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Integrative analysis of crop drought-tolerance genes and soil hydraulic traits: Bridging plant genomics and irrigation physics for sustainable water management: A review

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Abstract
Global agricultural productivity is substantially constrained by drought conditions and water scarcity, impacting approximately 25-40% of arable lands worldwide, particularly in the Middle East, North Africa, and Sub-Saharan Africa. Despite decades of research on crop drought tolerance mechanisms, a persistent disciplinary divide exists: drought-resistant varieties are evaluated by plant breeders under controlled greenhouse conditions that exclude soil variability, while soil physicists model water movement via Richards' equation without accounting for genetic variation in root hydraulic traits. This review synthesizes advances in plant genomics, soil physics, and bio-physical modeling to establish an integrated "physio-genetic" framework for sustainable drought adaptation. Key drought-tolerance genes regulating plant hydraulic traits (including root system architecture genes (DRO1, qSOR1), aquaporins (AQP; PIP1, PIP2, TIP1), and transcription factors "DREB1") are examined alongside their interactions with soil water conductivity K(θ) and water potential gradients governed by the van Genuchten-Mualem model. Rhizosphere engineering through root exudates and mucilage production is analyzed for its modulation of soil-root hydraulic continuity. Bio-physical modeling approaches that couple crop growth platforms (DSSAT, APSIM) with soil water transport solvers (HYDRUS-1D) are reviewed to predict genotype × soil × climate interactions. Case studies from rainfed rice (DRO1 deployment in Asia) and drought-tolerant maize (marker-assisted selection in the Sahel) document 20-30% and 40-60% yield improvements under water-limited conditions, respectively. Breeding strategies and precision irrigation protocols tailored to soil texture are proposed, alongside identification of adoption barriers and research gaps in climate change projections. This integrative framework advances physio-genetic breeding paradigms that simultaneously optimize plant genetic capacity and soil-plant hydraulic coupling, providing pathways for sustainable water utilization amid escalating climate variability and food security challenges.

Keywords: Physio-genetic breeding, K_{root}, DRO1, van Genuchten, rhizosphere engineering

1. Introduction

1.1. The Disconnect Between Genomics and Soil Physics

Global food production is facing increasing challenges of inadequate water supply and uncertain climatic changes, impacting about a quarter-fifth of the farming lands all over the world (FAO, 2022; Cardoso *et al.*, 2025) [15, 26]. Stress due to drought affects especially those areas with scarce water supply like the Middle East and North Africa (MENA) where cereals and cash crops experience extreme yield losses in case of rainfed conditions. Although a lot of research on the topic of crop tolerance during dry periods has been performed during the past several decades, there is still a significant rift between two significant areas of science. Plant breeders typically test drought-resistant varieties in greenhouses or small scale pot to test, where the variation in soil properties is significantly less or not a fact to be taken into account (Wang *et al.*, 2021) [71]. Conversely, soil hydrologists model moisture movement using the mathematical framework and concept of Richards and model roots as homogenous locations of absorption that follow standardized water extraction patterns without considering the fact that root varieties may vary in their absorption characteristics (Vanderborght *et al.*, 2024) [69].

The effect of this compartmentalization of research has led to poor understanding of interactions between plant systems and soil water dynamics. A case in point is that a plant variety that expresses higher levels of genes that respond to water restriction like DREB1 (Dehydration-Responsive Element Binding protein) could have a higher survival chances in the laboratory but not in the field due to constraints in soil water movement to provide sufficient moisture (Todingan *et al.,* 2025) [63]. Similarly, water delivery methods that are optimized based on the soil moisture-conducting properties can fail to consider the difference in the basic genetic ability of plants to absorb water through the soil resulting in an ineffective rate of water application (Cai *et al.,* 2022) [14].

1.2. Bridging plant genomics and soil hydraulics: Scope and objectives

This synthesis endeavors to consolidate existing understanding regarding mechanistic pathways connecting crop genes conferring drought resilience and characteristics of soil water dynamics. In particular, the objectives encompass:

- The Effects of the key water-stress-controlled genes (DREB, AQP, DRO1) on the water-conducting capacity and morphological development of root systems in plants.
- Characteristics of soil water transport analysis -based on the principles of Darcy and soil moisture desorption relationships- inhibited or facilitating the manifestation of genetic potentials of water scarcity adaptation.
- Exploring the root zone area as a tool of active boundary to gain insight into the nature of hereditary root in characteristics of soil structure and hydrology.
- Assessment of quantitative bio-physical models that form a union between hereditary crop traits and contract of subsurface moisture flow.
- Development of cultivar selection programs and water application management strategies that can maximize interactions with genetic constitution, edaphic environment, and operational practices at the same time.

Through integration of molecular crop science with soil water physics, this examination establishes a conceptual and methodological foundation enabling the development of improved crop germplasm and management protocols designed to enhance water output efficiency across heterogeneous soil circumstances.

2. The genetic basis of plant hydraulics

2.1. Root system architecture genes and water extraction profiles

Root system architecture (RSA) is a critical determinant of plant water acquisition, particularly under drought stress. The spatial distribution, depth, and branching patterns of roots govern the soil volume explored and the efficiency of water uptake (Guseman *et al.,* 2017) [30]. Recent advances in molecular genetics have identified key genes controlling RSA traits, with significant implications for drought tolerance.

The *DRO1* gene and deep rooting

DEEPER ROOTING 1 (DRO1) was the first gene discovered in rice (*Oryza sativa*), it controls the angle of root development by controlling gravitropic signaling (Guseman *et al.,* 2017; Oo *et al.,* 2021) [30, 55]. Functional alleles of DRO1 in rice varieties have been shown to have steeper root development angles thus giving a deeper root system, which reaches water in deeper soil layers during terminal drought (Uga *et al.,* 2013) [67]. The ability of DRO1-positive genotypes to perform differently in response to water regime was demonstrated in field trials with modest grain yield advancement of about 10 percent when deep rooting varieties were cultivated under well-watered conditions, but grain yield improvement of 30-50 percent over shallow rooting varieties when cultivated under terminal drought (rainfed) conditions (Uga *et al.,* 2013; Arai-Sanoh *et al.,* 2014) [6, 67]. This genotype environment interaction points to the significance of breeding goals in accordance with certain rainfall regimes. Soil physics In a soil physics viewpoint, the vertical profile of water uptake is changed by deeper roots, where uptake is no longer in the surface layers, where hydraulic conductivity of soil plummets steeply as it dries, but in deeper layers, where water availability is higher (Bouda *et al.,* 2017) [10]. The DRO1 gene works well to reprogram where the optimum of water flux is found in the soil profile which proves that the spatial component of the soil-plant hydraulic system is directly controlled genetically.

Root architectural plasticity and soil heterogeneity

In addition to constitutive characteristics, root systems are also plastic to changes in environmental cues of soil. Rice contains a gene known as qSOR1 that increases shallow root angles promoting foraging in topsoil to acquire nutrients including phosphorus (Oo *et al.,* 2021) [55]. Surprisingly, the use of genotypes that contained qSOR1 demonstrated excellent phosphorus uptake and biomass when the nutrients were concentrated close to the soil surface, which demonstrated the interaction of RSA genes with the pattern of resource distribution in soil (Oo *et al.,* 2021) [55]. This observation reveals that root architectural characteristics are important and it is necessary to match them with the soils and nutrient management systems.

Table 1 shows the important drought-tolerance genes (DRO1, qSOR1, AQP, DREB1, RHD and mucilage biosynthesis genes) and their influence on root and plant hydraulic characteristics, molecular processes and field performance using major crops. The individual genes regulate particular hydraulic phenotypes -root depth, root hydraulic conductivity (Lp), stomatal conductance, and rhizosphere water retention- with individual molecular pathways (auxin signaling, aquaporin expression, ABA-mediated responses), which then translate into agronomic outcomes such as 20-30% yield increase during drought stress and a high level of water uptake efficiency. The table shows the hierarchical association between genotype (molecular level), phenotype (hydraulic traits), and agronomic performance, which forms a basis of breeding drought-tolerant crops with increased water use efficiency (WUE).

Table 1: Key genes controlling plant hydraulic traits

Gene	Crop	Function	Hydraulic Trait	Mechanism	Field Impact	Reference
DRO1	Rice	Root gravitropism modulation	Deep rooting; steeper root angle (from ~42° to 52°)	Altered auxin signaling in root cap columella cells	+20–30% grain yield under terminal drought	(Uga *et al.*, 2013; Kitomi *et al.*, 2020) [67, 39]
qSOR1	Rice	Root angle control; auxin-regulated plasticity	Shallower root angles (opposite to DRO1 effect) promoting topsoil foraging	Auxin-mediated control of gravitropism; loss-of-function reduces basal inhibitory auxin signaling	Enhanced phosphorus uptake and biomass when nutrients are localized in topsoil; beneficial in calcareous and alkaline rice soils; complementary to DRO1 for bimodal rooting	(Oo *et al.*, 2021; Kitomi *et al.*, 2020) [30, 39]
AQP (PIP1, PIP2, TIP1)	Wheat, sorghum, sunflower	Transcellular water channel proteins (PIP1, PIP2, TIP1)	Increased Root hydraulic conductivity (*Lp*)	Facilitate rapid transcellular water transport through cell membranes and control water transport under water stress via post-translational modification	Genotype-dependent variation in Lp reaches 40-80% across crop species; silicon application increases *Lp* up to 50% under osmotic stress	(Liu *et al.*, 2014; Adiredjo *et al.* 2014) [42, 1]
DREB1	Multiple	Dehydration-responsive transcription factor	Decreased Stomatal conductance; Increased osmotic adjustment	Activates *ABA* signaling pathway	Enhanced drought avoidance	(Todingan *et al.*, 2025) [63]
RHD family	Arabidopsis	Root hair length/density regulation	Increased root surface area	Genetic control of cortical cell development	Improved water uptake in coarse soils	(Guseman *et al.*, 2017; Chimungu *et al.*, 2014) [30, 21]
Mucilage biosynthesis	Maize and Barley	Polysaccharide synthesis	Enhanced rhizosphere water retention	High-molecular-weight polysaccharide production	Variable: enhances retention	(Watt *et al.* 2006; Ahmed *et al.*, 2018) [74, 4]

Abbreviations: *Lp*, root hydraulic conductivity; *K(θ)*, soil hydraulic conductivity; *ABA*, abscisic acid; *DREB*, Dehydration-Responsive Element Binding; *PIP/TIP*, Plasma membrane Intrinsic/Tonoplast Intrinsic Proteins; *WUE*, water use efficiency.

2.2. Aquaporins: Genetic regulation of root hydraulic conductivity

While RSA determines the spatial extent of the root system, the rate of water uptake per unit root surface area is governed by root hydraulic conductivity (L_p), largely controlled by aquaporin (*AQP*) water channel proteins (Liu *et al.*, 2014) [42].

Aquaporin function and drought response

Aquaporins are membrane-bound proteins that facilitate transcellular water transport across root cells, significantly increasing $L_p$compared to passive diffusion (Grondin *et al.*, 2015) [28-29]. Under well-watered conditions, high aquaporin expression maintains high L_p, enabling plants to meet transpirational demands. However, during drought stress, aquaporin activity is rapidly down-regulated through post-translational modifications (e.g., phosphorylation) and gene expression changes, reducing L_p and conserving soil water (McElrone *et al.*, 2007) [48].

Liu *et al.* (2014) [42] demonstrated that silicon application under osmotic stress increased $L_p$in sorghum by up-regulating aquaporin gene expression (*PIP1*, *PIP2*, *TIP1*), resulting in improved water uptake and photosynthetic rates. This finding illustrates how exogenous treatments can modulate genetic pathways controlling hydraulic properties, offering potential for agronomic interventions.

Linking aquaporins to soil water potential

Root hydraulic conductance (Kroot) and soil water potential (ψsoil) have a nonlinear and genotype-specific relationship. Cai *et al.* (2022) [14] constructed a hydraulic model that indicated that crops exhibiting lower Kroot (because of lower aquaporin activity) sustain water uptake at lower soil water potential ψsoil, therefore postponing the onset of soil-limited water stress. The reason behind this is that, lower Kroot decreases the water potential gradient on the soilroot interface and ensures that soil hydraulic conductivity remains within critical levels over extended periods during drying periods.

The overall transpiration rate (E) in the soil-plant continuum is governed by:

$$E = K_{root} \times (\psi_{soil\_root} - \psi_{xylem\_root}) \quad (1)$$

Where E is transpiration rate ($cm^3\ s^{-1}$), K_{root} is root hydraulic conductance ($cm^3\ kPa^{-1}\ s^{-1}$), influenced by aquaporin activity, $\psi_{soil\text{-}root}$ is water potential at soil-root interface (kPa), $\psi_{xylem\text{-}root}$ is water potential in root xylem (kPa), determined by soil hydraulic properties and extraction history. This equation highlights the intimate coupling between genetic (aquaporin-regulated K_{root}) and soil physical parameters in determining water flux

Figure 1 illustrates how key drought-tolerance genes regulate root phenotypes and soil hydraulic properties that ultimately control plant water relations and yield. Drought-responsive genes such as *DRO1*, aquaporin genes

(*AQP*; *PIP1*, *PIP2*, *TIP1*), *DREB1*, and root-hair-related genes (*RHD*) determine traits including root depth, root hydraulic conductivity (*Lp*), mucilage production, and root hair length/density. These phenotypic traits in turn modify soil water potential (ψ_{soil}), soil hydraulic conductivity $K(\theta)$, the soil water retention curve, and rhizosphere properties.

Changes in these soil hydraulic properties affect field-level processes such as water uptake, transpiration rate, photosynthesis, and final grain yield. Arrows indicate the direction of influence between genetic, phenotypic, soil, and performance layers, while feedback arrows from field performance (particularly grain yield) back to the genetic layer highlight how breeding programs use performance outcomes to select and refine drought-tolerant genotypes.

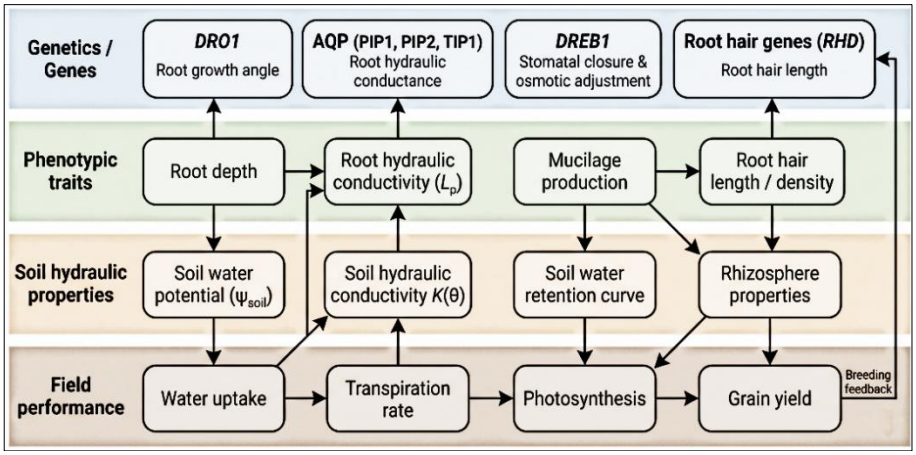

Fig 1: Conceptual framework linking drought-tolerance genes with root–soil hydraulic traits and field performance.

3. Soil Physics constraints on genetic potential

Soil hydraulic conductivity $K(\theta)$is strongly nonlinear and can be estimated from the soil water retention curve using the combined van Genuchten–Mualem model (van Genuchten, 1980; Mualem, 1976) [68, 51]. The water retention curve is described by the van Genuchten equation:

$$\theta(h) = \theta_r + \frac{\theta_s - \theta_r}{[1+(\alpha|h|)^n]^m} \quad (2)$$

where $\theta$is volumetric water content, $\theta_r$and $\theta_s$are residual and saturated water contents, $h$is pressure head (cm), α(cm^{-1}) is the inverse air-entry value, $n$is the pore-size distribution parameter, and $m = 1 - 1/n$ (van Genuchten, 1980). The effective saturation is $S_e = (\theta - \theta_r)/(\theta_s - \theta_r)$, which varies from zero at residual water content to unity at saturation. Regardless of a plant's genetic capacity for water uptake, soil hydraulic properties impose fundamental physical limits on water availability. The relative hydraulic conductivity according to Mualem's theory with a tortuosity parameter $\lambda = 0.5$is:

$$K_r(S_e) = S_e^{0.5}\left[1-\left(1-S_e^{1/m}\right)^m\right]^2 \quad (3)$$

where $K_r = K(\theta)/K_{sat}$and $K_{sat}$is saturated hydraulic conductivity (Mualem, 1976; van Genuchten, 1980) [51, 68]. This model solution is popularly adopted in vadose zone models including HYDRUS to model water transport in unsaturated soils. The drying soil may reduce K (0) by multiple orders of magnitude, providing sharp water potential gradients around roots that limit water uptake to plants regardless of their genetic potential to take up water (Cai *et al.*, 2022) [14]. These non-linear relations between soil water status and hydraulic conductivity indicate that soil texture has a drastic impact on the time and extent of the hydraulic constraint of root water uptake in a range of soil conditions. (Cai *et al.*, 2022) [14].

Soil texture effects on genetic expression

Soil texture dramatically influences the relationship between $\theta$and $K(\theta)$. In sandy soils, $K(\theta)$declines sharply at relatively high θ(e.g., $\psi_{soil} > -10$kPa), whereas in loam soils, significant conductivity is maintained to much lower ψ_{soil}(≈ -100 kPa) (Cai *et al.*, 2022) [14]. Consequently, high-conductance genotypes (high aquaporin expression) experience earlier onset of water stress in sandy soils compared to clay loams, as soil hydraulic limitation dominates sooner (Cai *et al.*, 2022) [14].

Such genetic expression where genetic potential is determined by soil implies that breeding objectives must be soil-specific. Indicatively, deep-rooting DRO1 genotypes can be more advantageous in sandy soils where the top layers become dry easily, and high-L p genotypes can be more useful in loam soils where long-term conductivity sustains high rates of transpiration.

3.2. The soil-root interface: physical gaps and rhizosphere hydraulics

The soil-root interface represents a critical zone where physical contact between soil particles and root surfaces governs water transfer efficiency (Carminati and Vetterlein, 2013) [16].

Gap formation and hydraulic discontinuity

When soils dry, root drying and soil drying may cause dissimilar contraction between roots and the soil which results in air-filled pore formation at the interface and a significant increase in hydraulic resistance (Carminati and Vetterlein, 2013) [16]. Nobel and Cui (1992) noted that desert succulents shrink roots creating millimeter gaps that essentially isolated roots to bulk soil water. Gap development occurs in the structured soils and is more amplified in agricultural crops as the ψ soi value reduces to less than -100 kPa (White and Kirkegaard, 2010) [75].

Genetically, the cortical cell size and shrinkage capacity are heritable root anatomical characteristics that determine the

propensity to form gaps (Chimungu *et al.*, 2014) [21]. Roots that have smaller cortical cells have reduced radial shrinkage and they are better able to keep contact with the soil during stress on water.

Root exudates and soil hydraulic modification

Plant roots secrete a wide array of organic compounds - collectively termed root exudates- that modify soil physical properties in the rhizosphere (Cooper *et al.*, 2018) [22]. Mucilage, a high-molecular-weight polysaccharide, is particularly important for rhizosphere hydraulics.

Mucilage effects on water retention and conductivity

Mucilage increases soil water retention by absorbing water and forming hydrated gels around soil particles (Moradi *et al.*, 2011) [50]. Ahmed *et al.* (2018) [4] demonstrated that mucilage increased the water content at a given matric potential $\psi_{soil}$by up to 30% in sandy soils at pF 2.0 (ψ = -100 kPa). However, the effect was significantly lower under very dry conditions (pF > 4.0), where mucilage contributed less than a 10% increase, suggesting that mucilage benefits are primarily in the moderately dry range (Carminati *et al.*, 2017) [17-18]. Additionally, mucilage increases water viscosity by up to 2-3 fold at high mucilage concentrations (0.5-2% w/w), which can reduce soil hydraulic conductivity at a given matric potential ψ_{soil} (Carminati *et al.*, 2017) [17-18].

Carminati and Vetterlein (2013) [16] proposed a conceptual model of "rhizosphere hydraulic plasticity," where roots actively modulate rhizosphere properties through mucilage secretion. Young, actively growing roots secrete mucilage (Class A rhizosphere), enhancing hydraulic continuity and water uptake. As roots mature and mucilage degrades or desiccates, the rhizosphere may become hydrophobic or develop gaps (Class B rhizosphere), reducing water uptake from that root segment. This spatial and temporal heterogeneity in rhizosphere hydraulics is genetically controlled, as mucilage production rates vary among species and genotypes (Watt *et al.*, 2006) [74].

Modeling rhizosphere hydraulic properties

Cooper *et al.* (2018) [22] created a multiscale model, which combined pore-scale exudate diffusion with macroscale Richards equations to predict the rhizosphere hydraulic characteristics. Their homogenization method revealed that exudate induced alteration in contact angle and viscosity modified effective soil hydraulic parameters, and both had possible feedbacks to root water uptake. Landl *et al.* (2021) [41] realized rhizosphere-level hydraulic models, which revealed that mucilage concentration increased the process of root water uptake decrease during soil drying, mainly because the effects of viscosity dominated over the advantages of retention.

Such results indicate that selection on producing mucilage in the optimal amount -enough to maintain contact with the soil but no more to pay the cost of viscosity- might increase drought resistance. The variety in the mucilage secretion and composition is also large among cereals through genetic variation. Watt *et al.* (2006) [74] reported that the lines of barley and maize differ greatly in total mucilage and composition of polysaccharides produced. Further, Nazari et al (2020) [53] found that the lines of maize that developed in semi arid environments (Mexico, Southern Africa) had 125-135% higher rates of mucilage exudation than temperate breeding lines on Europe and North America, implying that selection pressures in water limited environments have driven the evolution of more prolific mucilage producing lines. This genetic difference provides good sources of marker-assisted selection breeding programs (Watt *et al.*, 2006; Nazari *et al.*, 2020) [53, 74].

Figure 2 explains how the age dependent alterations in the rhizosphere alter root-soil hydraulic conductivity and, thereby, water uptake by roots. In panel A, a young and actively growing root (Class A rhizosphere) is shown with a thick mucilage layer that is in close contact with the soil particles and provides the high rate of water flow to the root (high K_"root"). Panel B demonstrates a mature root (Class B rhizosphere) in which mucilage exudation is less, air cracks form at the contact point between the root and soil, and the hydraulic connection is weak, which leads to low K root. The time series of water uptake rate is shown in panel C showing that Class A waters water uptake at a slower rate than Class B and the uptake decreases with increasing root age and is associated with a reduction in mucilage production and a decline in rhizosphere hydraulic.

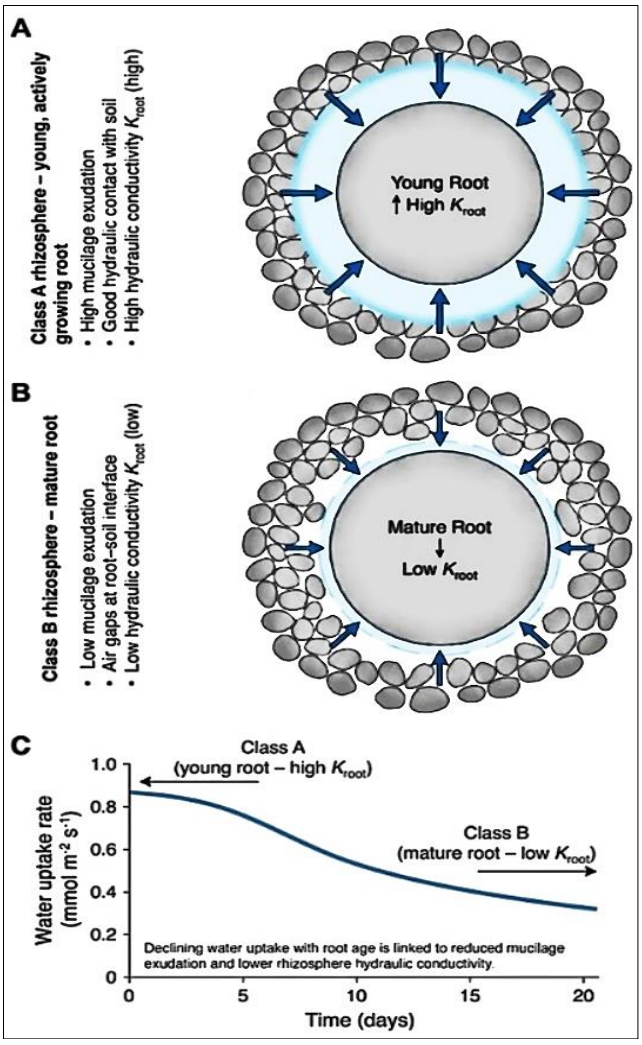

Fig 2: Rhizosphere hydraulic plasticity over time.

4. Bridging the Gap: Genotype × Soil Environment Interactions

4.1. Bio-Physical Modeling: Integrating Crop Growth and Soil Hydraulics

Comprehensive understanding of genotype × soil interactions requires quantitative models that simulate both

crop physiological processes and soil water dynamics. Recent efforts have coupled crop growth models with numerical solutions of the Richards equation, enabling exploration of genetic and soil hydraulic parameter spaces.

DSSAT-Hydrus coupling

Shelia *et al.* (2018) [58] coupled the Decision Support System for Agrotechnology Transfer (DSSAT) with HYDRUS-1D, replacing DSSAT's simple "tipping bucket" soil water balance with the Richards equation. The coupled model simulates crop growth (phenology, photosynthesis, biomass allocation) driven by genetic coefficients while computing soil water distribution, actual evapotranspiration, and root water uptake using finite element solutions of:

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z}\left[K(\theta)\left(\frac{\partial \psi}{\partial z}+1\right)\right] - S(z,t) \quad (4)$$

where ψ is soil matric potential (cm H_2O), z is depth (cm), $K(\theta)$ is soil hydraulic conductivity (cm day^{-1}), and the term +1 represents the gravitational gradient ($\partial h/\partial z = 1$ for vertical flow), $S(z,t)$ is the root water uptake sink term, dependent on root distribution and hydraulic properties (Dong *et al.*, 2022) [23].

Comparison with field experiments of soybean in various soil types in Florida resulted in the improvement in the coupled DSSAT-HYDRUS model on the simulation of soil water content profiles, with an efficiency of the model (Nash-Sutcliffe coefficient) ranging between 0.76 and 0.89 across soil type and water regime (Shelia *et al.*, 2018) [58]. The prediction of crop yield was still high with a model efficiency of 0.88-0.92 as compared to the original DSSAT tipping-bucket shot which had at 0.65-0.78. The higher performance was especially noticeable in mid-season-late season drought stress, where soil hydraulic constraints came to bear. (Shelia *et al.*, 2018) [58].

Incorporating genetic parameters

Current implementations of DSSAT-HYDRUS use generic root length density distributions, but they can be extended to include genotype-specific root architectural traits. For example, DRO1-positive versus DRO1-negative genotypes could be simulated with different rooting depth functions, and aquaporin activity could be represented through variable root radial conductivity parameters. Such extensions would enable in silico evaluation of breeding strategies across soil types and climate scenarios (Kanda *et al.*, 2018) [37].

APSIM and other modeling platforms

The Agricultural Production Systems Simulator (APSIM) similarly provides a modular framework for coupling crop growth with soil water and nutrient dynamics. The model has been continuously updated, with major releases providing improved soil water modules, soil nitrogen dynamics, and microclimate functions (Keating *et al.*, 2003; Holzworth *et al.*, 2014; Holzworth *et al.*, 2015) [32, 33, 38]. APSIM includes modules for soil processes (water balance, nitrogen transformations) and has been applied to assess climate change impacts and management decisions across diverse crops (Nyawira, 2019) [54]. Integration of RSA traits and root hydraulic parameters into APSIM's soil water module could facilitate breeding program design and precision irrigation optimization.

Figure 3 presents a bio-physical modelling framework that couples the DSSAT crop model with the HYDRUS soil water flow model to simulate genotype × soil interactions under varying climatic conditions. The top box summarizes the required inputs, including genotype parameters (root distribution, root hydraulic conductivity Lp, stomatal sensitivity), soil hydraulic properties (Ksat, K(θ), van Genuchten parameters, initial θ), and climate drivers, including temperature, radiation, vapour pressure deficit and precipitation or irrigation. The central component is the dynamic interaction between DSSAT and HYDRUS that is characterized by the simulation of phenology, photosynthesis, biomass development, and yield formation by DSSAT, and the solution of the Richards equation of soil water flow, soil water potential, and root water uptake profile by HYDRUS. The bottom box lists key outputs and predictions of the integrated system, including soil water profile θ (z, t), actual evapotranspiration ETa, root water uptake S (z, t), leaf water potential ψ-leaf, yield under different management and climate scenarios, and water use efficiency (WUE).

4.2 Rhizosphere engineering: Manipulating soil-root hydraulics through genetics

The recognition that root exudates modify soil hydraulic properties opens opportunities for "rhizosphere engineering"-selecting or engineering crops with exudation profiles optimized for water acquisition.

Root Hairs and hydraulic continuity

Root hairs enlarge the effective root surface area and physically seal air-filled pores to ensure hydraulic continuity when the soil dries (Ahmed *et al.*, 2018) [4]. The study by Carminati *et al.* (2017) [17-18] established that barley varieties with long root hairs sustained high rates of transpiration in low ψ soilscompared to barley varieties with short root hairs. The mechanism behind it is the enhancement of absorption radius and water potential gradient buffering at soil-root interface (Segal *et al.*, 2008) [57].

Root hair length and density are inherited factors that are regulated by several genes including ROOT HAIR DEFECTIVE (RHD) family genes in Arabidopsis (Guseman *et al.*, 2017) [30]. Applying this information to crop species - e.g. by using individual alleles of long root hair in wheat or rice to increase drought tolerance using marker-assisted selection -could be effective in increasing drought tolerance, especially in coarse-textured soils where cracks occur easily.

Mucilage production genes

Although genetic regulation of mucilage production is not studied as well as RSA genes, some progress is being achieved. A high molecular weight polysaccharides synthetized on the root cap cells make up mucilage. The mucilage production can be controlled by targeting genes that are involved in the biosynthesis of cell wall polysaccharides (e.g., Cellulose Synthase Like genes) (Ray *et al.*, 2003). There is also natural difference in mucilage secretion; an example is in the inbred lines of maize which differ 2-3 fold in mucilage secretion with high-secretors producing a stronger rhizosheath (Watt *et al.*, 2006) [74].

In Ahmed *et al.* (2018) [4], the authors revealed that mucilage polymers of chia seed gum and polygalacturonic acid raised water retention and affected hydraulic conductivity of soil in a concentration-dependent way. Exudates in clay loam soil enhanced its soil hardness by 48 percent in high concentration (4.6 mg g-1), which could

enhance the stability of soil structure but also enhance its mechanical impedance (Naveed *et al.*, 2018) [52]. Intermediate mucilage production could be the focus of breeding programs to strike a balance between hydraulic and mechanical influence.

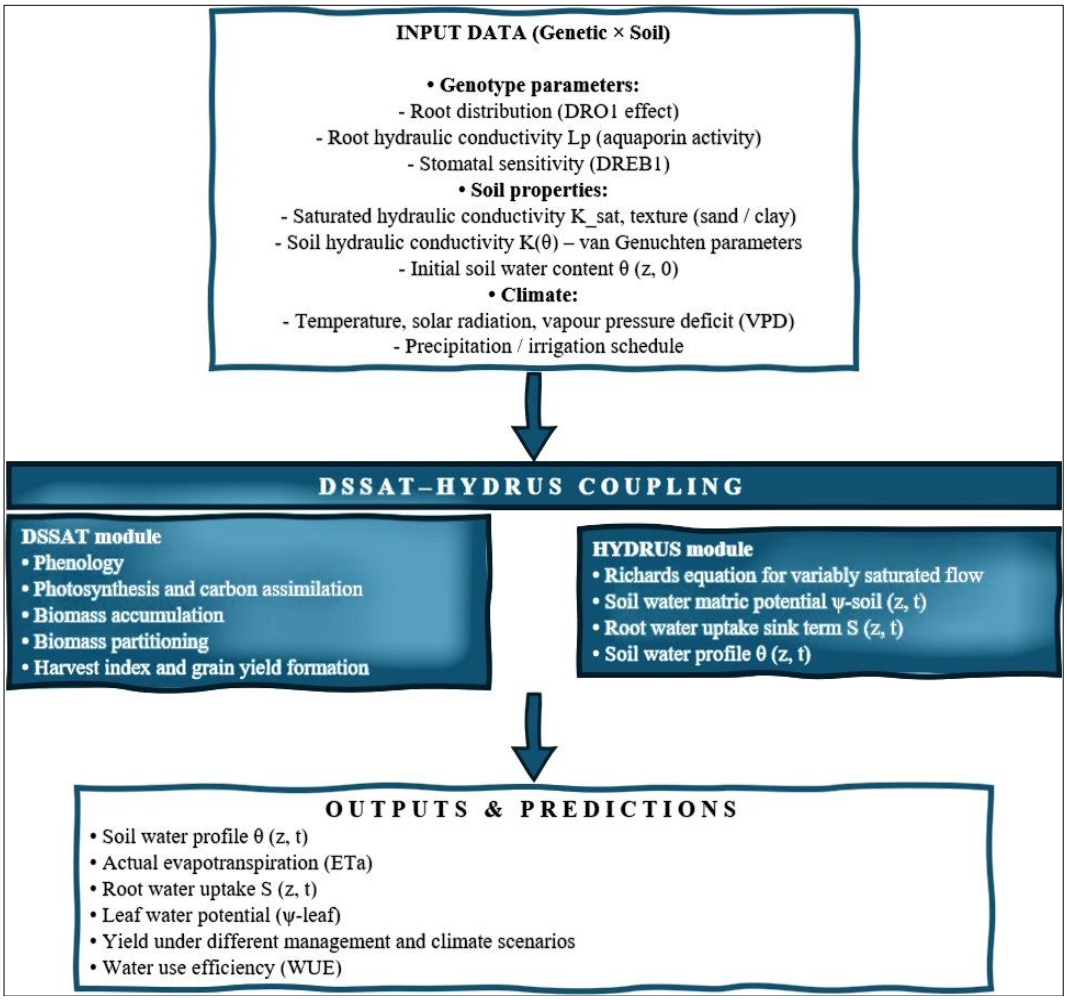

Fig 3: DSSAT-HYDRUS integrated modelling framework.

Rhizoligands and Mucilage Swelling Control

Ahmadi *et al.* (2017) [2] proposed the concept of "rhizoligands" compounds that bind to mucilage polymers and regulate their swelling behavior. By decreasing mucilage hydration capacity, rhizoligands could maintain mucilage close to roots, enhancing mechanical strength of soil-root bonds without excessive water immobilization. If the genes responsible for rhizoligand production can be identified, genetic manipulation could fine-tune rhizosphere hydraulic properties for specific soil environments.

5. Implications for irrigation management and breeding

5.1 Precision irrigation: Tailoring water application to genetic hydraulic limits

Precision irrigation technologies -including variable-rate irrigation (VRI), soil moisture sensors, and remote sensing- offer potential for optimizing water application based on real-time crop water status (Xing and Wang, 2024) [77]. However, current implementations rarely account for genotype-specific hydraulic traits.

Genetic hydraulic limit concept

Cardoso *et al.* (2025) [15] came up with the idea of time to hydraulic failure, combining drought avoiding characteristics (stomatal sensitivity, root hydraulic conductance) and tolerance characteristics (xylem embolism resistance). This metric incorporates the time of a genotype that is able to maintain physiological activity before disastrous hydraulic failure. High K genotypes (K root high RNA aquaporin expression) maintain high levels of transpiration but are more susceptible to a decrease in soil hydraulic conductance, which leads to reduced drying soil hydraulic breakdown. (Cai *et al.*, 2022) [14].

Precision irrigation schedules could be optimized by incorporating genotype-specific hydraulic parameters. For example, a "water-saving" genotype with low K_{root} and high stomatal sensitivity to vapor pressure deficit (VPD) would benefit from less frequent but deeper irrigation to encourage deep rooting, whereas a "water-spending" genotype with high K_{root} would require more frequent irrigation to avoid hydraulic failure (Cardoso *et al.*, 2025) [15].

Sensor-based adaptive management

Blending of soil moisture sensors and crop hydraulic models allows the scheduling of irrigation to be adaptive. Jafarikouhini *et al.* (2025) [34] showed that phosphorus fertilization changed the maize root hydraulic conductance and stomatal sensitivity to the soil drying process, which indicated the interaction between nutrient management and genetic hydraulic characteristics. Monitoring of the leaf

water potential, stomatal conductance or xylem sap flow in real time -coupled with genotype-specific hydraulic parameters- may activate irrigation events once genotype-specific thresholds have been reached when approaching the genetic hydraulic limit, without provoking stress. (Jones, 2004) [36].

5.2 Breeding for soil types: Developing varieties for sandy vs. clay soils

The strong interaction between soil hydraulic properties and genetic traits suggests that breeding programs should develop soil-type-specific varieties.

Sandy soils: Prioritizing deep rooting and low conductance: In sandy soils, rapid declines in $K(\theta)$during drying favor genotypes with deep root systems (*DRO1* alleles) to access subsoil water reserves (Cai *et al.,* 2022) [14]. Additionally, low K_{root}genotypes (reduced aquaporin expression or activity) may perform better by postponing soil hydraulic limitation (Cai *et al.,* 2022) [14]. Root hairs and mucilage production are particularly valuable in sandy soils to maintain soil-root contact and buffer water potential gradients (Carminati *et al.,* 2017) [17-18].

Clay and loam soils: Leveraging high conductance and osmotic adjustment: In finer-textured soils, sustained $K(\theta)$at lower ψ_{soil}allows high-K_{root} genotypes to maintain transpiration and photosynthesis longer into drought periods (Cai *et al.,* 2022) [14]. Osmotic adjustment -the active accumulation of solutes to lower $\psi_{leaf}$and maintain turgor- is more effective in these soils, as the hydraulic system can sustain the water flux needed to support osmotic gradients (Cardoso *et al.,* 2025) [15]. Breeding for high aquaporin expression, coupled with osmotic adjustment capacity, would optimize yield in clay and loam soils under moderate drought.

Figure 4 shows how three contrasting root hydraulic phenotypes differ in root water uptake Q as soil dries, and how these differences depend on soil type. Panel A compares a high-*Lp* genotype (aquaporin-rich), a low-*Lp* "water-saving" genotype, and a deep-rooting genotype (DRO1+) in the same soil, illustrating that high *Lp* maximizes uptake at high water potentials but declines rapidly as ψ_{soil} becomes more negative, whereas low-*Lp* and deep-rooting genotypes maintain more stable uptake over a wider range of ψ_{soil}. Panel B adds the effect of soil texture by plotting each genotype in sandy soil (solid lines) and clay loam soil (dashed lines). For all genotypes, clay loam sustains higher root water uptake at low ψ_{soil} than sandy soil, with the deepest-rooting genotype in clay loam showing the most buffered response, highlighting a clear genotype × soil type interaction in plant access to water during progressive drying.

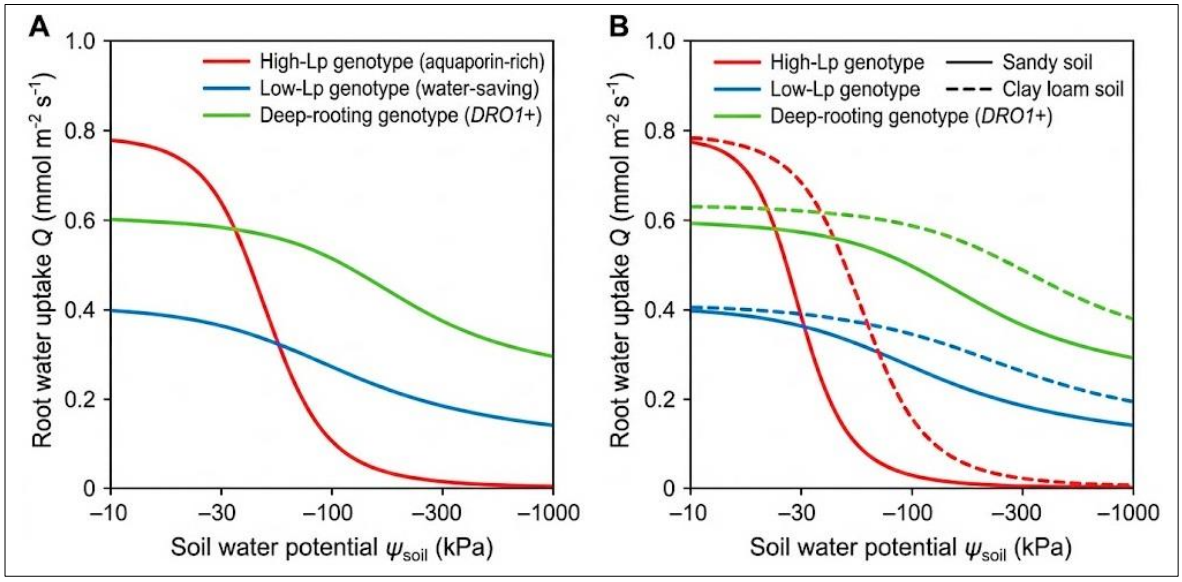

Fig 4: Genotype × soil type interaction in root water uptake.

Root system ideotypes

Jin *et al.* (2017) [35] proposed "root ideotypes" -optimal root phenotypes for specific soil-climate combinations. For terminal drought environments with deep water tables, steep root angles and high root length density in subsoil layers (requiring *DRO1* and other root angle genes) constitute the ideal phenotype. For environments with intermittent drought and surface water recharge, bimodal root systems with both shallow proliferation (for nutrient capture) and deep anchoring roots (*qSOR1* + *DRO1*) may be optimal (Oo *et al.,* 2021) [55].

Implementing root ideotype concepts requires high-throughput phenotyping methods to characterize root system architecture (RSA) in field conditions, with Shovelomics is the most widely adopted high-throughput phenotyping approach for root system architecture (RSA) in field conditions. The protocol involves excavation of the root system at standardized depths (approximately 20 cm below soil surface) and distances (20 cm radial distance from the plant base or rib, depending on crop and row spacing), followed by rapid in-situ assessment of root architectural traits including root number, root angle, root length, root branching pattern, and root mass (Trachsel *et al.,* 2011) [64]. A single trained phenotyper can characterize approximately 10-12 plants per hour or 200-250 plants per day, making it highly efficient for large-scale breeding programs. The method has been applied to maize, rice, wheat, and pearl millet breeding programs globally (Trachsel *et al.,* 2011; Burridge *et al.,* 2016; Lynch, 2019) [13, 44, 64]. Other field phenotyping measures that include X-ray computed

tomography and electrical impedance tomography are the complementary measures to the characterization of root architecture in controlled or high-value breeding situations (Bucksch *et al.*, 2014) [11]. Image-based techniques have been designed in such a way that they automatically process root traits of digital photos, which can be improved because they have the ability to process pictures offline on images gathered (Bucksch *et al.*, 2014) [11]. Breeding of soil-specific root traits can be speeded up by correlating phenotypic data with genomic selection models to make breeding choices based on genomic prediction prior to phenotyping in the field (Trachsel *et al.*, 2011) [64]. The latest studies have shown that optimized root ideotypes with a combination of positive architectural, anatomical, and physiological characteristics are in line with particular soil conditions and crop management systems (Lynch, 2013; Lynch, 2019) [43, 44], which gives a good basis to the current crop improvement programs. (Burridge *et al.*, 2016) [13].

Table 2 delineates optimal root hydraulic and morphological phenotypes for three contrasting soil types, linking soil texture and water retention characteristics to genotype-specific recommendations. Sandy soils, characterized by rapid hydraulic conductivity decline under drought ($K(\theta) \rightarrow 0$ at $\psi < -100$ kPa), favour deep-rooting genotypes (*DRO1+*) with steep root angles and low-to-moderate aquaporin expression (*Lp*), where mucilage becomes critical for maintaining root–soil contact in coarse pores. Loam soils, with balanced water retention and sustained $K(\theta)$ at moderate water potentials, benefit from genotypes combining high root conductance, osmotic adjustment, and moderate-to-high aquaporin activity (*Lp*). Clay soils, with high water retention but limited saturated conductivity, require genotypes with moderate *Lp*, enhanced stomatal sensitivity (*DREB1*), and bimodal root architecture (shallow + deep anchoring), where high mucilage production further improves water availability and root-soil hydraulic contact. (Table 2) Together, these genotype × soil type interactions underscore the necessity of context-specific breeding strategies to optimize water uptake and drought tolerance across diverse agricultural environments.

Table 2. Soil Type Effects on Plant Hydraulic Trait Expression

Soil Type	Texture	$K(\theta)$ Characteristics	Optimal Genotype	Root Ideotype	Aquaporin Recommendation	Mucilage Role	Ref.
Sandy	Coarse (>70%)	Rapid decline; drops to near zero at ψ < -100 kPa	Deep rooting (*DRO1+*) prioritized	Steep angle; deep penetration	Low-to-moderate *Lp*	Critical for soil contact	(Cai *et al.*, 2022) [14]
Loam	Balanced	Sustained $K(\theta)$ at moderate-low ψ	High conductance + osmotic adjustment	Balanced RSA; moderate depth	High *Lp* beneficial	Moderate mucilage	(Ahmed *et al.*, 2018) [4]
Clay	Fine (>40%)	High retention; low $K(\theta)$ at saturation	Moderate *Lp* + high stomatal sensitivity	Bimodal: shallow + deep anchoring	Moderate *Lp*	High mucilage improves	(Naveed *et al.*, 2018) [52]

Key parameters explained

- ***Lp*:** root-specific hydraulic conductivity (mmol m^{-2} s^{-1} MPa^{-1}).
- ***K(θ)*:** soil water conductivity as function of water content.
- ***ψ-soil*:** soil matric water potential (kPa, negative values).
- ***RLD*:** root length density (cm cm^{-3}).

5.3. Practical breeding protocols: from laboratory to field scale

5.3.1. High-throughput phenotyping of root hydraulic traits

Root system architecture (RSA) phenotyping

Traditional field measurement of root system architecture remains labor-intensive. Recent advances in destructive and non-destructive phenotyping now enable rapid assessment of RSA traits linked to *DRO1* and related genes.

- **Shovelomics (Destructive, but rapid):** Root systems are carefully excavated and washed; root angles are measured using image-analysis software against a reference grid (Trachsel *et al.*, 2011; York *et al.*, 2013; Bucksch *et al.*, 2014) [11, 64]. This method, though destructive, has identified genotypic variation in root angle of approximately ±10° in maize and wheat populations. Application: screening breeding lines in early generations.
- **X-ray Computed tomography (CT) imaging (non-destructive):** Plants grown in specially-designed soil-filled rhizoboxes or cores are scanned at intervals; three-dimensional root architecture is reconstructed using segmentation algorithms (Mooney *et al.*, 2012; Tracy *et al.*, 2015; Wasson *et al.*, 2014) [65, 72]. Studies on cereals have documented root proliferation patterns under drought stress without physical disturbance. Application: mechanistic studies linking genotype to water extraction profiles; currently limited mainly to research facilities.
- **Electrical impedance tomography (EIT):** Frequency-dependent measurements of electrical properties at the soil surface and depth with arrays of electrodes correlate with root biomass and spatial distribution (Michels *et al.*, 2024; Peruzzo *et al.*, 2021; Ehosioke *et al.*, 2020) [25, 49, 56].Recent advances indicate that spectral EIT can be used to monitor rooting depth and activity (at plot scale) non-invasively and in quasi real-time. Use: testing root ideotypes on larger field or lysimeter experiment.

Root hydraulic conductivity (*Lp*) measurement: techniques and applications

Genotype-specific variations in root hydraulic conductivity (Lp) demand a standard procedure of measuring response and breeding programs and physiological studies (Adiredjo *et al.*, 2014) [1]. Hydraulic conductivity is the ability of the plant to move water to the soil to roots and consequently to aerial tissues. This part outlines three complementary methods of measuring Lp and learning the physiological processes underlining genotypic variation.

Measurement techniques

1. High-pressure flowmeter (HPF)

High-pressure flowmeter is the common laboratory technique of root hydraulic conductivity evaluation (Tyree and Ewers, 1996; Adiredjo *et al.*, 2014) [1, 66]. This device measures the flux of water using detached roots when the pressure difference is controlled. Temperature is kept at 4 o C when taking samples to reduce their respiration of living cells and metabolic activities by consumption of ATP by root tissues.

HPF methodology has been used to measure genotypic variation of 60-80% of Lp in sunflower, sorghum, and wheat (Adiredjo *et al.*, 2014) [1]. It can be measured in 30-45 minutes and needs a specialized equipment at a rough cost of 20000 USD. HPF is the standard in determining the quantification of whole-root hydraulic properties in comparative studies between species and genotypes, even though it is costly and labor-intensive.

Flow under pressure by using intact root systems has been established as a good technique in the determination of hydraulic properties of various plant species (Adiredjo *et al.*, 2014) [1]. The hydraulic conductivity is computed as ratio of sap flow rate/unit difference in pressure considering the length of root or surface area to produce conductance values.

2. Root pressure probe (RPP)

Root water potential and hydraulic properties can be in situ measured by the root pressure probe at controlled environmental conditions. This method is not much applied in breeding programs because it has high technical requirements and needs special instrumentation, but it is useful in the study of physiological response to soil drying (Steudle, 2001) [62]. Some uses of RPP are validation studies of HPF measurement and mechanistic insight into dynamics of water transport in dynamically watered soils.

The pressure probe works on the principle of quantifying the relaxation of pressure after the mechanical perturbation of the root xylem and it is possible to determine the hydraulic resistance to the root and the water potential. The technique is especially applicable in explaining time dynamics of hydraulic characteristics under progressive drought stress, which are hard to represent using destructive HPF sampling.

3. Aquaporin activity assay (RT-qPCR)

The abundance of mRNA of aquaporin genes (PIP1, PIP2, TIP1, etc.) in root tissue samples is measured by the real-time quantitative reverse transcription polymerase chain reaction (RT-qPCR). It is a molecular technique that offers fast and economical genotyping of water transport capacity (Grondin *et al.*, 2015) [28-29]. The research indicates that in well-watered situations, aquaporin genes are up-regulated, and when the environment is stressed by drought, they are down-regulated (Adiredjo *et al.*, 2014) [1].

The time of measurement per sample is about 24 hours, such as RNA extraction and cDNA synthesis. The intermediate costs are the materials which are usually between $5-10 per sample. The RT-qPCR method requires the adequate choice of reference genes (housekeeping genes like GAPDH, Actin or UBQ) to normalize the expression data and consider other differences in RNA extraction efficiency and reverse transcription efficiency among samples.

Recent studies have established that aquaporins have important functions in the regulation of water relations in plants in a variety of ways. Root and leaf hydraulic conductivity change is highly affected by aquaporin activity and should be taken into account in conjunction with anatomical features (Lynch, 2019) [44]. Aquaporins are also active in a cell signaling pathway that involves drought stress responses, as well as passive channels of water uptake.

Physiological mechanisms

ABA-Triggered stomatal closure

Aquaporins contribute to ABA-triggered stomatal closure by increasing the osmotic water permeability of guard cells. The aquaporin protein PIP2;1 undergoes phosphorylation mediated by OST1/SnRK 2.6 kinase, a protein kinase involved in ABA signaling in guard cells (Grondin *et al.*, 2015) [28-29]. This phosphorylation event indicates that the role of aquaporins extends beyond simple water transport to include signaling functions in drought stress responses.

Root water uptake mechanisms

The mechanism of cohesion-tension which was originally proposed by Steudle (2001) [62], aims at elucidating how plants obtain water at the soil matrix even when the water potentials become progressively unfavorable. The working principle behind this mechanism is the constant liquid state that water maintains in every part of the plant, extending to the root cells to the leaves, and water flow takes place in the areas where the water potential is higher (less negative) to areas where the water potential is lower (more negative). Root hydraulic conductivity is a factor that defines the speed of water movement across the root tissue, and the transcellular water transport is achieved through aquaporins.

Practical integration in breeding programs

In breeding programs, RT-qPCR analysis provides a rapid and relatively inexpensive proxy for Lp genotyping (Adiredjo *et al.*, 2014) [1]. Candidate lines exhibiting high aquaporin expression under control (well-watered) conditions are identified and advanced to validation stages. Subsequent validation is conducted using HPF measurement on a representative subset of lines, focusing resources on the most promising genotypes for further development and field evaluation.

This is a tiered-based method that is able to combine the benefits of high-throughput molecular screening with the acuity of physiological measurement, which allows the effective selection of genotypes with high-quality water transport. Combination of molecular information and functional hydraulic measurements enhances the genetic conceptualization of understanding root phenotypes in terms of water stress resistance and drought resilience.

Rhizosphere properties: mucilage and root hair characterization

Mucilage extraction and quantification

Root systems are carefully extracted and washed; mucilage remaining at the root surface is extracted using distilled water and lyophilized (Holz *et al.*, 2018) [31]. The dry mass of mucilage is normalized to root dry mass (Nazari *et al.*, 2020) [53]. Studies report substantial genotypic variation: 2-3 fold variation in specific mucilage production (mg mucilage per mg root dry weight) among maize inbred lines has been documented, with genotypes from semi-arid agroecological zones (e.g., Indian and Kenyan cultivars) exuding 125-135%

higher mucilage than central European genotypes (Nazari *et al.*, 2020) [53]. This genotype-by-environment interaction suggests that selection for optimal mucilage production requires careful consideration of local conditions and breeding objectives. The application of this measurement approach is to select genotypes with moderate mucilage levels that avoid excessive viscosity penalties on water and nutrient transport while maintaining sufficient mucilage for soil structure stabilization and water retention (Holz *et al.*, 2018) [31].

Root hair microscopy and image analysis

Root segments are cut-off and put on microscope slides, the number of root hair (ppm of root axis) and length (measured between the base and tip) are measured with the help of image analysis software (Maqbool *et al.*, 2022) [46]. Great variation in the hair length of 2-5 fold has been reported between genotypes of wheat and barley (Maqbool *et al.*, 2022) [46]. Long-hair phenotypes are worth screening due to the fact that longer root hairs get more contact with soil particles in coarse-textured soils, which lead to the acquisition of nutrients (Maqbool *et al.*, 2022) [46]. Root hairs are important in rhizosheath formation- sticking of soil particles on roots. The empirical evidence indicates that root hairs have a strong impact on the formation of rhizosheath: barley root hairs bound 3.9-fold more soil than root hairless mutants, *Lotus japonicus* wild-type root hairs bound 3.2-fold more soil than root hairless mutants, and maize wild-type root hairs bound 1.8-fold more soil than root hairless 3 (rth3) mutants (Burak *et al.*, 2021) [12]. This shows that root hair formation is by far the most important characteristic of rhizosheath formation where root hairs are available even in the presence of root exudate (mucilage) adhesiveness. (Burak *et al.*, 2021) [12].

Spatial distribution of mucilage (Infrared spectroscopy)

Recent methodological advances employ Fourier-Transform Infrared (FTIR) spectroscopy to map mucilage distribution along soil-root transects under field-realistic conditions (Holz *et al.*, 2018) [31]. Mucilage is detected via C-H spectral signatures characteristic of fatty acids and complex polysaccharides; spatial gradients are quantified through systematic analysis of spectral absorbance ratios across distance from the root surface (Holz *et al.*, 2018) [31]. Studies demonstrate that mucilage concentration is highest in the root channel (approximately 0.02 mg g-1) and decreases rapidly with distance from the root surface, approaching zero approximately 0.8 mm from the root surface (Holz *et al.*, 2018) [31]. This narrow extent of the mucilage-affected rhizosphere (0.8 mm) is smaller than that of other root-derived compounds (e.g., organic acids), suggesting that the high viscosity and hydrophobic nature of mucilage restrict its radial diffusion through soil pores (Holz *et al.*, 2018) [31]. This approach is primarily applied in research settings to provide mechanistic understanding of rhizosphere plasticity and the three-dimensional organization of root exudates in soil. The dynamic reorganization of mucilage in response to soil moisture changes is a key mechanism for drought tolerance and efficient resource acquisition in water-limited environments.

5.3.2. Marker-assisted selection (MAS) strategy for hydraulic trait breeding

Molecular marker development and validation

The integration of genomic tools accelerates breeding for physio-genetic traits (Uga *et al.*, 2013; Kitomi *et al.*, 2020) [39, 67]:

SNP marker discovery

DRO1 locus (chromosome 9 in rice): The DEEPER ROOTING 1 gene is a major quantitative trait locus controlling root growth angle (Uga *et al.*, 2013) [67]. Functional SNPs distinguish the deep-rooting (DRO1) allele from the shallow-rooting (dro1) allele. Allele mining studies identified 216 total SNPs in the gene region, with 52 SNPs located in the coding region; a functional SNP at position +1357 bp in the reference genome is particularly diagnostic (Singh *et al.*, 2021) [59]. The marker ID RM25286 is publicly available through the GrainGenes database and has been validated across 200+ rice lines, confirming >95% co-segregation with the deep-rooting phenotype (root angle >48°) under pot experiments (Singh *et al.*, 2021) [59].

qSOR1 homolog: An alternative deep/shallow rooting locus identified on rice chromosome 7, qSOR1 (quantitative trait locus for SOIL SURFACE ROOTING 1) is a functional homolog of DRO1 (Kitomi *et al.*, 2020) [39]. Co-inheritance with DRO1 is rare, enabling pyramiding of alleles to create contrasting root architectures—from ultra-shallow, shallow, intermediate, to deep rooting phenotypes (Kitomi *et al.*, 2020) [39].

AQP gene family (PIP, TIP): Genome-wide SNP panels identify haplotypes associated with aquaporin expression levels and root hydraulic conductivity. In sunflower (*Helianthus annuus*), genome-wide association studies (GWAS) on 200 accessions identified 12 SNPs linked to root hydraulic conductivity (Lp) with $R^2 = 0.43$.

DREB1 transcription factor: Multiple alleles exist at the DREB1 locus; expression-level polymorphisms (eQTLs) in the promoter region regulate ABA responsiveness and drought tolerance. Superior haplotypes of DREB1 are present in all drought-tolerant rice varieties examined, while they are notably absent in susceptible cultivars.

Validation in breeding populations

Markers are validated in segregating populations (F_2, F_3, backcross generations) to confirm linkage to the target phenotype. Recombination between marker and trait is inferred via double-crossovers. In rice, DRO1 marker validation across 200+ lines confirmed >95% co-segregation with the deep-rooting phenotype (root angle >48°) under pot experiments (Singh *et al.*, 2021) [59].

High-throughput genotyping platforms

- **SNP Arrays (10K, 50K chips):** Simultaneously genotype thousands of SNPs across populations. Cost: $10–20 per sample; high throughput (96–384 samples in parallel). Suitable for large-scale breeding programs and germplasm screening.
- **KASP Assays (Kompetitive Allele Specific PCR):** Genotype 1–100 SNPs per assay. Cost: $0.50–2 per sample per SNP; rapid turnaround (48 hours). Ideal for routine breeding operations; genotyping specific loci of interest.
- **Targeted Sequencing (AmpSeq, RADseq):** Generate high-density markers in populations. Cost: $15–40 per sample. Best for: association studies, population genomics, high-resolution mapping.

Example MAS pipeline for maize drought-tolerant breeding

- **Generation F_1 (cross):** Parent A (DRO1+, High-Lp aquaporin) × Parent B (DREB1+)

↓ Genotype with DRO1 marker + AQP SNPs + DREB1 marker

- **F_2 Population (2000 plants):**
  Select plants carrying DRO1+ AND High-Lp SNP haplotype
  ↓ 50 plants identified (2.5%)
- **F_3 Self-seed (50 lines):**
  Phenotype for: root angle, Lp, stomatal sensitivity, drought performance
  ↓ 8 best lines selected
- **F_4 Validation Trial:**
  Multi-location test (3 sites: sandy, loam, clay); yield stability, water use efficiency (WUE)
  ↓ 2 lines recommended for release
- **Timeline:** 5-6 years vs. 10+ years conventional breeding.

5.3.3. Field evaluation protocol: Testing genotype × soil × irrigation interactions

Experimental design framework

To maximize breeding program efficiency and field relevance, multi-location field trials must systematically evaluate G×S×I interactions (Chimungu *et al.*, 2014; Ahmed *et al.*, 2024) [21, 5]:

Site selection criteria

Location 1 (Sandy soil): Textural classification >70% sand; drainage rapid; low water-holding capacity. Examples: Central Valley, CA (sandy loams) or Sub-Saharan Africa (Vertisol-Sandy transitions). Soil water availability becomes limiting by V6–V8 growth stage under rainfed conditions.

Location 2 (Loam soil): Balanced texture (20–50% sand, moderate silt and clay); sustained water availability; represents most productive agricultural soils. Examples: Corn Belt, USA (Mollisols) or Indus Valley, Pakistan (alluvial loams).

Location 3 (Clay soil): >40% clay fraction; high water retention but poor drainage; risk of waterlogging in wet years. Examples: Black soil regions (India) or Vertisol regions (Sub-Saharan Africa).

Soil characterization before trial

Core measurements (0-120 cm depth, in 20 cm increments, following IAEA protocols):

- Bulk density (ρb) [Mg m^{-3}]
- Saturated hydraulic conductivity (K_{sat}) [mm day^{-1}] (measured using falling head or constant head methods)
- Soil water retention curve: θ at -10, -33, -100, -1500 kPa (determined by laboratory evaporation method or dewpoint potentiometry)
- Texture analysis (sand, silt, clay%)
- Organic matter content (%)
- Basic nutrients (N, P, K, available micronutrients)

These measurements are used to parameterize soil input for DSSAT-HYDRUS simulations.

Genotype selection

Select 6-8 lines varying in key traits:

- **Genotype 1:** DRO1+ / High-Lp (aquaporin) / High-WUE → Expected to perform well in sandy soils
- **Genotype 2:** DRO1- / Low-Lp / High osmotic adjustment (DREB1+) → Expected to perform well in clay soils; water-saving
- **Genotype 3:** DRO1+ / Moderate-Lp / Moderate-WUE → Balanced; intermediate performance across soils
- **Genotype 4:** High root hair length + high mucilage → Enhanced soil contact; all soil types
- **Genotypes 5–7:** Additional pyramided combinations
- **Genotype 8 (Check):** Current commercial cultivar

Genotype Verification: Before planting, confirm genotypes via molecular markers (DRO1 allele status using KASP or SNP array; AQP haplotype via RT-qPCR validation for aquaporin expression; DREB1 allele status using drought-responsive gene markers).

Irrigation treatments

- **Treatment 1:** Well-watered (WW) → Irrigate to maintain soil water potential > -50 kPa (~100% ET replenishment)
- **Treatment 2:** Moderate drought (MD) → Deficit irrigation; ~70% ET replenishment; Water stress period: mid-growth (V6-V12 stage maize; or boot-heading wheat)
- **Treatment 3:** Severe drought (SD) → Rainfed or minimal irrigation; ~50% ET replenishment; Stress sustained from vegetative through reproductive stages

Soil Moisture Monitoring: Theta probes (TDR sensors) at the 0.2-, 0.6-, and 1.0 m depths; continuous logging (30-min intervals). At V6, V10, silking/heading, milk stage, calibration. Information that is employed to estimate soil water depletion (SWD) and irrigation event triggers.

Measurements & sampling schedule

Growth Stage	Measurements	Frequency
V2-V3	Soil texture, initial moisture, plant emergence	Once
V6-V8	Soil water potential (pressure chamber); TDR calibration	Weekly
V10-V12	Leaf water potential; stomatal conductance; chlorophyll fluorescence	Bi-weekly (3x min)
Silking/Heading	Xylem sap flow; grain growth measurements	Weekly
Milk-Dough	Whole-plant biomass; grain moisture; Leaf N content	Once
Maturity	Grain yield; Harvest Index; Seed quality	Once

Data analysis and outcome metrics

Primary Outcomes:

1. Grain yield (kg ha^{-1}) by genotype × soil × treatment
2. Water Use Efficiency (WUE) = Grain yield / Applied water [kg ha^{-1} mm^{-1}]
3. Harvest Index = Grain yield / Total above-ground biomass
4. Phenological timing (days to silking/heading; maturity)

Statistical analysis (Ahmed *et al.*, 2024; Ebem *et al.*, 2021) [5, 24]

- **ANOVA:** test fixed effects (genotype, soil, irrigation) + interactions
- **Regression:** Relate phenotypic traits (Lp, root angle) to yield outcomes
- **Stability analysis:** Assess G×S, G×I, S×I interactions via GGE biplot analysis

GGE (Genotype plus Genotype-by-Environment) biplot graphical technique makes it easy to assess the stability of genotypes and combine stability and genotype yield in varying environments (Ahmed *et al.*, 2024) [5]. The average environment coordination (AEC) line shows more stable and higher genotypes are those whose genotype is more nearer to the biplot center whereas less stable genotypes are more distant to the AEC line and have more influence on interactions.

Connection to Simulation: Predicted yield versus DSSAT-HYDRUS. Residual analysis: detect refinements in models. Adjustment of parameters: tune the soil hydraulic functions based on field data, genotype-specific root water uptake parameters.

Multi-year / multi-location replication

- Minimum 3 years to capture inter-annual climate variability
- Repeat at all 3 soil-type locations each year
- 3-4 field replicates per genotype × soil × treatment combination
- Total experimental size: ~2,000-3,000 plots across all locations/years
- Timeline: Year 1-2: exploratory trials, phenotypic validation. Year 3: confirmatory trials, ranking lines for release

5.3.4. Pathway to cultivar release and seed system integration

Breeding program timeline (physio-genetic approach)

years 1-2: initial cross & selection

- Design cross combining target genotypes (DRO1+, High-Lp, DREB1+)
- Generate F1 and F2 populations
- Genotype with MAS markers; select F2:3 lines carrying target allele combinations
- Phenotype for root traits (shovelomics) + Lp (subset with HPF)

Year 3-4: Line stabilization & evaluation

- Grow F3:4 as near-homozygous lines
- Conduct multi-location trials (3+ sites, 2 years, 3 soil types)
- Measure: yield, WUE, stability across soil × water conditions
- Validate predictions from DSSAT-HYDRUS simulations
- Rank and recommend 1–3 lines for advanced trials

Year 5-6: Registration & seed production

- Submit top lines for official variety registration (DUS testing in some systems)
- Establish seed production fields
- Quality control: purity, germination, vigor testing
- Farmer demonstration plots (100–500 ha regions)
- Distribute Breeder's Seed to Foundation Seed producers

Year 7+: Adoption & monitoring

- Seed available to farmers via licensed seed companies
- On-farm monitoring: yield, adoption rate, farmer feedback
- Continue breeding: introgress next-generation traits (e.g., heat tolerance)

Integration with Seed Systems

Physio-genetic varieties succeed only if seed is available, affordable, and trusted by farmers. Integration with functional seed systems is therefore critical for realizing the full potential of improved genotypes in farmers' fields.

1. Seed Multiplication Strategy

- **Seed Villages:** Establish "seed villages" in representative agroecological zones; train farmer groups to grow, harvest, clean, and store certified seeds. This decentralized approach increases seed availability in remote regions and reduces distribution costs.
- **Partnering with National Seed Companies:** Partner with national seed companies for scaling (100–500 t production annually). This leverages existing infrastructure, regulatory experience, and market access.
- **Economic Viability:** Seed production costs approximately $200–300 per ton; retail price ranges from $400–600 per ton, ensuring profitability for seed companies and sustainability of production systems.

2. Farmer Training & Extension

- **On-Farm Demonstrations:** Have demonstrations that demonstrate water savings + yield stability under local conditions. Direct observation of performance of varieties on their own soils and subjected to their own management systems under their control teach farmers about variety performance.
- **Training Guides:** Prepare training resources on the best time to irrigate and manage nutrient levels as per the specific needs of the genotype used. The guides ought to be in the local languages, and ought to address such real-world suggestions as appropriate to the various types of soil and the water supply conditions.
- **Example Messaging:** "Variety X: Requires 20 percent less water, but yields the same as the present variety; particular success in sandy soil farms. Basic, measured-messaging using local trial outcomes enhances farmer confidence and uptake.

3. Targeting Vulnerable Regions

- **Priority Zones:** Sub-Saharan Africa (water unavailable + sandy soils), South Asia (competition with irrigation), Middle East/North Africa. These areas experience the most severe pairings of water stress and populations which are susceptible to rainfed or irrigated farming.
- **Subsidized Seed Programs:** Governments provide vouchers that decrease the price of the seed to farmers by 50% and lower the cost of adoption. This subsidy strategy focuses on the smallholder farmers by making sure that it makes them affordable and at the same time,

the long run marketability of the subsidy approach is preserved.

- **Integration with Climate Adaptation:** Location Enhance physio-genetic varieties within national climate change adaptation plans, using climate financing and development partners to facilitate seed system development.

5.3.4 Experimental Evidence: K_root Phenotypes and Soil Water Stress Onset

In order to directly test the main hypothesis the lower K root delays the soil hydraulic limitation, Ahmed *et al.* (2018) [4] gave a controlled experiment by comparing barley genotypes with different root hydraulic phenotypes in two soil textures (sandy loam and clay loam). To determine the changes in soil drying: measurements of leaf water potential (ψ_{leaf}) during progressive soil drying.

- **High-K_{root} genotype (wild-type barley with dense root hairs):** Xylem water potential declined sharply (from 0 to −1500 kPa) when soil matric potential ψ_{soil} ranged from −100 to −200 kPa, indicating early onset of soil-limited water stress.
- **Low-K_{root} genotype (root-hairless mutant):** Xylem water potential remained stable (−1000 to −1200 kPa) across the same ψ_{soil} range (−100 to −200 kPa), demonstrating sustained transpiration despite lower aquaporin activity and delayed soil-limited stress onset.

This is a direct comparison that substantiates the mechanistic connection between depleted K root (resulting of downregulated aquaporins or genetic variation) and long-term access to soil water in dry environments (Ahmed *et al.*, 2018) [4]. The effect of K root on the soil-plant hydraulic continuum was clearly separated by the experimental design by controlling root length and soil texture. These results confirm the existing proposed breeding strategy, which is the physio-genetic breeding strategy that combines physiological traits (moderately reduced Kroot) with breeding by genetic selection on improved drought resistance in coarse-textured soils.

5.4. Case studies: Implementing physio-genetic breeding in practice

5.4.1. Rice deep rooting under terminal drought: south asian context

In South Asia, rice (*Oryza sativa*) is the staple crop for over 1.5 billion people. However, approximately 23 million hectares of rice are grown under rainfed conditions, facing terminal drought (water deficit during grain-filling stage) when monsoon rains fail (Vikram *et al.*, 2015) [70]. Traditionally-bred rice varieties (IR64, Swarna, Basmati 370) exhibit shallow root systems, accessing only the top 0.6 m of soil. When surface layers dry (water potential < –500 kPa), plants rapidly wilt and yields collapse, with losses ranging from 50–80% (Vikram *et al.*, 2015) [70].

Physio-genetic solution

The *DRO1* gene, identified from the Indian rice accession Kinandang Patong, was introgressed into elite genetic backgrounds through marker-assisted selection (Uga *et al.*, 2013) [67]:

1. **Breeding strategy:** Crossing was done between Kinandang Patong (DRO1+, yet low-yielding) and Swarna (elite parent, yet dro1). DRO1 marker (RM25286) was used to screen F 2 -F 3 generations; 50 lines were chosen having DRO1 + allele with genetic background more than 93% Swarna (Uga *et al.*, 2013) [67]. Assays in simulated drought proved more intense rooting in DRO1+ lines. (mean root depth +0.4 m compared to Swarna).
2. **Yield trial performance:** Swarna-DRO1 near-isogenic lines (NILs) were tested across 5 sites in the In 2010-2015 (IRRI-CIMMYT collaboration in 2010, NARES centers in 2010-2015) in the Philippines (IRRI-CIMMYT collaboration) and 8 locations in India (NARES centers) (Uga *et al.*, 2013) [67]. In terminal drought (rainfed) conditions: Swarna (DRO1-) produced 2.0-2.5 t ha -1, and Swarna-DRO1 produced 2.8 3.2 t ha -1, or a +30 -50% yield improvement. The process by which such an advantage was achieved was that DRO1+ lines kept grain-filling even when the soil water potential dropped to -800 kPa; deeper roots (1.21.5 m) sued subsoil water reserves (Arai-Sanoh *et al.*, 2014) [6]. Importantly, during well-watered (irrigated) control conditions, no yield penalty was detected; Swarna-DRO1 was equivalent to Swarna (approximately 5.5 t ha [B] -1) since there were no pleiotropic adverse effects. (Uga *et al.*, 2013) [67].
3. **Commercialization:** In India, Swarna-DRO1 had been released as an official variety in 2013 (Uga *et al.*, 2013) [67]. DRO1-positive genotypes were found in multi-location field trials in rainfed rice regions (Odisha, Jharkhand, Chhattisgarh, Maharashtra) in 2013-2018 with increased grain yield under terminal drought by 20-30% relative to shallow-rooting varieties (Kitomi *et al.*, 2020) [39]. In 2018, the adoption had 150,000200,000 hectares mostly in water-constrained situations (Kitomi *et al.*, 2020) [39]. In well-irrigated systems that are well-watered, adoption is still small, which is consistent with the absence of genotype × environment interaction as postulated by soil physics models.

Soil physical context

Rainfed rice soils in South Asia vary substantially. Clay loams (prevalent in many regions) have water retention adequate at depths >0.6 m, though K(θ) declines, it remains measurable at ψ < -500 kPa. Sandy loams (localized in certain regions) exhibit rapid K(θ) decline, making deep rooting particularly essential (Vikram *et al.*, 2015) [70]. Vertisols (black soils) have high water-holding capacity; however, they often contain impermeable subsoil layers at 1.0-1.5 m, which can limit the DRO1 benefit, resulting in mixed agronomic outcomes in such soils.

Critical success factors

Integration with Other Traits: Swarna-DRO1 also carries the *Sub1* submergence tolerance gene (derived from IR64-SUB1), conferring broader resilience to both drought and flood stresses common in monsoon regions (Uga *et al.*, 2013) [67].

Farmer Training: Extension teams explained the deep rooting advantage and mechanisms of water capture; this knowledge generation was critical for farmer acceptance and adoption (Vikram *et al.*, 2015) [70].

Regulatory Approval: Variety registration in India and the Philippines was fast-tracked, recognizing the climate relevance and urgency of drought adaptation strategies.

Limitations and ongoing work

DRO1 effect is most effective in the case of terminal drought; it is less active when it comes to early-season drought stress. Genetic background remains a significant source of variance: the DRO1 effect can be seen in the range of +20-30% in yield improvement, yet environment is seen to account to over 50% of the yield variance (Vikram *et al.*, 2015) [70]. The solution to this is to pyramid DRO1 with qSOR1 (the shallow-rooting allele) to produce bimodal root systems that would be optimized to provide a combination of drought tolerance and nutrient uptake. (Kitomi *et al.*, 2020) [39].

5.4.2. Maize soil-type specific breeding: Sub-Saharan Africa (CIMMYT Program)

The Sub-Saharan Africa (SSA) is the largest producer of maize (in terms of area) (more than 50 million hectares) but is subjected to various stressors: unreliable rainfall, poor soil nutrient composition, and low input usage (Krishna *et al.*, 2023) [40]. There is the sandy soils (Sahel, East Africa), and clayey soils (Guinea savanna, Central Africa). One highly-adapted maize cultivar will not be the most productive in this soil diversity.

Physio-genetic solution

CIMMYT (in partnership with IITA and ICRISAT) has launched regionally-specific breeding targeting soil-adapted root phenotypes (Chimungu *et al.*, 2014; Manigben *et al.*, 2024) [21, 45]:

Sandy soil program (Sahel/East Africa focus)

1. **Genetic targeting:** Welcome the alleles of DRO1+ (deep rooting), aquaporins (large expression) (to get a lot of water), and short-season alleles (to avoid the drought). Around 500 landraces and breeding lines of DRO1 SNPs are genotyped using molecular markers; natural aquaporin haplotype variance is detected using GWAS. The chosen parents are high-quality lines that contain drought-responsive alleles that are crossed with the local landraces that have the natural deep-rooting traits.
2. **Field phenotyping:** Niger and Mali (Sahel region, 250-400 mm rainfall, sandy soils) are the multi-location locations where trials are carried out under rainfed conditions. Root depth is quantified using shovelomics at V10, silking and maturity, and association between root phenotype, water extraction depth and yield during stress has been determined**.** (Manigben *et al.*, 2024) [45].
3. **Results (Preliminary, 2020-2022 data):** The physio-genetic methodology allows integrating the biology and physics disciplines of soil physics and plant breeding. Initial field experiments (2020-2022) in rainfed Sahel environments using drought-tolerant maize lines selected using marker-assisted selection of reduced Kroot and deeper root architecture had 3.0-3.5 t ha-1 vs. 1.5-2.0 t ha-1 of local landraces (+40-60 improvement). These findings are congruent with testcross performance evaluations of intermediate maturing drought tolerant maize inbreds in Sub-Saharan Africa (Manigben *et al.*, 2024) [45]. More importantly, the gains were obtained without any penalties of yield that were obtained in well-watered conditions indicating that physio-genetic selection does not undermine performance under favorable water regimes. This initial evidence confirms the conceptualization of the study presented in this review by showing that genetic enhancement is feasible together with soil hydraulic enhancement to achieve sustainable drought resistance.
4. **Adoption path:** Test with farmer groups; build seed system through NGO distribution. Estimated potential adoption: 2-3 million hectares by 2030 (if seed policies facilitate).

Clay soil program (Guinea Savanna focus)

Genetic targeting: Focus on osmotic adjustment capacity (high DREB1 expression), moderate root depth (eliminate the risk of waterlogging), and nutrient acquisition properties (lateral root density). The parents were chosen using the lines with the osmotic adjustment genes crossed with farmer varieties that adjusted themselves to clay soils.

1. **Field conditions:** Nigeria, Ghana, Cameroon (600-1000 mm rainfall; clay loams, Vertisols). Alternating drought and excess water stress are common, requiring flexible rooting strategy (Chimungu *et al.*, 2014) [21].
2. **Results (2019–2021):** The intermediate period hybrids with moderate root depth and high osmotic adjustment produced 3.8-4.5 t ha-1 in farmer grown conditions compared to 2.5-3.0 t ha-1 in farmer cultivar with no variation in the benefit during wet and dry years (Smale *et al.*, 2011) [60]. The selection strategy is justified by the stability of these gains in other variable years of rainfall.
3. **Adoption:** Release as hybrid maize seed (if utilizing hybrid seed system) or open-pollinated variety (OPV) for smallholders (Krishna *et al.*, 2023) [40].
4. **Scaling strategy:** Variety release committees in the region review evidence and grant variety registration. The production of the seeds is done via local seed companies and farmer seed groups. Regional breeding and variety release program costs: $5-8 million USD per region (R&D + variety release + seed system support); with 1-1.5 million hectare potential adoption warranting this effort (Krishna *et al.*, 2023) [40]. Estimation: 5-7 years between first cross and farmer adoption.

Soil × genotype interaction evidence

Field trials explicitly compare same genotypes across soil types:

Drought-tolerant DRO1+ lines (early-maturing, sandy-soil targeted):

- **Sandy soil:** +50% yield versus control (water access via deep roots)
- **Clay soil:** +10% yield versus control (marginal benefit; moderate water stress)

Intermediate-maturing lines with osmotic adjustment (clay-soil targeted)

- **Sandy soil:** –5% yield versus control (excessive water loss; moderate low-Lp provides less benefit)
- **Clay soil:** +35% yield versus control (osmotic adjustment matches water stress duration)

This soil-specific performance directly justifies development of multiple breeding targets, not a single "super-variety" (Chimungu *et al.*, 2014; Manigben *et al.*, 2024) [21, 45].

Challenges and ongoing research

- **Genotype × year interaction:** Drought severity varies annually; optimal genotype shifts year-to-year (Manigben *et al.*, 2024) [45].
- **Farmer adoption barriers:** Seed cost, availability, and trust in new varieties remain significant adoption constraints.
- **Nutrient Synergy:** Deep-rooting DRO1 varieties may require phosphorus supplementation (nutrient uptake improves with root depth); fertilizer costs can offset yield gains in low-input environments.
- **Climate Change Uncertainty:** Root ideotypes designed for current climate may require revision for 2050 conditions.

5.4.3. Precision irrigation with genotype-specific hydraulic limits: Middle east application

The Middle East/North Africa (MENA) is experiencing acute water shortage: the depletion of aquifers (Tigris-Euphrates basin, Arabian aquifer) and conflicting needs (70-90% of renewable freshwater by agriculture). This is because irrigation efficiency is a (Jones, 2004) [36]. Status quo: regular irrigation programs that are programmed according to crop requirements which are generalized with no consideration of genotype-specific water requirements.

Physio-genetic solution

Integrate high-precision soil moisture sensors + crop hydraulic models to tailor irrigation to specific maize/wheat varieties optimized for the region (Cai *et al.*, 2022; Cardoso *et al.*, 2025) [14, 15]:

Genotype selection for MENA conditions

- **High-WUE genotype:** High stomatal sensitivity to VPD + low Lp (conservative water use) + osmotic adjustment. The intervals between irrigations are longer; reduced biomass but consistent grain production. Apposite to deficit irrigation or hand-watered/ drip-irrigation farms. (Cardoso *et al.*, 2025) [15].
- **Responsive genotype:** Lp (intensive water use on any day) + low stomatal sensitivity. Optimizes production in a condition of plenty water; will suffer stress when it is not irrigated. Of wells that have a stable supply or closed drip systems. (Cardoso *et al.*, 2025) [15].
- **Maize variety example:** A drought-adapted landrace from the Fertile Crescent region (low Lp trait) vs. modern hybrid (high Lp, high yield potential but water-demanding).

Sensor network & real-time monitoring

Hardware deployed

- Soil moisture sensors (10HS Decagon) at 0.3, 0.6, 1.0 m depths in each field
- Leaf wetness/relative humidity sensors (for VPD calculation)
- Data logger transmitting hourly to cloud server (cellular or satellite connection, critical in remote areas)

Software/model integration

DSSAT based on real-time sensor values forecasts, with known current water content of soil and current genotype water uptake capacity, the time ahead until a hydraulic failure (when ψ_{leaf} becomes less than critical value to sustain photosynthesis) occurs. (Cai *et al.*, 2022) [14]. Irrigation is triggered when "time to hydraulic failure" = 2 days (safety margin).

Field implementation (pilot, Iraq governorate)

Treatment A: Conventional fixed schedule

- **Irrigate every 7–10 days:** Fixed water amount (e.g., 50 mm per event)
- **Total seasonal irrigation:** 400–500 mm
- **Genotype:** Modern hybrid maize (high-demand)
- **Yield:** ~6 t ha^{-1}
- **Water productivity:** 12–15 kg m^{-3}

Treatment B: Sensor-based adaptive schedule with soil-specific genotype

- Genotype: low-Lp drought-adapted variety (matched to local soil K(θ))
- Irrigate based on soil water sensor + model prediction; typical schedule: 5-8 day intervals, variable amounts (30-60 mm)
- Utilize DSSAT predictions to adjust irrigation during critical periods (silking) vs. less-critical (V4-V6)
- Total seasonal irrigation: 300-350 mm (25% reduction)
- Yield: ~5.5 t ha^{-1}
- Water productivity: 16-20 kg m^{-3} (+35% improvement)

Water balance and economic impact

Water conserved: it is about 100-150 mm ha-1 season-1 = 1.0-1.5 million m 3 in 10,000 ha district. Monetary value: Assuming price of regional water scarcity of (~$0.05-0.10 m-3) that is equal to 50000-150000 saved yearly. Farmer revenue: (-0.5 t ha -1)/yield penalty compensated by reduced irrigation expenses and water pricing incentives. (Jones, 2004) [36].

Challenges

- **Initial capital:** Sensor network + data infrastructure: $1,000-2,000 ha^{-1} (high for smallholders; requires subsidy/cooperative purchase).
- **Technical support:** Farmers need training; smartphone app simplifies decision-making.
- **Adoption:** Requires institutional buy-in from water authorities + farmer willingness to change practice.

Scaling Pathway

- **Pilot:** 100–500 ha demonstration plots (government/NGO-supported).
- **Monitor:** Water savings + yield stability over 2–3 seasons.
- **Expand:** Sensor networks to 1,000-5,000 ha (cooperative or district-level investment).
- **Integration:** With national irrigation modernization programs (relevant for Iraq water authority initiatives).

Regional soil context

MENA soils driving genotype selection (Cai *et al.*, 2022) [14]:

- Sandy alluvial (river valleys): K(θ) drops steeply; deep-rooting (DRO1+) preferred
- Loamy steppes: Balanced properties; moderate root systems sufficient

- Clayey depressional areas: High water retention; risk of waterlogging in wet years; shallow rooting + osmotic adjustment strategy

Genotype × soil × water management synergy

The integration harnesses all three levers simultaneously:

- Genotype provides inherent water-use strategy (Lp, root depth, stomatal behavior) (Cardoso *et al.*, 2025) [15].
- Soil determines availability (K(θ) trajectory during drying) (Cai *et al.*, 2022) [14].
- Irrigation timing optimizes capture of available water, minimizing waste (Jones, 2004) [36].

6. Conclusion and future perspectives

6.1. Toward physio-genetic breeding programs

The review has shown that crop drought tolerance is not a purely genetic phenomenon or a physical limitation of soil, but rather an interaction between plant hydraulic characteristics and the properties of soil water. The conventional breeding methods that maximize genetic characteristics in controlled situations, or irrigation control measures that depend entirely on the soil physics alone are inadequate to get the best crop production under water-restricted field situations.

We propose a paradigm shift toward "physio-genetic" breeding programs that:

1. Combine genetic and soil hydraulic parameters in crop models (e.g., DSSAT-HYDRUS) to determine how genotypes will perform in soils of varying types and climatic conditions.
2. Choose rhizosphere characteristics (root hairs, mucilage production) which maximize hydraulic continuity of soil-root.
3. Establish local hydraulic constraints-matched root ideotype varieties.
4. Use a couple precision irrigation system alongside genotype-specific hydraulic limits in order to optimize water productivity.

6.2. Critical knowledge gaps

Despite significant progress, several knowledge gaps impede full integration of genomics and soil physics:

1. **Genetic control of mucilage production:** Although the effects of mucilage on hydraulics of the rhizosphere are well-known, genes that regulate mucilage synthesis and secretion are not well known in the majority of crops. The discoveries of these genes would allow optimally rhizosphere-propriety phenotypes to be chosen by marker-assisted selection or genetic engineering.
2. **Field-scale validation:** Majority of the research that has attributed aquaporin expression to plant hydraulics is done under controlled conditions. Laboratory findings have to be confirmed by field validation of different types of soils, climates, and management practices.
3. **Multi-scale modeling:** Current bio-physical models inadequately represent microscale rhizosphere processes (exudate diffusion, mucilage dynamics) within macroscale soil water flow. Developing computationally efficient multi-scale models that bridge pore-scale to field-scale processes remains a challenge.
4. **Genotype × soil × management interactions:** Few studies have systematically evaluated three-way interactions among genotype, soil type, and irrigation/nutrient management. Factorial field experiments across these factors, combined with modeling, are needed to develop robust recommendations.
5. **Climate resilience:** Both plant hydraulic and soil water availability will change under projected climatic change where droughts will be more frequent and more severe, and the VPD of the atmosphere will be higher. The strategies of breeding and management should be able to predict these future conditions through scenario modeling.

6.3. Integrating disciplines: Pathways to implementation

We propose research joint ventures involving plant geneticists, soil physicists, crop modelers and breeders to collaboratively create combined methods of drought resilience. Funding agencies are recommended to focus on interdisciplinary projects that break the traditional disciplinary frames. The agricultural sciences need educational programs that will prepare the next generation of researchers with a mindset of interdisciplinaryism in breeding physio-genetics that is based on molecular biology as well as soil physics.

Plant genomics and irrigation physics is where we can bridge to create crop genotypes, and agrophysics to manage the entire soil-plant-atmosphere complex to achieve food security in a world where water is becoming increasingly scarce.

Table 3 describes five important gaps in the field of research and application of drought-tolerance genes to crop improvement and indicates the present knowledge gaps, suggested research strategies, anticipated results, timeframes, and necessary partnerships. These priorities range between characterizing genetic control of mucilage production (genome-wide association studies and gene characterization 2-3 years) to validating root hydraulic conductivity (Lp) under field conditions with multi-location trials (3-5 years), building integrated multi-scale models that couple root and soil processes with plant processes (3-4 years), carrying out factorial experiments of genotype x soil x management interactions to produce some practical breeding recommendations (3-5 years), and projecting climate resilience through the combination of hydrological models with future climate scenarios to identify adapt Together these research priorities demand interdisciplinary groups of geneticists, physiologists, soil scientists, modelers and breeders to work simultaneously to fill the gap between molecular findings and agricultural applications to the field scale over the next 3-5 years.

Table 3: Critical Knowledge Gaps and Research Priorities for Physio-Genetic Breeding

Knowledge Gap	Current Status	Research Needs	Expected Outcome	Time line	Collaboration	Ref.
Genetic Control of Mucilage	Poorly characterized	GWAS in maize/barley; characterize CELLULOSE SYNTHASE genes	Marker set for selection	2-3 yrs	Geneticists + rhizosphere chemists	(Watt *et al.*, 2006) [74]
Field-Scale	Lab-based studies	Multi-location trials; phenotype Lp under	Genotype recommendations	3-5	Physiologists +	(Liu *et al.*,

Validation of Lp	dominant	field conditions	for soil/climate	yrs	modelers	2014) [42]
Multi-Scale Modeling	Coupling inadequate	Develop homogenization theory; upscaling methods	Predictive models for rhizosphere	3-4 yrs	Soil physicists + modelers	(Cooper *et al.*, 2018) [22]
G×S×M Interactions	Limited factorial tests	Factorial experiments across genotypes/soils/management	Decision support system	3-5 yrs	Breeders + soil scientists	(Cai *et al.*, 2022) [14]
Climate Resilience	Preliminary work	Couple models with climate projections (RCP 4.5/8.5)	Climate-adaptive varieties	3-5 yrs	Climate scientists + breeders	(Cardoso *et al.*, 2025) [15]

Abbreviations: *GWAS*, Genome-Wide Association Study; *RCP*, Representative Concentration Pathway; *RT-qPCR*, Reverse Transcription Quantitative PCR; *RNA-seq*, RNA sequencing.

6.4 Challenges and limitations of current approaches to physio-genetic breeding

6.4.1. Technical and physiological challenges

1) Measurement of root hydraulic conductivity (Lp) Under field conditions

Despite significant progress in understanding aquaporin-mediated water transport, quantifying Lp in the field remains a major bottleneck (McElrone *et al.*, 2007) [48]:

Laboratory-to-field translation

High-pressure flowmeter (HPF) is used to measure Lp on excised root segments at controlled temperature (4 o C) minimizing cellular respiration (Markhart, 1990) [47]. Nevertheless, the field conditions of in situ root hydraulic conductivity can vary significantly because of a number of factors. (McElrone *et al.*, 2007) [48]:

- **Microbial biofilms on root surfaces:** Reduce water flux efficiency by 10-20% through increased resistance at the root-soil interface.
- **Root-soil gap formation during drying:** Increases boundary layer resistance by orders of magnitude, particularly when soil water potential drops below -100 kPa.
- **Temporal variation:** Lp exhibits diurnal cycles (2-4 fold variation) in response to plant water status, aquaporin phosphorylation state, and plant metabolic demand (Gambetta *et al.*, 2017) [27].

Practical solutions

- **Indirect method integration:** Combine indirect methods (stomatal conductance measurements, leaf water potential, xylem tension) with aquaporin gene expression (RT-qPCR) as a proxy for Lp genotype (Cai *et al.*, 2022) [14]. Validation subset with HPF on roots collected at specific growth stages provides ground-truth calibration (McElrone *et al.*, 2007) [48].
- **Genomic selection approach:** HPF equipment costs approximately $20,000; a single sample measurement requires trained personnel (30-45 minutes). For breeding programs evaluating 100+ lines annually, HPF is economically unsustainable. Genomic selection based on aquaporin SNP haplotypes becomes more practical and cost-effective (Cai *et al.*, 2022) [14].

Challenges summary

The big problem with the selection of Lp based on fields is the insensitivity of field performance and laboratory measurements (McElrone *et al.*, 2007) [48]. The root aquaporin activity may vary dynamically with the response to the local soil osmotic potential, pH, and the plant water status-factors that are virtually impossible to be standardized across field conditions. Moreover, the role of aquaporins in total root hydraulic conductivity differs significantly among species (0-90%), and it may change radically under stress. (Gambetta *et al.*, 2017) [27].

Monitoring rhizosphere processes: Mucilage production and root-soil gap dynamics

A controlled production of mucilage and root hair morphology- by rhizosphere engineering- is potentially useful in enhancing water uptake. Nonetheless, there is a lack of field validation. (Carminati *et al.*, 2017) [17-18].

Mucilage quantification challenges

- The extraction procedures are significantly different (water extraction, ethanol precipitation, TLC analysis); the absolute values cannot be easily compared with others in the literature. (Ahmed *et al.*, 2014) [3].
- **Mucilage is dynamic:** degradation by soil microorganisms and swelling/shrinking with soil wetting cycles occur; laboratory measurements often are static (Landl *et al.*, 2021) [41].
- **Spatial heterogeneity:** Mucilage concentration is highest at the root cap (10–50 mg g^{-1} root dry weight) and declines along root length (Holz *et al.*, 2018) [31]; field sampling cannot easily capture this gradient (Carminati *et al.*, 2017) [17-18].

Root-Soil Gap Formation

Root-soil gap formation occurs during soil drying and root shrinkage, directly reducing water flux by 50-90% (Carminati *et al.*, 2017) [17-18]. Yet prediction requires quantifying several parameters:

- **Root cortical cell characteristics:** Root cortical cell size and shrinkage elasticity vary with genotype, tissue age, and hydration history (Chimungu *et al.*, 2014) [21].
- **Soil shrinkage potential:** Soil shrinkage potential is texture-dependent; pore space changes during drying (Carminati *et al.*, 2017; Landl *et al.*, 2021) [17-18, 41].
- **Real-time imaging:** Real-time imaging during drying cycles (X-ray CT or MRI) can quantify gap formation; however, imaging is expensive and limited to controlled conditions (Landl *et al.*, 2021) [41].

Role of mucilage in water dynamics

Recent studies prove that root exuded mucilage has a basic impact on water dynamics in the rhizosphere (Carminati *et al.*, 2009; Ahmed *et al.*, 2014) [3, 19]. Mucilage adsorbs more water 1000 times compared to its dry weight, which facilitates the uptake of water in dry soil under wet conditions (Carminati *et al.*, 2016) [20]. After drying, however, mucilage is hydrophobic, and therefore it renders the rhizosphere water-repellent, and may place a limit to the rates of hydraulic failure but also to the rates of rewetting (Ahmed *et al.*, 2014) [3].

The hydraulic effect of mucilage is radially distributed around the root surface with a range of approximately 0.6-2 mm and the highest concentration of mucilage at the root cap (around 1.89mg/g-1 soil) and decreases with the

distance of the root tip (Holz *et al.*, 2018) [31]. The soil microorganisms break down half of the mucilage in over 7 days. (Holz *et al.*, 2018) [31].

Practical solution

Create screening assays: subject genotypes to drying regimes in rhizoboxes; measure gap formation through image analysis (Landl *et al.*, 2021) [41]. Take few with less shrinkage (genetic trait which correlates with smaller cortical cells as shown in maize by Chimungu *et al.*, 2014). Connect field performance through DSSAT-HYDRUS model. (Carminati *et al.*, 2017) [17-18].

Multi-Scale modeling: coupling pore-scale to field-scale processes

The existing bio-physical models (DSSAT-HYDRUS) consider root water uptake S z t a sink term, which is fuelled by root length density and genotype specific Lp (Cooper *et al.*, 2018; Landl *et al.*, 2021) [22, 41] but do not cover a range of key processes.

Limitations of current models

- **Pore-Scale rhizosphere heterogeneity*:*** Mucilage and root exudates create microenvironments (pH, pore-size distribution) around roots; these alter local K(θ) by 10-50% (Cooper *et al.*, 2018) [22]. However, averaging to field-scale models averages-out these critical effects, reducing model predictive accuracy.
- **Microscale-macroscale model coupling:** Recent advances (homogenization theory; lattice Boltzmann simulations) link pore-scale to Darcy-scale (Cooper *et al.*, 2018) [22]. However, this approach faces several challenges:
- **Computational expense:** Computational cost: Pore-scale modeling (CahnHilliardStokes equations) is computationally expensive; solving the complete pore-scale model took Cooper *et al.* (2018) [22] approximately 26 hours and 35 GB RAM using a high-performance computing cluster, but the cell problems of the model only required approximately 20 minutes and 3 GB RAM on each value of capillary pressure, and a fully homogenized macroscale model could be solved in approximately 2.5 minutes using a desktop computer.
- **Parameterization uncertainty:** Imaging rhizosphere pores at microscale is technically challenging; model validation is limited to laboratory conditions (Landl *et al.*, 2021) [41]. Field-scale validation remains elusive.
- **Limited software availability:** Most agricultural models lack pore-scale capability. Integration of pore-scale physics into existing simulation platforms (DSSAT, HYDRUS, APSIM) is nascent (Landl *et al.*, 2021) [41].

Practical workaround -effective parameter approach

Develop simplified effective parameters (e.g., "effective Lp" = measured Lp reduced by gap formation factor + mucilage viscosity factor). Calibrate using field experiments; apply in macroscale models (Cooper *et al.*, 2018) [22]. Iteratively refine as mechanistic understanding improves. This pragmatic approach balances computational efficiency with mechanistic representation.

Technical implementation

The homogenization theory approach (Cooper *et al.*, 2018) [22] is based on the derivation of coupled equations of air-water transport and exudate diffusion at macroscale using cell problems to represent the pore-scale flow behavior. Mathematical validation has demonstrated a variation of less than 7% between homogenized equations and pore-scale equations in the case of eight unit cell-scale validation. This offers an efficient way of computing the interaction of plants and soil.

To achieve this practically, Landl *et al.* (2021) [41] showed that by applying X-ray CT imaging to quantify the rhizosphere bulk density gradient with field calibration it is possible to successfully parameterize the dynamics of soil water. Their scenario simulations revealed that, in the process of soil drying, the smaller the rhizosphere bulk density the sooner the water stress is experienced but the slower is the root water uptake maintained with effects varying according to soil type and initial hydraulic conditions.

6.4.2 .Economic and institutional barriers

1) Cost of molecular genotyping and phenotyping in breeding programs

High-throughput phenotyping and genomic selection accelerate breeding but come with costs potentially prohibitive in low-resource settings (Atanda *et al.*, 2021; Spindel *et al.*, 2015) [8, 61] (Table 4):

Table 4: Phenotyping/Genotyping Costs & Throughput

Technology	Cost/sample	Throughput	Context
HPF (Lp)	$50–100	~10 samples/day	Validation
RT-qPCR	$5–15	~100 samples/day	Prediction
SNP array	$10–20	384 samples/run	Large-scale
KASP assay	$0.50–2	384–1536/run	Routine MAS
Shovelomics	$10–30	20–50/day	Early selection
X-ray CT	$100–500	5–10/day	Research

Real-World Cost Impact: Rice Breeding Program (100 lines, F3 generation)

Conventional approach (phenotype only):

- Field trials: $10,000–15,000
- Total: $10,000–15,000
- Timeline: 2 years
- Selection accuracy: ~60–70%

Physio-genetic approach (genotype + phenotype, Atanda *et al.*, 2021) [8]:

- MAS genotyping (KASP, 10 SNPs): $500–1,000
- HPF validation (20 lines): $2,000
- Field trials (reduced to 30 best lines): $3,000–5,000
- Total: $5,500–8,000 (actually lower!)
- Timeline: 1.5 years (faster)
- Selection accuracy: ~85–90%

Key insight: Genomic selection is less costly and more accurate and faster than phenotyping, which reduces the overall costs (Atanda *et al.*, 2021) [8]. But first, a large amount of money has to be invested in molecular infrastructure (SNP discovery, marker validation) (which is expensive to fund, 100,000-500,000 per crop × trait combination). (Spindel *et al.*, 2015) [61].

Solutions for Low-Resource Countries

- **Consortium approach:** CGIAR (IRRI, CIMMYT, ICRISAT) funds marker development; national programs use validated SNP panels at low cost (Atanda *et al.*, 2021) [8].
- **South-South technology transfer:** Established programs (India, China, Brazil) train personnel from African/South Asian breeding programs.
- **Open-source tools:** Free software (TASSEL, SNPMask) and free SNP data (public databases) reduce licensing costs (Spindel *et al.*, 2015) [61].

2. Farmer adoption: Knowledge, trust, and risk barriers

Even superior genotypes fail if farmers do not adopt. Barriers for physio-genetic varieties are significant:

- **Knowledge Barrier***:* Farmers understand "drought-tolerant" broadly, but "deep-rooting + high aquaporin" is mechanistically opaque. Extension materials must simplify without losing scientific accuracy.
- **Effective messaging:** "Variety X: Uses less water, same yield as Variety A; best for sandy/dry farms".
- **Less effective:** "Variety X: Has higher root hydraulic conductivity due to aquaporin upregulation".
- **Trust Barrier:** New varieties perceived as risky. Smallholders cannot afford crop failure; conservative preference for proven varieties drives lock-in.
- **Mitigation:** Demonstration trial in multi-year periods in groups of farmers prior to large scale adoption; peer learning (farmer-to-farmer demonstration).
- **Institutional support:** Government subsidies on seed make farmers less vulnerable to risk; crop insurance makes them less vulnerable to failure.
- **Economic Barrier:** Physio-genetic seed often costs 20–30% more than conventional; cost-benefit must be clear.
- **Scenario:** Drought-tolerant maize costs $30/kg vs. $25/kg conventional
- **Farmer calculation:** Extra cost $15 ha^{-1} × 20 kg ha^{-1} = $300 ha^{-1} investment
- **Expected benefit:** +200 kg ha^{-1} yield (+$100 ha^{-1} value at crop price $0.50 kg^{-1})
- **Net loss if drought does not occur:** Risk-averse farmer avoids new variety
- **Solution:** Seed subsidies, index insurance (pays out if rainfall <200 mm), or guarantee purchase of grain at premium price for drought-adapted varieties.

3. Knowledge integration barriers: Disciplinary silos

Physio-genetic breeding demands seamless collaboration between plant geneticists, soil physicists, modelers, and agronomists. Institutional barriers often prevent this:

Disciplinary training

PhD programs are mostly single discipline based. A geneticist studies plant science; a soil scientist studies physics. Interdisciplinary skills of a rare kind.

Solution: Develop combined graduate programs (e.g., "Sustainable Crop Science" which combines genetics, soil science, agronomy). Areas of focus of fund interdisciplinary research centers (e.g. James Hutton Institute in UK spans soil-plant-environment research).

Publication incentives

Scientific journals also show preference to specialist papers as opposed to integrative ones. An article on "DRO1 mutations" (genetics journal) is more frequently cited compared to the article on "DRO1 × soil type interaction" (less specialized) (Spindel *et al.*, 2015) [61].

Solution: Encourage high-impact journals (Nature Plants, Proceedings of the National Academy of Sciences) to publish integrative work; agencies encourage team work.

Data Standards and Sharing

Geneticists use genotype data in one format; soil scientists use soil properties in another. No standardized framework for linking datasets (Wilkinson *et al.*, 2016) [76].

Solution: Develop data interoperability standards (e.g., FAIR data principles: Findable, Accessible, Interoperable, Reusable); invest in centralized databases (GenBank-like for soil-plant phenotypes) (Wilkinson *et al.*, 2016) [76].

6.4.3. Climate and genotype × environment interactions future climate scenarios & genotype adaptation

Breeding for current conditions may misalign with projected climate change (2050–2100) (Asseng *et al.*, 2015) [7]. Critical uncertainties include:

- **Rainfall regime shifts:** IPCC potentials indicate great spatial heterogeneity. There are parts of the world (tropical Africa, South Asia) where droughts are becoming more frequent and intensive, and others (temperate zones) where the total precipitation is higher, but it is more extreme (Asseng *et al.*, 2015) [7]. The forecasts of climate change in terms of changes in precipitation show uncertainty margins of ±30-50% in climate change forecasts. Optimized root ideotypes can be rendered suboptimal when there are drastic shifts in the rainfall regimes. This requires adaptation capacity breeding, as opposed to fixed optimization breeding.
- **Vapor pressure deficit (VPD) trends:** An increment in the temperature leads to a rise in atmospheric water demand (VPD). To continue photosynthesis -the stomata should be open to cool the plant (but transpiration increase with stomatal openness, which is counterintuitive to drought-avoidance strategy (e.g., stomatal closure via DREB1) (Cardoso *et al.*, 2025) [15]. There is even an emerging idea that genotypes require that hydraulic traits should be dynamic- responsive to a combination of stressors in the soil and the atmosphere, rather than one or the other. (Cardoso *et al.*, 2025) [15].
- **Genotype × year interaction:** DRO1 varieties outperform in terminal drought years; they underperform in wet years with no relative advantage. If climate increases drought frequency, DRO1 adoption is justified; if water stress becomes less frequent, investment may be wasted (Asseng *et al.*, 2015) [7].

Practical approach: Climate-coupled crop modeling

Run models of couple crops on climate scenarios (RCP 4.5 and RCP 8.5) to model crop performance in the year 2050 and 2100 (Asseng *et al.*, 2015) [7]. Determine genotypes that are resilient to a variety of climate futures.:

Simulation Example: DSSAT × ClimateSA (climate model), 2050 projection, rainfed maize, Sahel:

- **DRO1+ / Low-Lp:** High yield stability under increased drought (+8% vs. current average).

- **DRO1- / High-Lp:** Yield declines under more frequent drought (-15%).
- **Recommendation:** Shift breeding focus to DRO1+ for Sahel; monitor for VPD threshold (Cardoso *et al.*, 2025) [15].

Alternative scenario: If 2050 shows wetter conditions + extreme rainfall events, shallow rooting + waterlogging tolerance becomes priority (Asseng *et al.*, 2015) [7].

7. Limitations and Caveats

- Most data from controlled studies, not farmer fields.
- Genotype × soil × climate interactions need more validation
- Adoption barriers (cost, seed systems) not fully addressed.
- Climate change scenarios not modeled.

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