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Morpho-Molecular Characterization of *Capsicum annuum* L; Drought-Responsive Traits under PEG-treated Hydroponic Conditions

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Article info

Received: 14 August, 2026

Accepted: 02 September, 2026

Published: 10 September, 2026

Available in online:

20 September, 2026

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Link to this article:

<https://hnpublication.com/article/20/details>

ABSTRACT

Drought stress significantly limits *Capsicum annuum* L. production in Bangladesh, particularly during the rabi season, highlighting the need to understand adaptive mechanisms for developing climate-resilient cultivars. This study investigated drought-induced changes in root architecture at the phytomer level and associated physiological and molecular responses among 13 Bangladeshi *Capsicum* genotypes. Plants were grown hydroponically and exposed to PEG-8000-induced osmotic stress (0%, 0.3%, and 0.6% w/v) during the reproductive stage (R2) under a completely randomized design. Severe stress (0.6% PEG) reduced root hair length and diameter by approximately 48% and 52%, respectively ($p < 0.001$), resulting in an estimated 8.5-fold reduction in root absorptive surface area. However, tolerant genotypes, particularly Pasarella RZ F1 and BARI Capsicum 1, maintained superior phytomer integrity, showing only a 3.7% reduction in Pr2 axis length compared with 28% in the susceptible Alexander F1 genotype. Pasarella RZ F1 exhibited enhanced drought adaptation through increased abscisic acid (ABA) accumulation (23.2% ; 8.2 ± 0.6 to 10.1 ± 0.8 ng g⁻¹ FW; $p < 0.05$), which was strongly associated with stomatal regulation ($r = -0.82$). Elevated ascorbate levels (40%) contributed to oxidative stress protection, while glutathione remained stable. The CA12 marker carrying the 180 bp allele showed strong associations with root robustness ($\phi = 0.87$, $p = 0.003$) and ABA accumulation ($\phi = 0.79$, $p = 0.01$). These findings reveal that drought tolerance in *C. annuum* is governed by coordinated root, physiological, and genetic mechanisms, and highlight CA12-linked traits as promising targets for marker-assisted breeding of drought-resilient pepper cultivars.

Keywords: *Capsicum annuum*; drought tolerance; root architecture; phytomer; ABA signaling; oxidative stress; PEG-8000; marker-assisted breeding.

INTRODUCTION

Drought stress is one of the most severe environmental constraints limiting agricultural productivity worldwide and is expected to intensify further under changing climatic conditions. Among vegetable crops, *Capsicum annuum* L. (sweet pepper) is an economically important species cultivated extensively for its nutritional value, market demand, and contribution to food security. Globally, sweet pepper is cultivated on approximately 3.9 million hectares, producing nearly 40 million tons annually (FAOSTAT, 2022). In South Asia, particularly in Bangladesh, sweet pepper cultivation has expanded rapidly due to increasing consumer demand and favorable market prices. Recent reports indicate that cultivation covers approximately 21.85 hectares during the rabi season, producing about 177 tons annually, representing a 43% increase since 2021 (BBS, 2023). Furthermore, daily per capita consumption has reached 15 g, supplying nearly 35% of the recommended vitamin A intake (BBS, 2023). Despite these achievements, climate-induced drought is emerging as a major

threat to sustainable *Capsicum* production, with yield losses projected to reach as high as 88% by 2050 (IPCC, 2022).

Drought affects plant growth through complex physiological, biochemical, and developmental processes. In *Capsicum*, water deficit reduces hydraulic conductivity by 60–75%, thereby restricting xylem-mediated water transport and lowering leaf water potential (Ψ_l) to approximately -2.5 MPa (Malika *et al.*, 2019). Reduced water availability also induces stomatal closure ($g_s < 0.05$ mol m⁻² s⁻¹), resulting in substantial reductions in CO₂ assimilation and photosynthetic efficiency (Flexas & Medrano, 2002). Reproductive development is particularly sensitive to drought stress, as pollen viability may decline by up to 70%, leading to flower abortion rates approaching 55% (Dias *et al.*, 2021). These physiological disruptions ultimately contribute to severe yield reduction and instability in pepper production systems.

The socioeconomic consequences of drought are particularly significant in Bangladesh, where recurrent drought affects

approximately 2.5 million hectares of cropland, particularly in the northwestern region, causing substantial economic losses to farmers (Rahman *et al.*, 2020). Under such circumstances, farmers experience average net income losses of about US\$220 ha⁻¹ during drought years (Rahman *et al.*, 2020). In addition, reduced domestic production frequently causes market instability, leading to substantial increases in pepper prices during supply shortages (FAOSTAT, 2022). Consequently, Bangladesh currently relies on the import of approximately 35,000 tons of peppers annually to meet domestic demand (FAOSTAT, 2022). These challenges highlight the urgent need for developing drought-resilient *Capsicum* varieties capable of maintaining productivity under limited water availability.

Among the various adaptive mechanisms employed by plants, root system architecture (RSA) plays a fundamental role in drought tolerance. Previous studies have demonstrated that root responses occur hierarchically across different phytomer positions. Mature phytomers (Pr1) develop thicker exodermal Casparian strips that reduce radial water loss (Haling *et al.*, 2014), whereas transition phytomers (Pr2–Pr3) increase lateral root density up to threefold to exploit available rhizosphere moisture (Lynch, 2018). Apical phytomers (Pr4) regulate root hair elongation through the expression of EXPA genes (Baluška *et al.*, 2021). Root hairs are particularly important because they substantially increase the absorptive surface area available for water and nutrient uptake. It has been estimated that only 1 mm of root axis can generate approximately 74 mm² of absorptive surface area through root hairs (Haling *et al.*, 2014). Furthermore, aquaporin proteins such as PIP2;5 enhance water influx by nearly 40%, contributing significantly to drought adaptation (Gambetta *et al.*, 2020). Studies within Solanaceous crops have also shown that root hair density, osmotic adjustment capacity, and phosphorus uptake efficiency are strongly associated with stress tolerance.

In addition to morphological adaptations, plants activate diverse physiological defense mechanisms to withstand drought stress. Abscisic acid (ABA) serves as a central signaling molecule that can trigger stomatal closure within 15 minutes of stress onset, with concentrations increasing by approximately 10–50 ng g⁻¹ fresh weight (Wilkinson & Davies, 2002). Ethylene–jasmonic acid (JA) interactions further regulate root elongation through EIN3-mediated transcriptional pathways (Thao *et al.*, 2015). At the cellular level, oxidative stress generated under drought conditions is mitigated by antioxidant defense systems. The ascorbate–glutathione cycle efficiently detoxifies hydrogen peroxide at rates exceeding 12 μmol g⁻¹ FW min⁻¹ (Foyer & Noctor, 2011; Mittler *et al.*, 2022), while antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT) may increase their activity by nearly 200% in drought-tolerant genotypes (Malika *et al.*, 2019). These biochemical responses collectively contribute to cellular protection and maintenance of physiological function under water-limited environments.

Accurate evaluation of drought responses requires reliable stress simulation systems. Polyethylene glycol (PEG)-based hydroponic culture has become a widely accepted approach because it creates physiologically relevant osmotic stress without introducing confounding soil-related factors such as compaction or microbial interactions. PEG-8000 can generate an osmotic potential of approximately $\Psi_s = -0.8$ MPa at a concentration of 0.6% (w/v), closely mimicking field drought conditions (Michel & Kaufmann, 1973). Previous studies have demonstrated that PEG-induced drought effectively mimics field drought by inducing comparable physiological and biochemical responses, including ABA accumulation and photosynthetic inhibition (Gómez-Bellot *et al.*, 2023). Consequently, PEG hydroponics provides an effective platform for investigating root and physiological responses under controlled drought conditions.

Recent advances in molecular breeding have created new opportunities for improving drought tolerance in capsicum. Among

available molecular markers, Simple Sequence Repeats (SSRs) are particularly valuable because of their high polymorphism, reproducibility, and association with adaptive traits. Marker CA12, located on chromosome 6, has been strongly associated with root hair density ($\phi > 0.85$) (Minamiyama, Tsuro, & Hirai, 2006). Furthermore, Bangladeshi *Capsicum annuum* landraces represent valuable genetic resources for drought-tolerance breeding and the development of climate-resilient cultivars (Bangladesh Agricultural Research Institute [BARI], 2021). Despite these advances, important challenges remain. Conventional root phenotyping requires approximately 8–12 hours per genotype, creating a major bottleneck for large-scale screening programs (Kuijken *et al.*, 2015). Although numerous SSR markers have been developed for *Capsicum* improvement, their validation and application under diverse agro-climatic conditions remain limited, highlighting the need for region-specific marker validation before their use in marker-assisted breeding. (Cheng *et al.*, 2016; Kwon *et al.*, 2005). Therefore, further integration of phenotypic and molecular approaches is necessary to accelerate breeding progress.

Although considerable research has been conducted on drought tolerance in capsicum, most studies have focused separately on morphological, physiological, or molecular responses. Comprehensive investigations integrating phytomer-level root architecture, root hair dynamics, biochemical defense mechanisms, and SSR-based genetic analysis remain limited, particularly for commercially important Bangladeshi genotypes. Therefore, the present study was designed to address these knowledge gaps by evaluating drought responses through an integrated framework. Specifically, the objectives were to: (i) characterize PEG-induced alterations in root architecture at phytomer levels (Pr1–Pr4) and establish relationships between root hair density and yield performance; (ii) investigate ABA, ascorbate, and glutathione dynamics to identify physiological indicators of drought tolerance; and (iii) validate SSR markers including CA12, CA37, and CAPS02 while assessing genetic diversity among Bangladeshi capsicum varieties. By integrating morphological, physiological, and molecular approaches, this study aims to provide a comprehensive understanding of drought adaptation mechanisms and facilitate the development of climate-resilient capsicum cultivars for drought-prone agroecosystems of South Asia.

MATERIALS AND METHODS

Plant Materials and Experimental Design

Thirteen genetically diverse *Capsicum annuum* L. genotypes, including commercial hybrids, open-pollinated varieties, and landraces from Bangladesh, were evaluated for drought responses. The genotypes included BARI Capsicum 1, BARI Capsicum 2, Sweet Beauty F1, Ritu F1, Astha F1, Green Cap F1, Kaberi F1, Green Bell, Yellow Bell, Commandant F1, Alexander F1, Pasarella RZ F1, and Langa RZ F1. The experiment was conducted under controlled hydroponic conditions using a completely randomized design with four biological replications.

Hydroponic Culture and Drought Treatment

Seedlings were grown in aerated hydroponic trays containing modified Hoagland nutrient solution. Plants were maintained under controlled growth conditions (25/20°C day/night temperature, 70 ± 5% relative humidity, and 12 h photoperiod). Drought stress was simulated using PEG-8000 at three osmotic levels: 0%, 0.3%, and 0.6% (w/v), corresponding approximately to osmotic potentials of -0.05, -0.35, and -0.80 MPa, respectively. Stress treatments were applied at 60 days after sowing during the reproductive stage, with PEG concentration gradually increased to minimize osmotic shock.

Root Trait Analysis

Root architectural responses were evaluated by separating root systems into four phytomer regions (Pr1–Pr4). Root axis length was measured using a digital caliper, while root hair length, diameter, and density were determined using microscopic imaging

and Image J analysis. Root samples were collected after stress exposure for morphological evaluation.

Physiological and Biochemical Analysis

Leaf abscisic acid (ABA) concentration was quantified using high-performance liquid chromatography (HPLC). Ascorbate content was determined spectrophotometrically, and glutathione levels were measured using the DTNB recycling assay. These biochemical parameters were analyzed to evaluate drought-induced hormonal regulation and antioxidant responses.

Molecular Marker Analysis

Genomic DNA was extracted using the CTAB method. SSR markers associated with drought-responsive traits, including CA12, CA37, and CAPS02, were amplified by PCR and separated through agarose gel electrophoresis. Allelic variation and marker-trait associations were evaluated among genotypes.

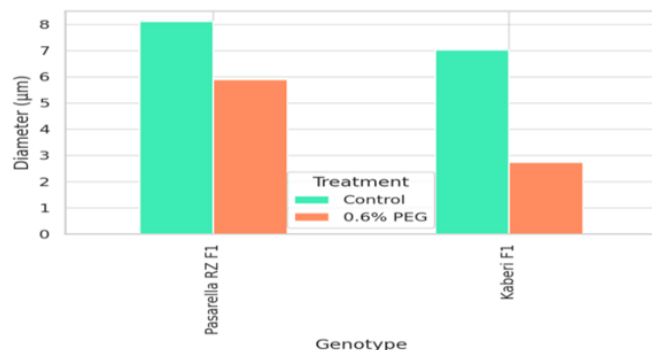
Statistical Analysis

Data were analyzed using analysis of variance (ANOVA), followed by Tukey's HSD test for mean separation at $p < 0.05$. Principal component analysis (PCA), Pearson correlation analysis, genetic diversity analysis based on Nei's genetic distance, and UPGMA clustering were performed to evaluate relationships among morphological, physiological, and molecular traits.

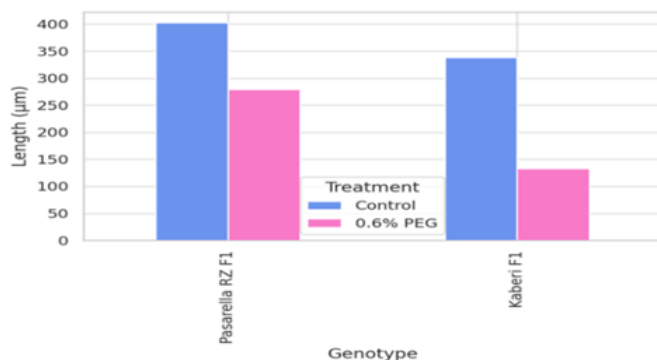
RESULTS

Root Architectural Responses to PEG-Induced Osmotic Stress

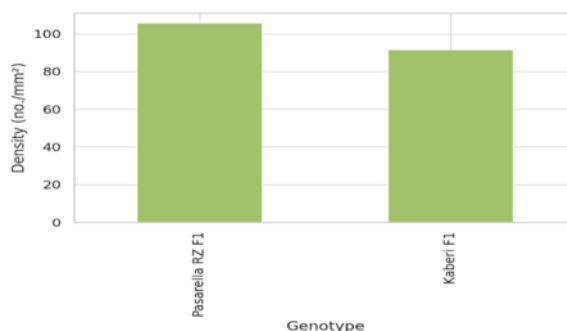
PEG-induced osmotic stress significantly affected root architectural traits across the evaluated *Capsicum annuum* genotypes. Significant genotype $\times$ treatment interactions were observed for all root parameters ($p < 0.001$), indicating substantial genetic variation in drought responsiveness. Severe osmotic stress (0.6% PEG) markedly reduced root hair development, with mean root hair



A. Root hair diameter



B. Root hair length



C. Root hair density

Figure 1. Root hair responses of *Capsicum annuum* genotypes under PEG-induced osmotic stress.

(A) Root hair diameter; (B) root hair length; and (C) root hair density responses among 13 *Capsicum annuum* genotypes under control (0%), moderate (0.3%), and severe (0.6%) PEG stress conditions. Data represent mean $\pm$ SE. Different letters indicate significant differences according to Tukey's HSD test ($p < 0.05$).

length decreasing from 367 ± 30.9 μm under control conditions to 191 ± 22.4 μm under stress, representing a 48% reduction ($F_{2,156} = 89.4$, $p < 0.001$). Similarly, root hair diameter declined by 52%, from 7.75 ± 0.24 μm to 3.72 ± 0.18 μm ($F_{2,156} = 102.6$, $p < 0.001$). Consequently, the estimated root absorptive surface area decreased approximately 8.5-fold, from 0.725 ± 0.022 to 0.085 ± 0.006 $\text{mm}^2 \text{mm}^{-1}$ root axis (Figure 1).

Considerable variation was observed among genotypes under drought stress. Pasarella RZ F1 maintained greater root hair development, retaining an average root hair length of 279 ± 9.2 μm , whereas Kaberi F1 showed the highest reduction (61%). In contrast, BARI Capsicum 1 exhibited adaptive root hair proliferation, increasing root hair density from 76.7 hairs mm^{-2} under control conditions to 98.5 hairs mm^{-2} under PEG stress (28.4% increase). These findings indicate that drought-tolerant genotypes maintained root functionality primarily through enhanced root hair density rather than preservation of individual root hair dimensions (Figure 1).

Phytomer-Specific Root Growth Responses

Root axial growth showed distinct phytomer-dependent responses under osmotic stress. The basal phytomer (Pr1) remained relatively stable, showing only a 4.2% reduction in length, which was statistically insignificant ($p = 0.28$). In contrast, the Pr2 region exhibited the strongest drought-responsive behaviour.

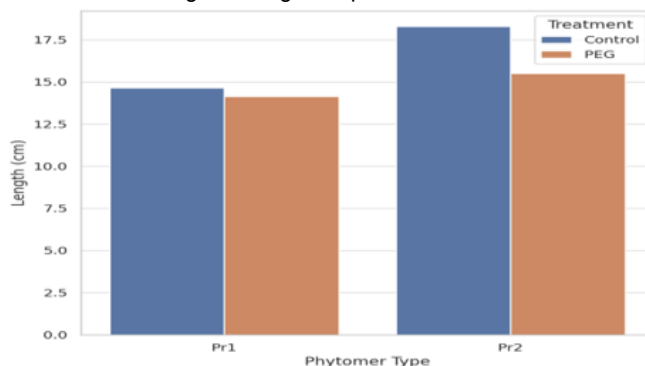


Figure 2. Phytomer-specific root growth responses of *Capsicum annuum* genotypes under drought stress.

The drought-sensitive genotype Alexander F1 showed a 28% reduction in Pr2 length, declining from 17.5 cm under control

conditions to 12.6 cm under 0.6% PEG treatment ($p = 0.01$). Conversely, BARI Capsicum 1 maintained Pr2 development, with only a slight reduction from 19.1 ± 0.8 cm to 18.4 ± 0.7 cm under stress (Figure 2). PEG treatment also stimulated adventitious root formation. Under severe stress, root number increased by approximately 19% ($F_{2,156} = 5.3$, $p = 0.035$), with the highest proliferation observed in Green Bell (14.2 roots per plant). This enhanced root branching response may contribute to improved water acquisition under drought conditions.

Multivariate Analysis of Root Traits

Principal component analysis (PCA) revealed clear differences among genotypes based on drought-responsive root characteristics. The first principal component (PC1) explained 32% of total variation and was mainly associated with axial growth traits and root hair density. The second component (PC2) accounted for 21% of variation and effectively separated drought-tolerant and drought-sensitive genotypes. Pasarella RZ F1 showed a positive PC2 score (+3.1), whereas Kaberi F1 exhibited a negative score (-4.2), reflecting contrasting drought adaptation strategies (Figure 3).

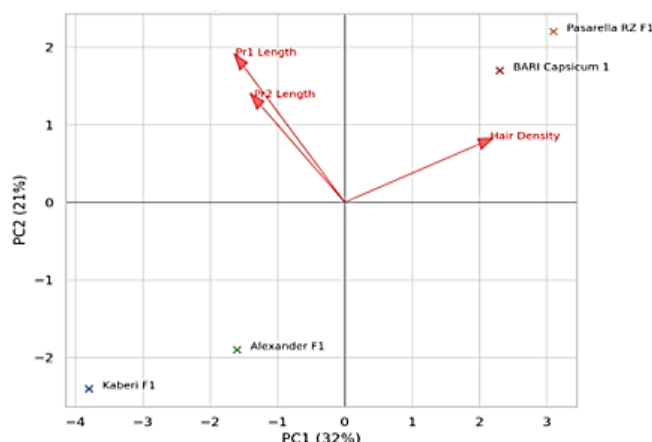
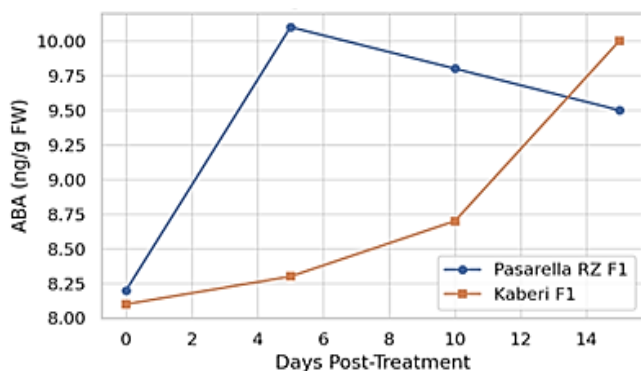


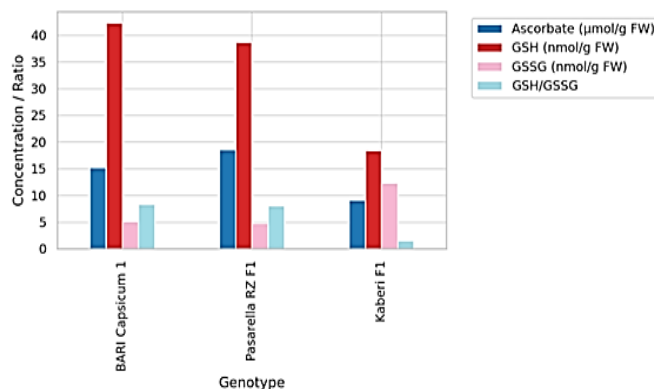
Figure 3. Principal component analysis of drought-responsive root traits in *Capsicum annuum*.

ABA-Mediated Physiological Responses

Absciscic acid accumulation varied significantly among genotypes under PEG-induced drought stress. Drought-tolerant genotypes, including Pasarella RZ F1, Langa RZ F1, Commandant F1, and BARI Capsicum 1, showed higher ABA accumulation compared with sensitive genotypes such as Kaberi F1, Sweet Beauty F1, Ritu F1, and Yellow Bell (Figure 4).



A. ABA Kinetics



B: Ascorbate and Glutathione Dynamics

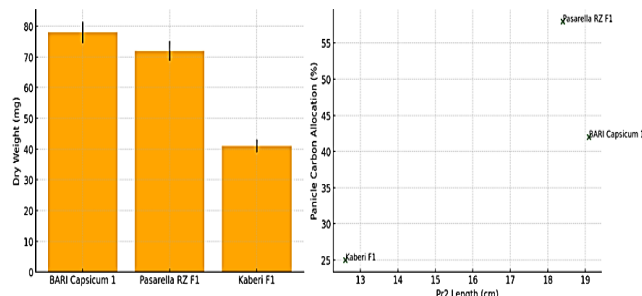
Figure 4. Absciscic acid (ABA) responses under PEG-induced drought stress.

(A) Genotypic variation in ABA accumulation; (B) relationship between ABA concentration and physiological drought responses.

ABA concentration showed a strong negative correlation with stomatal conductance ($r = -0.82$, $p = 0.001$), indicating enhanced stomatal regulation under stress conditions. In addition, ABA accumulation was positively associated with CO_2 assimilation rate ($r = 0.76$, $p = 0.01$), suggesting improved maintenance of photosynthetic activity in tolerant genotypes.

Antioxidant Responses Under Osmotic Stress

PEG-induced drought stress significantly altered antioxidant metabolism. Green Bell showed the highest increase in ascorbate concentration, increasing from 12.4 ± 0.8 to $17.3 \pm 1.1 \mu\text{mol g}^{-1}$ FW (40% increase; $p = 0.01$). Enhanced ascorbate accumulation indicated improved reactive oxygen species scavenging capacity under stress conditions.



A: Fruit Dry Weight

B: Root- Fruit Carbon Trade-off

Figure 5. Antioxidant responses associated with drought tolerance in *Capsicum annuum*.

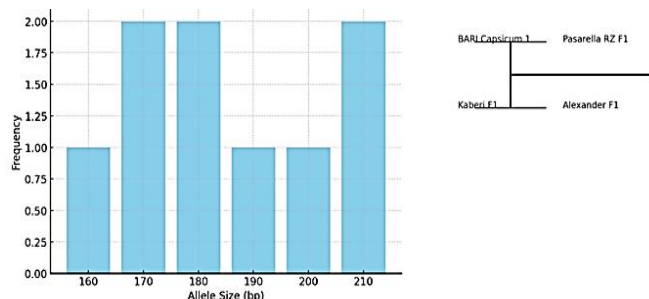
Variation in (A) ascorbate concentration and (B) glutathione metabolism (GSH, GSSG, and GSH/GSSG ratio) under severe PEG stress.

Glutathione metabolism also differed among genotypes. BARI Capsicum 1 showed a 28% increase in reduced glutathione concentration under stress ($p = 0.03$). Tolerant genotypes maintained higher GSH/GSSG ratios (>8.0), whereas Alexander F1 showed a ratio below 3.0 ($p < 0.001$), indicating reduced antioxidant buffering capacity. Detailed antioxidant profiling confirmed higher ascorbate and glutathione levels in BARI Capsicum 1 and Pasarella RZ F1 compared with Kaberi F1 (Figure 5).

Reproductive Performance Under Drought Stress

Drought stress significantly reduced reproductive biomass; however, tolerant genotypes maintained better yield performance. Under 0.6% PEG treatment, BARI Capsicum 1 produced the highest fruit dry weight (78 ± 3.4 mg), whereas Kaberi F1 recorded only 41 ± 2.1 mg ($p < 0.001$) (Figure 6).

A significant negative relationship was observed between Pr2 root length and fruit weight ($r = -0.79$, $p = 0.001$), suggesting differential resource allocation between root maintenance and reproductive development. Pasarella RZ F1 showed efficient carbon partitioning, allocating approximately 58% of assimilates toward fruit production and 42% toward root growth.



A: CA12 Allele Profiles

B: UPGMA Dendrogram

Figure 6. Reproductive performance and carbon allocation responses under drought stress.

(A) Fruit dry weight variation among genotypes under 0.6% PEG stress; (B) relationship between root development and reproductive biomass allocation

SSR Marker Variation and Trait Associations

SSR analysis revealed substantial genetic variation among the evaluated genotypes. CA12 was the most informative marker, producing six alleles (160–210 bp) with a PIC value of 0.72, whereas CA37 produced four alleles (190–240 bp) with a PIC value of 0.65 (Table 1).

The 180 bp allele of CA12 was uniquely detected in BARI Capsicum 1 and Pasarella RZ F1, while the 210 bp allele of CA37 was associated with Commandant F1. Marker–trait analysis showed that CA12 had strong associations with root hair density ($\phi = 0.87$), Pr2 length ($\phi = 0.73$), and ABA accumulation ($\phi = 0.68$). CA37 showed strong associations with ABA accumulation ($\phi = 0.81$) and Pr2 length ($\phi = 0.81$), whereas CAPS02 showed comparatively weaker relationships.

Table 1. SSR Marker-Trait Associations (ϕ coefficients)

Serial No	Marker	Allele (bp)	Root Hair Density	Pr2 Length	ABA (0.6% PEG)
1	CA12	180	0.87	0.73	0.68
2	CA37	210	0.52	0.81	0.81
3	CAPS02	145	0.31	0.42	0.29

Genetic Structure and Integrated Drought Response

Population structure analysis separated drought-tolerant and drought-sensitive genotypes into distinct genetic groups. BARI Capsicum 1 and Pasarella RZ F1 clustered together, whereas Kaberi F1 and Alexander F1 formed a separate group, with significant genetic differentiation between clusters ($D = 0.38$, $p = 0.002$).

DISCUSSIONS

Drought tolerance in *Capsicum annuum* is a complex trait governed by coordinated morphological, physiological, biochemical, and genetic mechanisms. In the present study, PEG-induced osmotic stress significantly affected root development, physiological regulation, antioxidant activity, and reproductive performance among the evaluated genotypes. However, the magnitude of these responses varied considerably, indicating substantial genetic differences in drought adaptation capacity. The tolerant genotypes, particularly BARI Capsicum 1 and Pasarella RZ F1, maintained better performance under stress through

integrated regulation of root architecture, hormonal adjustment, oxidative protection, and genetic factors.

Root architectural modification represents one of the earliest and most important adaptive responses of plants exposed to water limitation. In this study, drought stress significantly reduced root hair length, diameter, and estimated absorptive surface area, demonstrating that root hair development is highly sensitive to osmotic stress. Root hairs increase the effective soil–root contact area and contribute significantly to water and nutrient acquisition under drought conditions (Haling et al., 2014). Similar reductions in root hair growth under water deficit have been reported in several crop species, where maintenance of root hair traits was associated with improved drought adaptation (Lynch, 2018). The considerable variation observed among *Capsicum* genotypes suggests that root hair plasticity is an important component of drought tolerance.

Although severe stress reduced root hair size in most genotypes, tolerant varieties maintained greater root functionality through alternative strategies. Pasarella RZ F1 preserved longer root hairs under stress, whereas BARI Capsicum 1 increased root hair density, indicating that different genotypes may employ distinct mechanisms to maintain water uptake capacity. Such variation in root system architecture provides valuable genetic resources for improving drought resilience. Previous studies have emphasized that drought-adapted plants often optimize root traits through increased branching, deeper rooting, and enhanced root hair formation rather than relying on a single root characteristic (Lynch, 2018).

The phytomer-based analysis further revealed that drought responses were not uniform throughout the root system. The Pr2 region showed the greatest sensitivity to osmotic stress, whereas tolerant genotypes maintained greater Pr2 elongation compared with sensitive genotypes. Preservation of active root growth zones may enable continued exploration of available water resources under drought conditions. Root developmental plasticity is considered a key mechanism allowing plants to adjust growth patterns according to environmental limitations (Comas et al., 2013). Therefore, the maintenance of Pr2 development in BARI Capsicum 1 may contribute to its superior drought performance.

Drought adaptation also involves complex physiological regulation, particularly through abscisic acid (ABA)-mediated responses. In the present study, drought-tolerant genotypes showed enhanced ABA accumulation under PEG stress, with Pasarella RZ F1 exhibiting a significant increase in ABA concentration. The negative association between ABA content and stomatal conductance indicates that increased ABA accumulation promoted effective stomatal regulation, thereby reducing water loss under stress conditions. ABA is a central drought-signaling molecule that regulates stomatal closure, root responses, and expression of stress-responsive genes (Wilkinson & Davies, 2002). Similar genotype-dependent differences in ABA accumulation and water-use regulation have been reported in pepper and other Solanaceous crops under drought stress (Malika et al., 2019; Dias et al., 2021).

Interestingly, tolerant genotypes maintained higher ABA accumulation while retaining better photosynthetic performance, suggesting efficient stress regulation rather than excessive growth inhibition. This balance between water conservation and carbon assimilation is critical for maintaining productivity under drought conditions. Genotypes with delayed or insufficient ABA responses may experience excessive water loss, leading to greater physiological damage and reduced reproductive performance.

Drought-induced oxidative stress is another major limitation affecting plant growth and productivity. Water deficit enhances reactive oxygen species (ROS) accumulation, which can damage cellular membranes, proteins, and photosynthetic systems. In this study, tolerant genotypes exhibited improved antioxidant capacity through increased ascorbate accumulation and higher glutathione redox status. The ascorbate–glutathione pathway plays a central

role in detoxifying ROS and maintaining cellular redox balance under environmental stress (Foyer & Noctor, 2011). Similar enhancement of antioxidant defense mechanisms has been reported in drought-tolerant pepper genotypes, where increased antioxidant activity was associated with reduced oxidative injury and improved stress tolerance (Malika et al., 2019).

The differences in antioxidant responses among genotypes further explain their contrasting drought performance. BARI Capsicum 1 and Pasarella RZ F1 maintained higher GSH/GSSG ratios, indicating stronger cellular protection capacity under stress. In contrast, sensitive genotypes such as Kaberi F1 showed reduced antioxidant buffering ability, suggesting greater oxidative damage during drought exposure. These findings demonstrate that antioxidant regulation is an important physiological determinant separating tolerant and sensitive *Capsicum* genotypes.

Drought stress frequently causes significant reproductive losses by reducing flower retention, fruit development, and biomass accumulation. Despite exposure to severe osmotic stress, tolerant genotypes maintained higher fruit dry weight compared with sensitive varieties. The improved reproductive performance of BARI Capsicum 1 suggests that efficient root function and physiological regulation contributed to sustained carbon availability for reproductive development. Similar relationships between root traits, antioxidant activity, and yield stability under drought have been reported in pepper and other vegetable crops (Dias et al., 2021).

The molecular analysis further strengthened the identification of drought-responsive genotypes. SSR markers revealed substantial genetic variation among the evaluated materials, with CA12 showing strong associations with root hair density, Pr2 development, and ABA accumulation. SSR markers are valuable tools for drought breeding because of their reproducibility, codominant inheritance, and ability to detect genetic variation linked with adaptive traits (Cheng et al., 2016). However, marker-trait associations identified under controlled conditions require further validation under field environments before their application in breeding programs.

The presence of favourable alleles, particularly CA12 (180 bp) and CA37 (210 bp), in drought-performing genotypes suggests their potential usefulness for marker-assisted selection. Integration of molecular markers with physiological and phenotypic screening can accelerate the identification of superior breeding materials and improve the efficiency of drought tolerance improvement programs. Overall, the findings demonstrate that drought tolerance in *Capsicum annuum* is not controlled by a single mechanism but results from coordinated interactions among root architectural plasticity, ABA-mediated regulation, antioxidant defense, and genetic variation. The superior performance of BARI Capsicum 1 and Pasarella RZ F1 under PEG-induced drought stress highlights their potential as valuable genetic resources for developing climate-resilient pepper cultivars. The integrated approach combining phytomer-level root analysis, physiological characterization, and molecular marker evaluation provides a comprehensive framework for future drought tolerance breeding in *Capsicum*.

CONCLUSIONS

This study demonstrates that drought tolerance in *Capsicum annuum* is regulated through the coordinated interaction of root architectural plasticity, physiological adjustment, antioxidant defense, and genetic variation. PEG-induced osmotic stress significantly reduced root hair development and absorptive capacity; however, drought-tolerant genotypes maintained superior root performance through improved root hair density and preservation of critical phytomer growth, particularly the Pr2 region. Physiological analyses revealed that enhanced ABA accumulation, efficient stomatal regulation, and improved antioxidant capacity contributed to drought adaptation by maintaining cellular stability

and reducing oxidative damage. Among the evaluated genotypes, BARI Capsicum 1 and Pasarella RZ F1 exhibited superior drought resilience by sustaining root development, antioxidant balance, and reproductive performance under stress conditions.

Molecular characterization further identified CA12 and CA37 SSR markers as potential indicators associated with drought-responsive traits, including root architecture and ABA accumulation. These findings highlight the value of integrating root phenotyping, physiological screening, and molecular markers for identifying drought-resilient *Capsicum* genotypes. The identified tolerant genotypes and associated markers provide valuable resources for future marker-assisted breeding programs aimed at developing climate-resilient pepper cultivars for drought-prone environments.

ACKNOWLEDEMENT

This research was supported by the Ministry of Science and Technology, Bangladesh Government (Grant No: R&D-2410150) and Department of Agriculture, City University of Bangladesh.

CONFLICT OF INTEREST

The authors have no conflict of interest among them.

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How to cite: Bayazid, K.N., Ferdous, J., Mahmud, Q.M., Bir, M.S.H. and Ullah, M.A. 2026. Morpho-molecular characterization of *Capsicum annuum* L; drought-responsive traits under PEG-treated hydroponic conditions, *Journal of Contemporary Agriculture and Bioscience* 3(1), 24-30.

