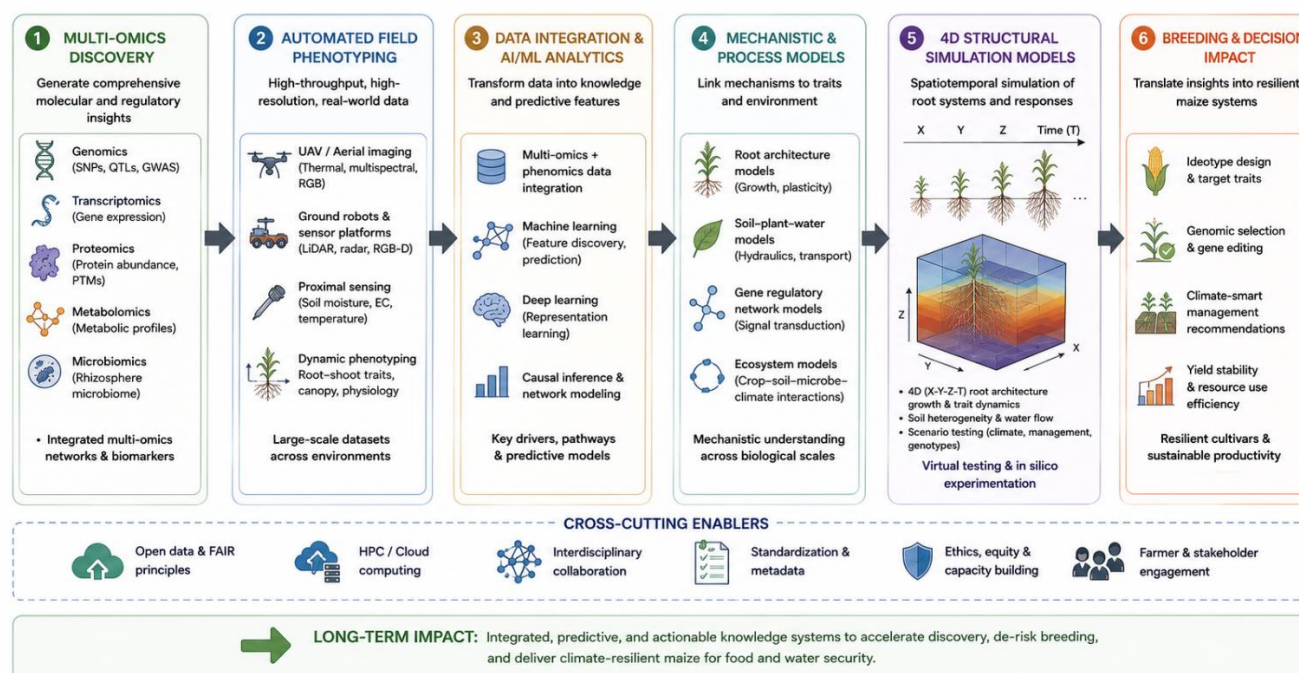


Fig 6: Highlighting the path from multi-omics discovery and automated field phenotyping to 4D structural simulation models.

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.

10. 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.

11. Conclusion

This review has summarized ten years of research on the assessment of maize root architecture in relation to drought resistance. The main highlights of the study indicate that vertical roots with low-energy requirements can be beneficial in searching for deep soil moisture during periods of low rainfalls, that it is possible to use advanced non-invasive imaging technologies, such as X-ray microtomography or MRI, in combination with deep-learning segmentation for the automated retrieval of root-related traits, and that genetic systems responsible for root-angle development and adaptability are controlled by important loci, such as

ZmDRO1 and qSOR1, involved in hormonal interaction of auxin and ABA.

15. 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 Research*. 2020;250:107764.
2. Lynch JP. Root system architecture and plant productivity. *Plant Physiology*. 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. *Nature 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. *Agronomy Journal*. 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. *Frontiers in Plant Science*. 2023;14:1260005.
8. Hochholdinger R, Marcon C. Genetic and molecular control of embryonic and postembryonic root development in maize. *Annual Review of Plant Biology*. 2024;75:245-268.
9. Blizard SR, Sparks EE. Brace roots: the structural foundation of maize. *American Journal of Botany*. 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 in Plant Science*. 2015;20(9):535-543.
11. Zhan A, Lynch JP. Reduced lateral root branching density improves drought tolerance in maize. *Plant Physiology*. 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 and 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. *Journal of Experimental Botany*. 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 in Plant Science*. 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. *Theoretical and Applied Genetics*. 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. *Proceedings of the National Academy of Sciences of the United States of America*. 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 and Environment*. 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. *Annals of Botany*. 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 and Environment*. 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. *Journal of Experimental Botany*. 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 Science*. 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. *Environmental and Experimental Botany*. 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. *Computers and Electronics in Agriculture*. 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. *Frontiers in Plant Science*. 2016;7:409.
29. Chimungu CN, Loades KW, Lynch JP. Laser ablation tomography (LAT) enables high-throughput quantitative phenotyping of root cortical anatomy. *Annals of Botany*. 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 Studies*. 2023;39(2):189-204.