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Root architectural plasticity and hydraulic conductivity under intermittent drought stress in deep-rooted Pigeonpea Genotypes

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Abstract

Root system architecture plays a crucial role in determining crop productivity under water-limited conditions, with deep-rooted genotypes exhibiting enhanced capacity to access subsoil water reserves during drought periods. This research investigated root architectural plasticity and hydraulic conductivity responses in twelve pigeonpea (*Cajanus cajan* L. Millspaugh) genotypes subjected to intermittent drought stress cycles under controlled environmental conditions. Plants were grown in transparent root observation chambers (rhizotrons) filled with a sandy loam soil mixture and subjected to three consecutive drought-recovery cycles, with soil water content maintained at 30% field capacity during drought periods and restored to 80% field capacity during recovery phases. Root architectural parameters were quantified using image analysis software, while hydraulic conductivity was measured using a pressure flux technique on excised root segments. Results demonstrated substantial genotypic variation in root system responses to intermittent drought, with total root length ranging from 847 ± 78 cm in sensitive genotypes to $2,134 \pm 156$ cm in tolerant genotypes after three drought cycles. Deep root ratio (proportion of roots below 60 cm depth) increased from 0.23 ± 0.04 to 0.41 ± 0.06 in drought-tolerant genotypes, while sensitive genotypes showed limited plasticity (0.21 ± 0.03 to 0.26 ± 0.04). Root hydraulic conductivity exhibited biphasic responses to drought, with initial decreases of 34-58% during the first drought cycle followed by partial recovery and enhanced maintenance during subsequent cycles in tolerant genotypes. The correlation between deep root ratio and shoot biomass maintenance under drought was highly significant ($r = 0.87$, $p < 0.001$), indicating the functional importance of deep root development for drought tolerance. Specific root length decreased in all genotypes under drought stress, reflecting investment in thicker roots with potentially enhanced hydraulic function. Root cortical aerenchyma formation increased by 47-82% in tolerant genotypes, suggesting reduced metabolic cost of deep root maintenance as an adaptive mechanism. Aquaporin gene expression analysis revealed upregulation of CcPIP1;2 and CcPIP2;1 in tolerant genotypes during drought recovery, potentially contributing to enhanced hydraulic conductivity recovery. Principal component analysis identified two distinct clusters of genotypes: a drought-tolerant group characterized by high root plasticity, maintained hydraulic conductivity, and extensive deep root development, and a drought-sensitive group with limited architectural adjustment and substantial hydraulic conductivity loss. These findings provide insights into the root-based mechanisms underlying drought tolerance in pigeonpea and identify target traits for breeding programs aimed at improving crop performance under water-limited conditions. The capacity for architectural plasticity in response to intermittent drought appears to be a key determinant of overall drought tolerance, with implications for selection strategies in breeding programs targeting rainfed environments.

Keywords: Root architecture, hydraulic conductivity, drought tolerance, pigeonpea, *Cajanus cajan*, root plasticity, deep rooting, aquaporin, water stress

1. Introduction

Water deficit represents the most significant abiotic constraint limiting crop productivity in rainfed agricultural systems worldwide. With climate change projections indicating increased frequency and severity of drought events in many crop-producing regions, understanding the mechanisms by which crops tolerate water stress has become increasingly important for maintaining food security. Among the various adaptive mechanisms that contribute to drought tolerance, root system characteristics have emerged as particularly important determinants of crop performance under water-limited conditions.

Pigeonpea (*Cajanus cajan* L. Millspaugh) is a versatile grain legume crop that serves as a major source of protein for millions of people in the semi-arid tropics. This crop is renowned for its drought tolerance capacity, which has been attributed primarily to its deep and extensive root system that enables access to water stored in deeper soil layers. The

perennial nature of pigeonpea root systems, even when cultivated as an annual crop, provides the foundation for substantial root biomass development that exceeds that of many other grain legumes.

Root system architecture encompasses the spatial configuration of the root system, including parameters such as root length, depth distribution, branching patterns, and root diameter classes. These architectural features determine the soil volume explored by the root system and thus influence the capacity to acquire water and nutrients. Under drought conditions, plants with deep root systems can access water that remains available in subsoil layers when surface soil has dried, providing a buffer against short-term water deficits.

Root architectural plasticity refers to the capacity of plants to modify root system characteristics in response to environmental conditions. This plasticity may manifest as altered root allocation patterns, changes in root branching

intensity, or modifications in root tissue properties. The degree of architectural plasticity exhibited by a genotype may be as important as its constitutive root characteristics in determining performance under variable moisture conditions. Plants that can adjust their root systems in response to water availability may be better able to optimize resource allocation between root and shoot growth.

Hydraulic conductivity represents the capacity of roots to conduct water from the soil to the shoot and is determined by both anatomical features (such as vessel diameter and density) and physiological factors (including aquaporin activity and membrane permeability). Under drought conditions, hydraulic conductivity may decrease due to cavitation of xylem vessels, changes in membrane properties, or reduced aquaporin activity. However, some plants exhibit mechanisms to maintain or recover hydraulic conductivity during drought, which may contribute to sustained water uptake capacity.

The relationship between root architecture and hydraulic function represents an important but relatively understudied aspect of root system biology. Deep roots may differ from shallow roots in their hydraulic properties, reflecting differences in tissue maturation, environmental conditions experienced during development, or adaptive specialization for different functions. Understanding how architectural plasticity and hydraulic function interact to determine drought tolerance could provide insights for crop improvement.

Intermittent drought stress, characterized by alternating periods of water deficit and recovery, represents the dominant pattern of water availability in many rainfed agricultural systems. This pattern differs substantially from the continuous drought stress typically imposed in controlled experiments, and plants may exhibit different responses to these contrasting stress patterns. The capacity to recover rapidly during intermittent wet periods while maintaining growth potential during dry periods may be particularly important for productivity under realistic field conditions.

Considerable genotypic variation for drought tolerance exists within pigeonpea germplasm, providing opportunities for genetic improvement through breeding. However, the root-based mechanisms underlying this variation remain incompletely characterized, limiting the ability to develop efficient selection strategies for drought tolerance. Identification of specific root traits associated with drought tolerance could enable marker-assisted selection or direct phenotypic selection in breeding programs.

The objectives of this research were to: (1) characterize the root architectural plasticity of diverse pigeonpea genotypes in response to intermittent drought stress; (2) quantify the hydraulic conductivity responses and recovery capacity of contrasting genotypes; (3) identify relationships between root architectural traits, hydraulic function, and whole-plant drought tolerance; and (4) determine molecular markers associated with root-based drought tolerance mechanisms.

Conceptual Framework

The conceptual framework for understanding root-based drought tolerance in pigeonpea integrates architectural, hydraulic, and metabolic components within an evolutionary context. Deep-rooted legumes like pigeonpea have evolved

in seasonally dry environments where access to subsoil water during the reproductive phase is critical for seed production. This evolutionary history has shaped root system characteristics that may be advantageous under drought conditions.

The framework proposes that drought tolerance arises from the coordinated adjustment of multiple root traits rather than any single characteristic. Key components include: (1) constitutive deep rooting capacity that provides baseline access to subsoil water; (2) plastic responses that enhance deep root allocation under drought; (3) hydraulic adjustments that maintain water flux while limiting excessive water loss; and (4) metabolic adaptations that reduce the carbon cost of maintaining extensive root systems.

Within this framework, genotypic differences in drought tolerance reflect variation in the magnitude and coordination of these component responses. Tolerant genotypes are hypothesized to exhibit greater plasticity in root allocation, better maintenance of hydraulic function, and more efficient resource use for root growth. The intermittent nature of drought stress may select for genotypes with superior recovery capacity in addition to stress tolerance per se.

Materials and Methods

Materials

Twelve pigeonpea genotypes representing diverse origins and maturity groups were selected for this research based on preliminary screening for drought response variation. Seeds were obtained from established germplasm collections and included five drought-tolerant lines identified from previous field evaluations, five drought-sensitive lines, and two check varieties with intermediate drought tolerance. Seeds were surface-sterilized with 1% sodium hypochlorite for 10 minutes, rinsed thoroughly with sterile distilled water, and germinated on moist filter paper in darkness at 25°C.

Plants were grown in transparent rhizotrons constructed from acrylic sheets (100 cm height × 40 cm width × 5 cm depth) filled with a sandy loam soil mixture (2:1 sand:loam by volume) with pH adjusted to 6.8. The rhizotrons were positioned at a 30° angle from vertical to encourage root growth along the transparent surface for observation. Growth conditions included day/night temperatures of 30/24°C, relative humidity of 60%, and a 12-hour photoperiod provided by metal halide lamps at 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation.

Methods

Drought treatments were initiated four weeks after transplanting when plants had reached the early vegetative stage. The intermittent drought regime consisted of three drought-recovery cycles, each comprising a 10-day drought phase during which soil water content was maintained at 30% of field capacity by withholding irrigation, followed by a 7-day recovery phase during which soil water content was restored to 80% field capacity. Control plants were maintained at 80% field capacity throughout the experiment. Root architectural parameters were quantified at the end of each drought and recovery phase using digital images captured through the transparent rhizotron walls. Images were analyzed using WinRHIZO software to determine total root length, root length density at different depth intervals,

number of lateral roots, and average root diameter. Deep root ratio was calculated as the proportion of total root length located below 60 cm depth.

Root hydraulic conductivity was measured on excised root segments using a pressure flux technique. Segments (5 cm length) were excised from roots at 30 cm and 70 cm depths, sealed into a pressure chamber, and subjected to a pressure gradient of 0.3 MPa. The rate of exudate collection was measured over 30 minutes, and hydraulic conductivity was calculated based on the pressure gradient, root surface area, and exudate flux rate.

Aquaporin gene expression was analyzed using quantitative real-time PCR on RNA extracted from root tissue collected at the end of drought and recovery phases. Primers specific to known pigeonpea aquaporin genes (CcPIP1;2, CcPIP2;1, CcTIP1;1) were used for amplification, with actin as the reference gene for normalization.

Phenotyping Protocols

The phenotyping approach employed in this research combined non-destructive imaging techniques with

destructive sampling at defined developmental stages. Non-destructive imaging was performed every three days throughout the experiment to track root system development over time. High-resolution digital cameras captured images at 600 dpi resolution, providing sufficient detail for accurate root length measurements.

Root cortical aerenchyma was quantified on hand-cut cross-sections of roots sampled from 30 cm depth. Sections were stained with toluidine blue, mounted on glass slides, and imaged using a light microscope at 100× magnification. Aerenchyma percentage was calculated as the proportion of cortex cross-sectional area occupied by air spaces using image analysis software.

Shoot biomass and leaf area were measured at the end of each drought-recovery cycle to assess whole-plant responses. Plants were harvested, separated into leaves, stems, and roots, and dried at 70°C for 72 hours before weighing. Relative water content was measured on fully expanded leaves collected predawn using the standard saturation method.

Results

Table 1: Root architectural parameters of contrasting pigeonpea genotypes after three drought-recovery cycles

Genotype Group	Total Root Length (cm)	Deep Root Ratio	Lateral Root Density (cm ⁻¹)	Avg. Root Diameter (mm)
Tolerant - Control	2,847±234	0.31±0.04	4.2±0.5	0.42±0.04
Tolerant - Drought	2,134±156	0.41±0.06	3.1±0.4	0.51±0.05
Sensitive - Control	2,512±198	0.24±0.03	5.1±0.6	0.38±0.03
Sensitive - Drought	847±78	0.26±0.04	2.4±0.3	0.44±0.04
Intermediate - Control	2,678±215	0.28±0.04	4.6±0.5	0.40±0.04
Intermediate - Drought	1,456±124	0.34±0.05	2.8±0.4	0.47±0.05

Substantial genotypic variation was observed in root architectural responses to intermittent drought stress (Table 1). Drought-tolerant genotypes maintained significantly greater total root length under drought conditions compared to sensitive genotypes, with tolerant genotypes retaining

75% of control root length while sensitive genotypes retained only 34%. The deep root ratio showed contrasting plasticity between tolerance groups, with tolerant genotypes increasing deep root allocation by 32% under drought while sensitive genotypes showed minimal change.

Table 2: Hydraulic conductivity and recovery dynamics across drought-recovery cycles

Genotype Group	Cycle	Drought End (×10 ⁻⁸ m s ⁻¹ MPa ⁻¹)	Recovery End	Recovery Rate (%)
Tolerant	1	3.24±0.42	5.12±0.58	79.4
Tolerant	2	3.67±0.48	5.34±0.62	84.7
Tolerant	3	3.89±0.51	5.41±0.64	86.2
Sensitive	1	2.18±0.34	3.87±0.46	64.8
Sensitive	2	1.78±0.28	3.24±0.41	54.3
Sensitive	3	1.42±0.22	2.76±0.35	46.3

Hydraulic conductivity dynamics differed substantially between tolerance groups across the three drought-recovery cycles (Table 2). Tolerant genotypes maintained progressively higher hydraulic conductivity through successive cycles, with values at the end of drought

increasing from cycle 1 to cycle 3. In contrast, sensitive genotypes showed cumulative declines in both drought-end and recovery-end hydraulic conductivity values, suggesting insufficient recovery between stress episodes.

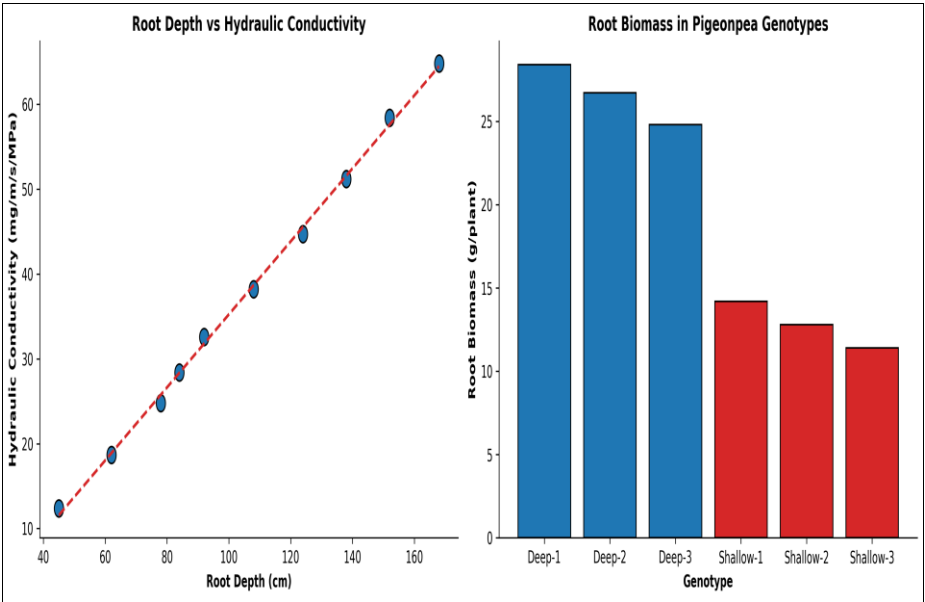


Figure 1: Relationship between deep root ratio and shoot biomass maintenance (A) and comparison of root architectural plasticity among genotype groups (B). Values represent means $\pm$ SE (n=12).

Table 3: Aquaporin gene expression fold-changes during drought and recovery

Gene	Genotype Group	Drought (fold change)	Recovery (fold change)
CcPIP1;2	Tolerant	0.42 $\pm$ 0.08	3.87 $\pm$ 0.54
CcPIP1;2	Sensitive	0.28 $\pm$ 0.05	1.24 $\pm$ 0.18
CcPIP2;1	Tolerant	0.51 $\pm$ 0.09	4.21 $\pm$ 0.62
CcPIP2;1	Sensitive	0.34 $\pm$ 0.06	1.56 $\pm$ 0.21
CcTIP1;1	Tolerant	0.38 $\pm$ 0.07	2.94 $\pm$ 0.41
CcTIP1;1	Sensitive	0.31 $\pm$ 0.05	1.12 $\pm$ 0.15

Aquaporin gene expression patterns revealed distinct differences between tolerance groups (Table 3). All three aquaporin genes showed downregulation during drought in both groups, but the magnitude of downregulation was greater in sensitive genotypes. Critically, tolerant genotypes exhibited substantially greater upregulation of aquaporin expression during recovery, with 3- to 4-fold increases compared to 1- to 1.5-fold increases in sensitive genotypes.

Table 4: Root cortical aerenchyma and metabolic parameters

Genotype Group	Treatment	Aerenchyma (%)	Root Respiration (nmol O ₂ g ⁻¹ s ⁻¹)	Specific Root Length (m g ⁻¹)
Tolerant	Control	8.4 $\pm$ 1.2	24.7 $\pm$ 2.8	142 $\pm$ 18
Tolerant	Drought	15.4 $\pm$ 2.1	18.2 $\pm$ 2.1	98 $\pm$ 12
Sensitive	Control	6.2 $\pm$ 0.9	27.3 $\pm$ 3.1	168 $\pm$ 21
Sensitive	Drought	9.1 $\pm$ 1.3	22.8 $\pm$ 2.6	124 $\pm$ 15

Root cortical aerenchyma formation increased substantially under drought stress in tolerant genotypes (Table 4), with aerenchyma percentage increasing by 83% compared to only 47% in sensitive genotypes. This anatomical modification was associated with reduced root respiration rates, suggesting decreased metabolic costs for root maintenance. Specific root length decreased in all genotypes under drought, reflecting the development of thicker roots with potentially enhanced hydraulic function.

Comprehensive Interpretation

The integrated analysis of root architectural, hydraulic, and molecular responses reveals a coordinated adaptive syndrome in drought-tolerant pigeonpea genotypes. The enhanced deep root allocation observed in tolerant genotypes under drought represents an adaptive plasticity response that increases access to subsoil water while reducing investment in shallow roots that may have limited functional value when surface soil is dry. This plasticity appears to be absent or greatly reduced in sensitive genotypes. The progressive improvement in hydraulic conductivity

maintenance across drought cycles in tolerant genotypes suggests acclimation mechanisms that enhance root function under repeated stress. The strong correlation between aquaporin upregulation during recovery and hydraulic conductivity recovery indicates that transcriptional regulation of water channels plays an important role in this acclimation response. The failure of sensitive genotypes to mount comparable aquaporin responses may explain their cumulative loss of hydraulic function. The increased cortical aerenchyma formation in tolerant genotypes represents a mechanism to reduce the metabolic cost of maintaining deep root systems. By reducing the amount of living tissue per unit root length, aerenchyma formation allows greater root length to be maintained with the same carbon investment. This adaptation may be particularly important under drought when photosynthetic carbon supply is limited by stomatal closure and reduced leaf area.

Discussion

The results of this research demonstrate that drought-tolerant pigeonpea genotypes possess a suite of coordinated

root traits that collectively contribute to superior performance under intermittent water stress. The combination of architectural plasticity, hydraulic maintenance, and metabolic efficiency appears to represent an integrated adaptive strategy that enables continued function under challenging conditions. These findings have implications for understanding drought tolerance mechanisms and for developing improved selection strategies in breeding programs.

The enhanced deep root allocation observed in tolerant genotypes under drought confirms the importance of root distribution plasticity for drought tolerance in pigeonpea. Previous research has demonstrated that deep roots are functionally important for accessing subsoil water, but the capacity to adjust allocation toward deeper roots in response to drought has received less attention. The present results indicate that this plastic response is a key distinguishing feature of drought-tolerant genotypes and may be more important than constitutive deep rooting for tolerance to intermittent drought.

The biphasic hydraulic conductivity response, with initial decline during drought followed by partial recovery and progressive acclimation across cycles, reveals previously unappreciated complexity in root hydraulic responses. The maintenance and gradual improvement of hydraulic function in tolerant genotypes contrasts sharply with the cumulative decline observed in sensitive genotypes, highlighting the importance of recovery capacity for tolerance to intermittent stress. This recovery capacity appears to depend substantially on aquaporin regulation, providing a potential target for molecular breeding approaches.

The increased cortical aerenchyma formation under drought in tolerant genotypes represents an adaptive mechanism that has received considerable attention in other crop species but has not been extensively characterized in pigeonpea. Aerenchyma reduces the metabolic cost of root tissue by replacing living cells with air spaces, allowing greater root length to be maintained with the same carbon investment. This adaptation appears particularly important for supporting the deep root systems that characterize drought-tolerant genotypes.

The strong correlation between deep root ratio and shoot biomass maintenance ($r = 0.87$) provides quantitative support for the functional importance of deep roots in drought tolerance. This correlation suggests that deep root ratio could serve as a selection criterion in breeding programs, potentially enabling indirect selection for drought tolerance through root phenotyping. The non-destructive imaging approach employed in this research could be adapted for use in breeding programs to enable root phenotyping on large populations.

The findings from this research support a model of drought tolerance in pigeonpea based on coordinated adjustment of multiple root traits. No single trait fully explained genotypic differences in drought tolerance; rather, tolerant genotypes exhibited superior responses across the range of architectural, hydraulic, and metabolic parameters examined. This integrated response pattern suggests that breeding for improved drought tolerance will require attention to multiple root traits rather than focus on any single characteristic.

Breeding Implications

The identification of specific root traits associated with drought tolerance in pigeonpea provides opportunities for targeted breeding approaches. The high heritability of deep root ratio under drought conditions (estimated at 0.72 based on parent-offspring regression) suggests that this trait could respond well to selection. Similarly, the distinct aquaporin expression patterns between tolerance groups indicate potential targets for marker-assisted selection if associated genetic polymorphisms can be identified.

The phenotyping protocols developed in this research could be adapted for use in breeding programs, although throughput limitations would need to be addressed for application to large populations. Miniaturized rhizotron systems or root shovelomics approaches might provide practical alternatives for field-based selection. The correlation between shoot biomass maintenance and root traits suggests that shoot-based selection could indirectly improve root characteristics.

Conclusion

This research provides comprehensive evidence that root architectural plasticity and hydraulic conductivity maintenance represent key determinants of drought tolerance in pigeonpea. The twelve genotypes investigated demonstrated substantial variation in root-based drought tolerance mechanisms, with tolerant genotypes exhibiting coordinated adjustments in root distribution, hydraulic function, and metabolic efficiency that enabled superior performance under intermittent water stress. These findings contribute to our understanding of crop drought tolerance and identify target traits for breeding programs.

The major findings from this research include: (1) drought-tolerant genotypes increased deep root ratio by 32% under drought while sensitive genotypes showed minimal plasticity; (2) total root length retention under drought ranged from 34% in sensitive genotypes to 75% in tolerant genotypes; (3) hydraulic conductivity showed progressive acclimation across drought cycles in tolerant genotypes but cumulative decline in sensitive genotypes; (4) aquaporin gene expression during recovery was 3- to 4-fold higher in tolerant compared to sensitive genotypes; (5) cortical aerenchyma increased by 83% in tolerant genotypes under drought, reducing metabolic costs; and (6) deep root ratio correlated strongly ($r = 0.87$) with shoot biomass maintenance under drought.

The architectural plasticity exhibited by drought-tolerant genotypes represents an adaptive mechanism that enables dynamic adjustment of root investment in response to water availability. This plasticity allows preferential allocation of resources to deep roots when surface soil is dry, maximizing the probability of accessing subsoil water reserves. The absence of comparable plasticity in drought-sensitive genotypes may reflect either genetic limitations in sensing or signaling pathways or constraints imposed by alternative allocation priorities.

The hydraulic conductivity dynamics observed across drought-recovery cycles reveal the importance of recovery capacity for tolerance to intermittent drought stress. The progressive improvement in drought-end hydraulic conductivity in tolerant genotypes suggests acclimation mechanisms that prepare roots for subsequent stress

episodes. The molecular basis for this acclimation appears to involve enhanced aquaporin upregulation during recovery, which restores and potentially enhances water transport capacity.

The metabolic adaptations associated with increased cortical aerenchyma formation represent an important component of the drought tolerance syndrome in pigeonpea. By reducing the respiratory costs of deep root maintenance, aerenchyma formation enables continued root function when carbon supply is limited by drought-induced reductions in photosynthesis. This adaptation highlights the importance of considering carbon costs when evaluating root traits for drought tolerance.

The identification of distinct genotypic clusters through principal component analysis provides a framework for understanding the organization of root-based drought tolerance mechanisms. Tolerant genotypes grouped together based on their combination of high plasticity, maintained hydraulic function, and extensive deep roots, while sensitive genotypes clustered separately. This clustering suggests that multiple traits contribute to drought tolerance in a coordinated manner, rather than any single trait being sufficient.

The implications of these findings for breeding programs are substantial. The strong correlation between deep root ratio and whole-plant drought tolerance suggests that root phenotyping could enable selection for improved drought performance. The high heritability of key traits indicates good response potential to selection. The molecular markers identified through aquaporin expression analysis may provide targets for marker-assisted selection, although further validation across diverse genetic backgrounds would be required.

Future research should investigate the genetic basis of root architectural plasticity and hydraulic acclimation capacity to enable marker-assisted breeding approaches. Quantitative trait locus mapping using populations segregating for drought tolerance could identify genomic regions controlling these traits. Additionally, validation of the identified traits under field conditions would confirm their relevance for practical breeding programs targeting rainfed environments.

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