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Research article

Harnessing root phenotyping and root growth plasticity of landraces of maize (*Zea mays* L.) for enhancing waterlogging tolerance in fragile and challenging agro-ecologies of Eastern Himalaya

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ABSTRACT

Maize is a major crop of the Eastern Himalayan Region (EHR) which faces significant environmental challenges including waterlogging (WL) under changing climate. Through microcosm and field experiments, this study aimed to evaluate the phenotypic plasticity and adaptive mechanisms of maize landraces under WL conditions at the seedling and flowering stages. Based on the response coefficient and waterlogging tolerance coefficient 14 landraces at the seedling stage were found to be WL tolerant whereas RCM-12-19, RCM-32-19, and RCM-16-19, emerged as WL tolerant at both stages. At seedling stage, Root Length ratio (RLR) has increased under WL stress to the tune of 98.4 % while Root Mass Ratio (RMR) has ranged from 0.09 to 0.47 for control and from 0.10 to 0.55 under WL. Root:shoot ratio varied from 0.10 to 0.88 and 0.11–1.23 under control and WL, respectively and a total of 19 genotypes reflected tolerance trait under WL. Phenotyping of key root traits (brace root angle (BA1), branching, and crown root number) revealed their substantial contribution to stress resilience, as confirmed by principal component analysis (PCA) and regression models. PCA indicates, for root tissue density (RTD) and root fineness (RF) at seedling stage, genotypes like RCM-34-19, RCM-10-19, RCM-23-19, RCM-42-19, and RCM-31-19 are closely associated with the second principal component (PC2). Whereas, at

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flowering stage, RCM-39-19, RCM-52-19, RCM-34-19, RCM-32-19, RCM-2-19, RCM-43-19, RCM-5-19, RCM-45-19, RCM-47-19, and RCM-50-19 exhibited strong positive loadings on (PC2) for the trait BA1. The results indicate that brace- and crown roots exhibit genotype-dependent architectural plasticity, which reduces the metabolic cost of soil exploration by increasing BA1, branching of brace roots (BB), and the number of brace roots (BO) while decreasing above-ground whorls (BW); thereby improving nutrient uptake from topsoil under WL stress. RCM-12-19, RCM-32-19, RCM-16-19, and RCM-23-19 demonstrated rapid root growth and branching after WL stress at the flowering stage, supporting their potential for breeding WL-tolerant maize. These findings align with the "steep, cheap, and deep" (SCD) root ideotype, where reduced crown root number and deeper root architecture improve nutrient uptake and yield. Genotype RCM-11-19 apart from scoring high through visual scoring was also found to have the highest dry biomass (76.7 g plant-1) and grain yield (12.2 g plant-1) under WL conditions. This research identifies critical root traits and promising genotypes for developing WL-tolerant maize, contributing to sustainable crop production in rain-fed EHR environments.

1. Introduction

The Eastern Himalayan region (EHR) being a mountainous region of varied altitudes is quite challenging agro-landscape for crop cultivation under changing climatic patterns. Among all the climatic anomalies, intense rainfall-induced transient and long-term flooding is potentially increasing to assume serious abiotic stress for arable crops under hill slopes cum valley lands of EHR. The Southeast Asian region experiences crop failures due to soil water logging due to erratic rainfall and changing climate, resulting in yield reductions of 25%–100 % [1]. Unprecedented land degradation and intense nutrient leaching in the backdrop of heavy rainfall *vis.* a *vis.* acid soil induced nutrient imbalances are a real cause of concerns that affect crop production and productivity in the region [2,3]. Maize (*Zea mays* L.) being the second most important staple crop of the EHR after rice, is ideally cultivated during summer and Kharif seasons [3,4]. Maize crop establishment and productivity are substantially impacted by these stresses resulting in sub-optimal growth performance, lower yields, and crop failures of indigenous landraces [4]. Although rain-fed maize crops are primarily grown during the monsoon season, they are highly susceptible to waterlogged anaerobic soil conditions in the root zone. This sensitivity arises from the negative impact of poor drainage on different stages of crop growth, overall affecting plant health, and maize grain yield [5]. Maize growth and grain yield were most sensitive to waterlogging at the jointing stage among the various growth stages of maize which is followed by the seedling, tasseling, and milk maturity stages [6].

Waterlogging (WL) refers to a condition where soil becomes fully saturated with water, leading to adverse alterations in its properties. These changes can significantly impede a plant's ability to survive [7]. The effect of waterlogging stress on anatomical, physiological, and biochemical attributes of tolerant maize cultivars is well documented [8,9]. WL significantly diminishes root respiration, root and shoot growth, seedling growth, and biomass accumulation along with disruption of the plant-nutrient pathway [10–12]. Additionally, it triggers overproduction of reactive oxygen species (ROS) which damage the chloroplast membrane lipid structure and the activities of photosynthetic enzymes and accelerate leaf senescence [13].

Root system architecture (RSA) is pivotal in maize for optimizing nutrient and water uptake efficiency, directly influencing plant development, biomass growth, and yield by serving as the critical interface between plant and soil [14,15]. The arrangement of primary roots and their branches, originating from both roots and stems, is essential for optimum shoot physiology, ideal biomass growth, metabolism, and adaptability to environmental stress [16,17]. Traits such as root angle, depth, lateral root branching, and aerenchyma formation are particularly crucial in mitigating anaerobic stress in waterlogged soils, a growing challenge due to climate change and variable water availability. Steeper root angles and optimal crown root numbers enhance rooting depth, leading to improved water and nitrogen uptake, lodging resistance, and reduced inter-root competition. Plasticity in RSA allows roots to adapt to stress by altering growth patterns, such as extending deeper or enhancing lateral roots to access oxygen and nutrients in less saturated soil layers. These adaptive traits, regulated by hormonal pathways involving auxins and abscisic acid (ABA), enhance resilience to waterlogging and other abiotic stresses. Therefore, in recent times use of root traits as indicators for screening maize genotypes for waterlogged tolerance is gaining importance. High-throughput field-based phenotyping methods like shovelomics, have revolutionized RSA assessment in maize by enabling visual scoring of traits [18]. This technique focuses on the root crown as it contains key traits that influence a plant's ability to capture resources. It enables the visual scoring of up to 10 root architectural traits, including root number, angle, and branching patterns, which are essential for understanding plant-soil interactions and resource utilization. This high-throughput approach helps identify genetic variation in root traits, aiding breeding programs aimed at improving drought tolerance and overall crop productivity [19].

The EHR harbours a range of crop landraces that are well-adapted to challenging climatic conditions like flood, drought, cold, acidic soil, and more. Therefore, it is imperative to promptly subject this diverse germplasm to thorough screening to utilize and harness its genetic potential for various breeding programs aimed at stressful environments. These landraces displayed a wide range of root morphological traits and plant types. Selecting genotypes with root traits that are well-suited to the target environment is essential for optimizing overall plant performance and productivity. Therefore, it is crucial to develop a robust RSA for optimal root distribution and organization, which maximizes water and nutrient uptake in a limited environment. Currently, root phenotyping is a focal point for researchers; especially to identify optimum RSA to combat abiotic stresses, particularly moisture stress and drought [20,21,22]. Considering the rich diversity of maize landraces in the EHR, adapted to varying rainfall zones, there is a compelling need to assess their susceptibility to waterlogging at different growth stages. Therefore, this study aims to catalog distinctive maize landraces based on root architecture, focusing on their response to waterlogged conditions during seedling and flowering stages. Through comprehensive phenotypic evaluation, the research seeks to identify genotypes with optimal RSA, crucial for mitigating the adverse effects of waterlogging and enhancing maize productivity in challenging environments.

2. Material and methods

2.1. Plant materials and location of the experiment

A total of 452 landraces of maize were collected from different parts of the NEH region of India, including Manipur, Meghalaya, and Mizoram for the present study. These landraces were collected from the germplasm pool of respective ICAR-RC for Regional centers and directly from farmers during exploration visits. These landraces were initially selected to capture the broad genetic and phenotypic diversity, geographical distribution, environmental adaptability, and traditional knowledge provided by local farmers. Two distinct sets of experiments: (i) the microcosm (pot) and (ii) field experiment in the Randomized Complete Block Design (RCBD) were conducted to evaluate the tolerance of maize landraces to waterlogging stress at both seedling and flowering stages. Both experiments were, conducted at Lamphelpat farm of ICAR-RC-NEH Region, Manipur Centre (latitude: 240 45′ N, longitude: 930 54′ E and altitude: 774 m above mean sea level; map as shown in Supplementary Fig. S1 for three consecutive years i.e., from 2018 to 2020. The graphical representation of three years of rainfall data documented during the crop duration is presented in Supplementary Fig. S2.

2.2. Screening of landraces for waterlogging tolerance

2.2.1. Microcosm experiment for screening at the seedling stage

The selection process for the maize landraces used in the present study was methodical and based on previous performance under WL conditions at the seedling stage over multiple experimental cycles. Initially, 452 maize landraces along with one popular hybrid (HQPM-5), for comparison were planted in plastic pots (30 cm diameter × 21 cm base diameter × 27 cm height) during April 2018 to assess their WL tolerance at seedling stage. In the current study, each pot contained three plants of each landrace, with three replications. All the pots were uniformly filled with water, maintained at 4–5 cm above the soil surface, at the 6–8 leaf stage of the plants. This water level was consistently maintained for 15 days [23,24]. The chosen water level effectively mimics natural waterlogging scenarios, where excess water saturates the soil, reducing oxygen availability for roots. The 6–8 leaf stage was selected as it represents a crucial developmental period preceding the reproductive phase. Stress during this stage has been shown to significantly influence yield components, making it an ideal window for assessing genotype responses to waterlogging [25]. These conditions provide a realistic framework to evaluate resilience under transient waterlogging events, which are increasingly prevalent in regions like the Eastern Himalayas due to erratic rainfall and climate variability.

The soil texture was clay loam (32 % sand, 35 % silt, and 33 % clay) having pH 5.87, organic carbon content of 2.03 %, available N, P, and K 6.42, 6.34, and 181.4 kg ha^{-1} respectively. Following the 15-day waterlogging treatment, only 227 landraces survived and were shortlisted for further evaluation. In April 2019, these 227 landraces were replanted under identical WL conditions for a second round of assessment. From this group, 35 landraces were selected for the present study. The selection of this subset was based on their consistent performance under WL stress and seed availability. During April 2020, these selected landraces were subjected to the same WL condition as before, with water level maintained at 4–5 cm above the soil surface for 15 days at the 6–8 leaf stage. The experiment was replicated three times. Concurrently, the same set of germplasm was also planted under non-stress control conditions, where pots were managed without flooding simulation. Instead, soil moisture was maintained by watering the pots at regular intervals to ensure optimal growth. These conditions were replicated three times to provide a reliable comparison and validation of plant performance under waterlogging and non-stress environments.

2.2.2. Field experiment for screening at the flowering stage

In the first year of the study, i.e. March 2018, all 452 landraces were planted to assess their tolerance to WL conditions at the flowering stage. The plot size was 5.4 m^2 for each landrace; row-to-row and plant-to-plant distances were maintained at 60 cm and 20 cm, respectively. Artificial flooding was induced at the time of flowering stage, with water level up to 20–25 cm above the soil surface for 10 days. After 10 days of continuous artificial flooding at field conditions, only 42 landraces were able to be maintain and established out of 452 landraces. The majority of landraces either failed to flower or the anther silking interval (ASI) was too extended to maintain the population through controlled pollination due to stress. In March 2019, the 42 surviving landraces were reassessed under identical WL conditions. The experiment was replicated three times.

2.3. Root phenotyping

2.3.1. Seedling stage

For the present study, a total of 35 landraces (based on the result of the pot experiment) were selected and planted during March 2020. The plot size was 5.4 m^2 for each landrace; row-to-row and plant-to-plant distances were maintained at 60 cm and 20 cm, respectively. The plants were then subjected to artificial flooding up to 20–25 cm above the soil surface continuously for 10 days (treatment) at the time of flowering. Simultaneously, the same set of landraces was also grown under control conditions for comparison and validation. The experiment was replicated three times. After 15 days of WL stress at the 6–8 leaf stage, seedlings from each genotype were carefully uprooted and dissected into shoots and roots. To minimize root damage and recover as many coarse and fine roots as possible, the surrounding soil was gently loosened using hand tools, following established protocols [26]. Then the roots were carefully washed with water to remove any adhering soil and then air-dried. Fresh and air-dried roots were spread on a fiber plate equipped with an Epson root scanner (EPSON V700), ensuring minimal overlap and meticulous handling. The root images were obtained using WinRHIZO professional software (Reagent Instruments, Quebec, Canada) to analyze various root morphological and two-dimensional architectural traits [21,27,28,29]. These traits include total root length (TRL), root surface area (RSA), root volume (RV), average root diameter (RD), number of tips (Ntips), number of forks (N forks), number of crosses (N cross), and number of links (Nlinks). The roots and shoots of the maize seedlings were separated and then subjected to subsequent scanning. Following this, they were further subjected to drying in a hot air oven at a temperature of 72 °C for 48 h or until a consistent weight was achieved. This process was carried out to obtain the dry biomass of the seedlings. The calculation of Total Dry Matter (TDM) during the active growth stage involved the summation of the dry weight of both the shoot and root components of the crop. The root-to-shoot ratio was determined by dividing the dry weight of the roots by the dry weight of the shoots.

The TRL was calculated using the following formula: Length = number of pixels in the skeleton multiplied by the pixel's dimension. WinRHIZO calculates the average root diameter based on the total projected root length and area. The average diameter was calculated using the formula: Diam_{avg} = Projected area/total root length. Additionally, functional traits like root length ratio (root length by whole plant dry weight, cm g^{-1}), root mass ratio (root dry weight by whole plant dry weight, g g^{-1}), root fineness (root length by root volume, g cm^{-3}), root tissue density (root dry mass by root volume, g cm^{-3}) were also calculated based on the aforementioned measurements.

2.3.2. Flowering stage

The roots of representative plants from each plot were extracted by excavating a cylindrical column of soil with a diameter of 40 cm and a depth of 25 cm around the roots from the field experiment. The plant base served as the horizontal center of the soil cylinder during the harvest, following the methodology outlined by Trachsel et al. [19]. The excavated root crowns underwent a quick shaking process followed by a low-pressure water rinse to thoroughly cleanse any soil adhering to the roots. Subsequently, a visual assessment was conducted on the fresh and soil-free roots from the field experiment to determine the following characteristics: the number of above-ground whorls (BW), the number of brace roots (BO), the angle of the first and second arm of brace roots originating from the first and second whorl concerning horizontal (BA1, BA2, etc.), the branching of brace roots (BB), and the numbers crowns (CN), crown angles (CA), and crown branching (CB) of crown roots. Each attribute was assigned a value between one and nine based on the visual assessment [30]. A rating of one denotes low root numbers, shallow root angles (10°), and poor branching density (0.5 lateral root cm^{-1}) while a rating of nine indicates higher numbers, sharp root angles (90°), and higher branching density (7 lateral roots cm^{-1}).

2.4. Dry biomass and grain yield

The mean dry biomass (DB) and grain yield (GY) per plant (g) of each genotype were recorded to estimate the overall potential of the genotypes under WL conditions.

2.5. Phenotypic plasticity and waterlogging tolerance index

The comprehensive evaluation and identification of tolerant maize landraces to the WL condition was established through the calculation of response coefficient (RC) or phenotypic plasticity index and waterlogging tolerance coefficient (WTC). WTC has been validated through various studies across different crops, demonstrating its effectiveness and reliability as an index for assessing waterlogging tolerance [31,32]. By integrating multiple physiological indicators, the WTC provides valuable insights into the performance and recovery potential of genotypes under waterlogged conditions. The Response Coefficient (RC) as phenotypic plasticity index [22,33] was calculated for each genotype as given in Eq (1):

$$RC = V_C / V_T \tag{Eq. 1}$$

Where V_C and V_T are the average values of traits obtained under the control and treatment (waterlogging) conditions.

If the RC value is equal to 1, it has indicated no response to the treatment; while RC<1 and RC>1 indicated tolerance and susceptibility to the treatment, respectively.

Waterlogging tolerance coefficient (WTC) was used to measure WL tolerance. WTC of samples was calculated using the following formula Eq. (2) [34],:

$$WTC = \text{Mean value of treatment} / \text{Mean value of control} \tag{Eq. 2}$$

2.6. Statistical analysis

A heatmap and principal component analysis (PCA) were estimated based on the response mechanism of maize to WL. The PCA was conducted using IBM SPSS statistics version 20. The heatmap was created using R Studio and an enhanced version of the "gplot" tool. To clearly distinguish between the high and low correlations, orthogonal transformations to the reduced factors were created using varimax rotation. For multi factorial comparison, Pearson's correlation, PCA, and heat map depicting agglomerative hierarchical clustering (AHC) were used to display the correlation between the various parameters and their relationship in both control and WL conditions. Stepwise linear multiple regression (SLMR) analysis was also computed to evaluate the relationships between the response variables (primary root traits) and grain yield using the formula below (Eq. (3)):

$$Yi = \beta 0 + \beta 1\ xi1 + \beta 2\ xi2 + \beta p\ xip + \varepsilon \tag{Eq. 3}$$

Where, i = no. of observations, Yi = dependent variable or predicted variable, xi = explanatory variables, β0 = y-intercept (constant term), i.e., the value of y when both xi1 and xi2 are 0. β1and β2 = the regression coefficients that represent the change in y relative to a one-unit change in xi1 and xi2, respectively. βp = slope coefficients for each explanatory variable. ϵ = the model's error term (also known as the residuals).

3. Results

3.1. Extent of root growth and its plasticity at seedling stage in a microcosm experiment

Root length ratio (RLR) ranged from 36.23 to 298.87 under control conditions and 94.32 to 771.39 under waterlogging (WL) conditions (Table 1). Most cultivars exhibited an RLR response coefficient (RC) of less than 1, indicating their adaptive nature to WL stress (Fig. 1). On average RLR has significantly increased under WL stress to the tune of 98.4 % whereas the root mass ratio (RMR) has ranged from 0.09 to 0.47 for control and from 0.10 to 0.55 under WL condition (Table 1). Out of 35 cultivars, 19 showed tolerance reaction against WL for RMR with RC values less than 1. RMR has also increased significantly to the tune of 7.69 % under WL stress. The maximum WTC for RLR was recorded for RCM-13-19 (5.28), followed by RCM-19-19(4.85) and RCM-39-19(4.54) while the lowest WTC was observed for RCM-15-19(0.70). The Highest WTC for RMR was exhibited by RCM-45-19 (5.01) followed by RCM-3-19 (2.52) and RCM-26-19 (2.23) and the lowest value were recorded for RCM-34-19 (0.42) (Table 1). From Tables 1 and it can be observed that root fineness values ranged from 21.71 to 176.53 under control and 27.13–397.09 under WL conditions and there was a significant increase of 10.69 % under WL stress. A total of 15 cultivars out of 35 exhibited RC values less than 1 for root fineness indicating their tolerance against WL conditions (Table 1). The mean value of root tissue density (RTD) under the control conditions ranged from 0.04 to 0.93, whereas the mean value under WL conditions varied from 0.02 to 0.26 (Table 1). Only 9 genotypes out of 35 showed an RC value for RTD is less than 1 (Table 1), indicating their tolerance against WL stress. In general, WL stress has significantly increased RTD to the tune of 46 % (Table 1). The highest WTC for root fineness was found in HQPM- 5 (18.29), followed by RCM-43-19 (3.18) and RCM-44-19 (3.09), while the lowest value was exhibited by RCM-21-19 (0.21). The highest WTC for RTD was observed in RCM-49-19 (4.19), followed by RCM-43-19 (2.40) and HQPM-5 (2.31), while the minimum value was shown by RCM-21-19 with a value of 0.13.

The mean value of the root:shoot ratio varied from 0.10 to 0.88 and 0.11–1.23 under control and WL conditions, respectively (Table 1). Nineteen (19) genotypes reflected tolerance reaction for the trait against the WL condition. R/S ratio has increased to the tune of 16.2 % under WL stress over control (Table .1). RCM-45-19 showed the highest value of WTC for root-to-shoot ratio (8.47) followed by RCM-26-19 (3.22) and RCM-3-19 (3.10). The lowest value of WTC for the root-to-shoot ratio was exhibited by the genotype RCM-34-19 (0.28). A gradual decline to the tune of 13.2 % has been recorded in the mean values of chlorophyll content expressed in terms of SPAD chlorophyll meter reading (SCMR) in most of the cultivars under the WL condition is evident in this study. Mean chlorophyll content significantly decreased under WL stress and ranged from 2.80 to 13.43 and 2.93–7.10 SCMR, respectively for control and WL conditions (Table 1). The genotype RCM-52-19 (1.40) exhibited the maximal value of WTC for SCMR which was closely followed by RCM-16-19 (1.35) and RCM-39-19 (1.31) while the lowest value was observed in RCM-10-19 with a value of 0.26 (Table 1).

The root and shoot dry weight (RDW and SDW) varied across genotypes under control and WL conditions. RDW ranged from 0.11 to 0.76 and 0.03–0.97 under control and WL conditions, respectively and it noted that RDW has been significantly decreased to the tune of 17.14 % (Table 1). A total of 14 genotypes showed RC<1 for SDW, showing an adaptive fitness to WL stress. The mean values of SDW ranged from 0.31 to 3.74 and 0.27–2.57, respectively under control and WL conditions, and a significant decline of 29.7 % was witnessed under WL stress (Table 1). Nine out of 35 genotypes have shown RC values less than 1 for RDW which indicates their adaptive nature towards the WL condition at the seedling stage. The WTC for SDW was highest in genotype RCM-21-19 (3.45), followed by RCM-10-19 (2.09) and RCM-23-19 (1.83), while the lowest value was seen in genotype HQPM-5 (0.15) for shoot dry weight (Table 1). Comparative images of root growth, illustrating the root architecture of selected genotypes under both control and WL conditions during the seedling stage, are presented in Supplementary Fig. 3. Cultivars like RCM-45-19 (3.68), RCM- 10–19 (2.26), and RCM-21-19 (1.70) demonstrated higher WTC values for the root dry weight, whereas genotype HQPM-5 exhibited the lowest WTC value (0.06).

3.2. Root phenotyping through visual scoring at flowering stage (field experiment)

The WL had a significant impact on the root trait scores of various maize cultivars compared to the control (Table 2). Root images comparing the root architecture (main root, brace root, and crown root) of some cultivars at the flowering stage under control and WL conditions revealed notable differences in root traits (Supplementary Fig. 4). The score of BW ranged from 1 to 4 and 0–6 under control and WL conditions, respectively. RCM-34-19 exhibited the highest score under WL condition but the lowest score was observed in RCM-8-19 (1) under both conditions. For BO, the score varied from 2.5 to 8.5, with HQPM-5 gaining the highest score (8.5) under control whereas, under WL condition the score ranged from 0 to 9, with RCM-1-19 and RCM-47-19 obtaining the highest score. The score of BA1 ranged from 2.5 to 5.5 under control condition but showed a decreasing trend ranging from 0 to 5 under the WL condition.

Table 1

Root parameters and chlorophyll content of 35 maize landraces under control (non-stress) and waterlogged (stress) conditions at seedling stage.

Genotypes	Root length ratio		Root mass ratio		Root fineness		Root tissue density		Root: Shoot		Chlorophyll content		Root dry weight (g)		Shoot dry weight (g)	
	C	WL	**C**	WL	**C**	WL	**C**	WL	**C**	WL	**C**	WL	**C**	WL	**C**	WL
RCM-8-19	244.24^{bcd}	291.51^{cdef}	0.30^{cd}	0.46^{bcd}	61.58^{a}	27.13^{j}	0.08^{a}	0.04^{a}	0.08^{e}	0.04^{h}	6.58^{bc}	5.85^{c}	0.32^{cd}	0.29^{cd}	0.73^{cd}	0.34^{cd}
RCM-11-19	122.54^{gh}	261.79^{efg}	0.41^{abc}	0.36d^{ef}	56.71^{b}	47.68^{f}	0.19^{b}	0.07^{b}	0.19^{b}	0.07^{g}	4.13^{e}	3.70^{e}	0.55^{a}	0.30^{cd}	0.79^{bcd}	0.53^{bcd}
RCM-2-19	203.25^{de}	364.33^{bc}	0.37^{bc}	0.37^{cde}	68.95^{a}	44.44^{e}	0.13^{a}	0.05^{a}	0.13^{d}	0.05^{h}	8.65^{a}	5.80^{c}	0.46^{ab}	0.33^{cd}	0.78^{bcd}	0.56^{bcd}
RCM-23-19	164.61^{efg}	160.38^{h}	0.21^{fg}	0.14^{g}	151.38^{c}	145.95^{b}	0.20^{c}	0.13^{c}	0.20^{b}	0.13^{e}	5.70^{cd}	6.65^{b}	0.11^{f}	0.12^{f}	0.41^{de}	0.74^{bcd}
RCM-41-19	102.36^{gh}	350.34^{bcd}	0.20^{fg}	0.22^{fg}	38.03^{f}	78.19^{c}	0.08^{a}	0.05^{a}	0.08^{e}	0.05^{h}	3.65^{f}	3.06^{f}	0.29^{de}	0.15^{ef}	1.13^{ab}	0.51^{bcd}
RCM-4-19	119.11^{gh}	487.64^{ab}	0.16^{g}	0.22^{fg}	89.60^{d}	54.29^{e}	0.12^{a}	0.02^{a}	0.12^{d}	0.02^{i}	4.50^{e}	3.60^{e}	0.14^{ef}	0.19^{ef}	0.70^{cd}	0.67^{bcd}
RCM-31-19	98.43^{h}	161.21^{h}	0.20^{fg}	0.17^{fg}	88.81^{d}	106.46^{b}	0.18^{b}	0.12^{b}	0.18^{b}	0.12^{e}	7.45^{ab}	6.05^{bc}	0.47^{ab}	0.31^{cd}	1.93^{a}	1.45^{a}
RCM-44-19	152.28^{efg}	444.61^{ab}	0.29^{de}	0.29^{def}	23.72^{h}	73.23^{d}	0.05^{a}	0.05^{a}	0.05^{f}	0.05^{h}	4.25^{e}	4.10^{de}	0.62^{a}	0.17^{ef}	1.51^{ab}	0.40^{de}
RCM-16-19	121.18^{gh}	485.82^{ab}	0.19^{fg}	0.38^{cde}	107.33^{c}	31.35^{i}	0.17^{b}	0.02^{a}	0.17^{c}	0.02^{i}	5.13^{de}	6.93^{b}	0.21^{ef}	0.23^{de}	0.87^{bcd}	0.37^{de}
RCM-36-19	134.74^{fgh}	164.96^{h}	0.34^{bcd}	0.20^{fg}	73.70^{e}	33.30^{i}	0.19^{b}	0.04^{a}	0.19^{b}	0.04^{h}	3.63^{f}	4.25^{de}	0.45^{ab}	0.21^{def}	0.87^{bcd}	0.86^{bcd}
RCM-39-19	169.77^{efg}	771.39^{a}	0.20^{fg}	0.29^{def}	32.20^{g}	56.59^{e}	0.04^{a}	0.02^{a}	0.04^{g}	0.02^{i}	4.03^{e}	5.28^{cd}	0.23^{def}	0.17^{ef}	0.93^{bcd}	0.43^{de}
RCM-21-19	135.34^{fgh}	133.33^{h}	0.39^{abc}	0.24^{fg}	176.53^{a}	36.50^{h}	0.51^{d}	0.07^{b}	0.51^{a}	0.07^{g}	3.38^{f}	3.65^{e}	0.20^{ef}	0.34^{cd}	0.31^{ef}	1.07^{bc}
RCM-50-19	143.01^{efg}	306.26^{def}	0.37^{bc}	0.25^{efg}	36.76^{f}	74.26^{c}	0.10^{a}	0.06^{a}	0.10^{e}	0.06^{h}	4.07^{e}	4.09^{de}	0.76^{ab}	0.20^{def}	1.26^{ab}	0.61^{bcd}
RCM-42-19	89.88^{h}	158.22^{h}	0.16^{g}	0.19^{fg}	101.02^{c}	99.44^{b}	0.18^{b}	0.12^{b}	0.18^{b}	0.12^{e}	3.53^{f}	4.08^{de}	0.31^{de}	0.32^{cd}	1.60^{ab}	1.38^{a}
RCM-15-19	165.54^{efg}	115.82^{h}	0.27^{de}	0.24^{fg}	41.34^{e}	33.83^{i}	0.07^{a}	0.07^{b}	0.07^{f}	0.07^{g}	3.70^{f}	3.75^{e}	0.32^{cd}	0.37^{cd}	0.87^{bcd}	1.20^{ab}
RCM-51-19	191.72^{def}	361.93^{bc}	0.24^{ef}	0.36^{def}	43.33^{e}	78.73^{c}	0.05^{a}	0.08^{b}	0.05^{f}	0.08^{f}	4.85^{de}	4.30^{de}	0.39^{bc}	0.26^{de}	1.23^{ab}	0.46^{de}
RCM-6-19	194.02^{def}	146.20^{h}	0.30^{cd}	0.17^{fg}	57.58^{b}	38.98^{h}	0.09^{a}	0.04^{a}	0.09^{e}	0.04^{h}	5.83^{cd}	4.75^{de}	0.39^{bc}	0.31^{cd}	0.91^{bcd}	1.56^{a}
RCM-52-19	76.54^{h}	105.95^{h}	0.27^{de}	0.21^{fg}	49.75^{d}	44.11^{e}	0.18^{b}	0.09^{b}	0.18^{b}	0.09^{f}	4.13^{e}	5.80^{cd}	0.35^{cde}	0.23^{de}	0.95^{bcd}	0.84^{bcd}
RCM-34-19	42.24^{i}	95.10^{h}	0.47^{a}	0.20^{fg}	84.49^{d}	67.35^{d}	0.93^{e}	0.14^{c}	0.93^{a}	0.14^{d}	4.53^{e}	3.63^{e}	0.49^{ab}	0.23^{de}	0.56^{de}	0.94^{bcd}
RCM-9-19	130.21^{fgh}	163.63^{h}	0.22^{fg}	0.22^{fg}	110.18^{c}	54.54^{e}	0.18^{b}	0.07^{b}	0.18^{b}	0.07^{g}	4.55^{e}	3.18^{f}	0.19^{ef}	0.30^{cd}	0.69^{cd}	1.05^{bc}
RCM-1-19	170.75^{efg}	336.71^{cde}	0.25^{de}	0.32^{def}	69.69^{e}	65.60^{d}	0.10^{a}	0.06^{a}	0.10^{e}	0.06^{h}	4.90^{de}	4.03^{de}	0.25^{def}	0.18^{ef}	0.76^{bcd}	0.39^{de}
RCM-19-19	36.23^{i}	175.80^{gh}	0.13^{g}	0.13^{g}	29.07^{g}	49.69^{f}	0.10^{a}	0.04^{a}	0.10^{e}	0.04^{h}	8.78^{a}	7.08^{ab}	0.56^{a}	0.18^{ef}	3.74^{a}	1.20^{ab}
HQPM-5	39.54^{i}	152.22^{h}	0.21^{fg}	0.10^{g}	21.71^{i}	397.09^{a}	0.11^{a}	0.26^{d}	0.11^{e}	0.26^{a}	7.33^{ab}	5.70^{cd}	0.47^{ab}	0.03^{g}	1.82^{bc}	0.27^{e}
RCM-5-19	298.87^{a}	490.30^{ab}	0.31^{cd}	0.38^{cde}	75.64^{e}	38.93^{h}	0.08^{a}	0.03^{a}	0.08^{e}	0.03^{i}	4.73^{e}	3.53^{f}	0.23^{def}	0.17^{ef}	0.49^{de}	0.27^{e}
RCM-45-19	86.41^{h}	231.56^{fg}	0.09^{g}	0.46^{bcd}	56.21^{b}	33.45^{i}	0.06^{a}	0.07^{b}	0.06^{f}	0.07^{g}	6.60^{bc}	5.30^{cd}	0.16^{ef}	0.57^{a}	1.52^{ab}	0.66^{bcd}
RCM-32-19	156.83^{efg}	350.96^{bcd}	0.39^{abc}	0.33^{def}	48.12^{d}	57.57^{e}	0.12^{a}	0.05^{a}	0.12^{d}	0.05^{h}	5.08^{de}	4.38^{de}	0.32^{cd}	0.33^{cd}	0.51^{de}	0.66^{bcd}
RCM-28-19	129.85^{gh}	180.97^{gh}	0.25^{de}	0.17^{fg}	43.99^{e}	72.19^{d}	0.08^{a}	0.07^{b}	0.08^{e}	0.07^{g}	4.13^{e}	4.47^{de}	0.31^{de}	0.18^{ef}	0.94^{bcd}	0.90^{bcd}
RCM-13-19	87.79^{h}	463.55^{ab}	0.21^{fg}	0.32^{def}	59.97^{b}	88.22^{c}	0.15^{b}	0.06^{a}	0.15^{c}	0.06^{h}	4.88^{de}	4.05^{de}	0.54^{ab}	0.18^{ef}	1.96^{ab}	0.39^{de}
RCM-3-19	64.41^{hi}	287.86^{def}	0.11^{g}	0.28^{def}	106.61^{c}	74.98^{c}	0.18^{b}	0.07^{b}	0.18^{b}	0.07^{g}	5.48^{cd}	4.35^{de}	0.21^{ef}	0.24^{de}	1.71^{bc}	0.63^{bcd}
RCM-43-19	251.97^{bc}	407.73^{abc}	0.29^{de}	0.36^{def}	31.17^{g}	99.13^{b}	0.04^{a}	0.09^{b}	0.04^{g}	0.09^{f}	5.36^{cd}	4.38^{de}	0.21^{ef}	0.21^{def}	0.51^{de}	0.37^{de}
RCM-10-19	87.00^{h}	94.32^{h}	0.26^{de}	0.27^{def}	43.96^{e}	39.99^{h}	0.13^{a}	0.12^{b}	0.13^{d}	0.12^{e}	13.43^{a}	3.55^{f}	0.43^{bc}	0.97^{b}	1.23^{ab}	2.57^{a}
RCM-49-19	221.54^{de}	200.78^{gh}	0.30^{cd}	0.55^{bc}	29.09^{g}	60.42^{e}	0.04^{a}	0.17^{c}	0.04^{g}	0.17^{b}	2.80^{f}	2.93^{f}	0.46^{ab}	0.71^{ab}	1.05^{bcd}	0.58^{bcd}
RCM-12-19	167.78^{efg}	220.04^{fg}	0.21^{fg}	0.41^{bcd}	83.10^{d}	108.02^{b}	0.10^{a}	0.20^{d}	0.10^{e}	0.20^{a}	4.53^{e}	3.58^{f}	0.39^{bc}	0.56^{ab}	1.45^{ab}	0.79^{bcd}
RCM-26-19	106.82^{gh}	323.64^{cde}	0.20^{fg}	0.45^{bcd}	56.33^{b}	99.58^{b}	0.11^{a}	0.14^{c}	0.11^{e}	0.14^{d}	6.05^{bc}	5.30^{cd}	0.29^{de}	0.30^{cd}	1.16^{ab}	0.37^{de}
RCM-47-19	162.46^{efg}	213.04^{fg}	0.34^{bcd}	0.23^{fg}	60.03^{b}	43.07^{de}	0.12^{a}	0.05^{a}	0.12^{abc}	0.05^{abc}	6.60^{bc}	7.10^{ab}	0.33^{cd}	0.30^{cd}	0.65^{de}	1.02^{bc}
Mean	139.12	276.00	0.26	0.284	65.93	72.98	0.15	0.081	0.371	0.431	5.34	4.635	0.35	0.29	1.10	0.773
LSD ($p = 0.05$)		0.35		0.23		0.26		0.89		0.15		0.31		0.09		0.16

Duncan's Multiple Range Test indicated significant differences among treatments, as shown by the varying alphabetical superscripts. Genotypes with the same superscript letter are not significantly different at the 5 % level.

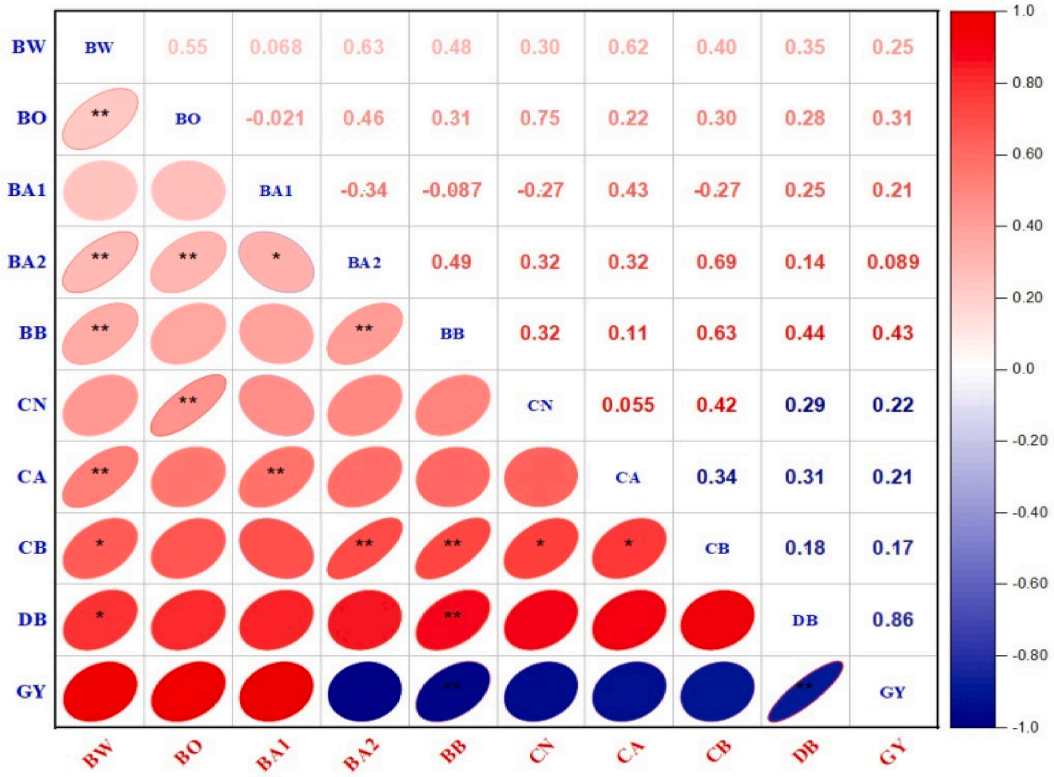

Fig. 1. Correlogram showing the correlation coefficients (r) between the root parameters in maize maturity stage under the control condition.

RCM-2- 19 and RCM-11-19 exhibited the highest score while RCM-8-19 showed the lowest value for BA1 under WL condition. Similarly, for the trait BA2, the score under control and WL conditions were at par with a score ranging from 0 to 7.5 and 0–7, respectively. The score for the trait BB exhibited a sharp decrease from 5 to 8 under control compared to the WL condition (ranging from 0 to 8). However, the score range for CN increased from 2.5 to 6.5 under control to 4.5–8.0 under WL condition. Similar trends of comparable scores were observed for CA and CB under both control and WL conditions.

RCM-8-19 was reported to have the lowest score for 4 characters out of 8 root characters studied under control conditions. RCM-23-19, RCM-4-19, RCM-16-19, RCM-36-19, and HQPM 5 genotypes performed better under normal growth conditions and exhibited higher scores for 3 or more traits. Under the WL condition, genotype RCM-11-19 scored the highest among 8 root characters studied, suggesting a tolerant nature to waterlogging. Some more promising lines having a high visual score for different root traits under WL conditions were RCM-34-19, RCM-1-19, RCM-13-19, RCM-12-19, and RCM-26-19. However, genotype RCM-8-19 again showed the lowest score for 6 root characters out of 8 studied, indicating its susceptible nature to WL.

3.3. *Correlation, clustered heatmaps and principal component analysis (PCA)*

3.3.1. *Seedling stage*

The correlogram depicting the correlation matrix for some major root traits under both control and WL conditions (Supplementary Figs. S5 and S6) at the seedling stage revealed a significant positive correlation among traits. Under control condition, the root-to-shoot ratio and root mass ratio exhibited the strongest positive correlation ($r = 0.99$). Significant positive correlation was observed between root-to-shoot ratio and root tissue density ($r = 0.55$), root fineness and root tissue density ($r = 0.49$), root mass ratio and root tissue density ($r = 0.45$), root mass ratio and root length ratio ($r = 0.32$), and root-to-shoot ratio and root length ratio ($r = 0.24$). Under the WL condition, the correlation between the root-to-shoot ratio and root mass ratio was the strongest and most significant ($r = 0.98$). A positive correlation was also noted between root fineness and root tissue density ($r = 0.73$), root mass ratio and root length ratio ($r = 0.37$), root-to-shoot ratio and root length ratio ($r = 0.28$), and root tissue density and root-to-shoot ratio ($r = 0.07$). These correlations indicate coordinated responses among root traits, reflecting their functional and structural interdependence during stress adaptation.

The PCA consolidated these findings by aggregating root traits variability into two principal components (PCs) under both conditions. Under control conditions, PC1 and PC2 explained 79.45 % of the total variance (Table 3). The root mass ratio (0.987) had the highest loading on PC1, followed by the root-to-shoot ratio (0.984) and root tissue density (0.496). For PC2, the highest loading was contributed by the root tissue density (0.823) followed by root fineness (0.688). The loading plot (Supplementary Fig. S7) indicates positive loadings of both PC1 and PC2 for root fineness and root tissue density, with genotypes viz. RCM-21-19 and RCM-34-19 have

Table 2

Visual scoring (0–9 scale) of primary root traits, dry biomass (DB) and grain yield (GY) of 35 genotypes under control and WL conditions.

Genotypes	BW		BO		BA1		BA2		BB		CN		CA		CB		Dry biomass (g/plant) at harvest		Grain yield (g/plant)	
	C	WL	**C**	WL	**C**	WL	**C**	WL	**C**	WL	**C**	WL	**C**	WL	**C**	WL	**C**	WL	**C**	WL
RCM-8-19	1^{c}	0^{e}	3^{def}	0^{e}	2.5^{ef}	0^{e}	4.5^{abc}	0^{e}	5^{abc}	0^{e}	3^{def}	5^{c}	4^{c}	4^{c}	6^{bc}	7^{ab}	90.9^{d}	46.8^{d}	26.4^{e}	7.9^{c}
RCM-11-19	3^{abc}	4^{ab}	5^{abcd}	6^{ab}	3.5^{cde}	5^{ab}	0^{e}	6.5^{ab}	5.5^{ab}	8^{a}	4^{abcd}	6^{ab}	6^{ab}	7^{a}	4.5^{cd}	8^{a}	109.1^{ab}	76.7^{ab}	33.8^{bc}	12.2^{ab}
RCM-2-19	3^{abc}	2^{bc}	5^{abcd}	6^{ab}	5^{abc}	5^{ab}	0^{e}	6.5^{ab}	5.5^{ab}	6^{ab}	4^{abcd}	5.5^{bc}	7^{a}	7^{a}	5^{bc}	7.5^{ab}	108.0^{ab}	65.3^{bc}	32.0^{cd}	10.6^{bc}
RCM-23-19	4^{ab}	3^{abc}	6^{abc}	8.5^{a}	3^{def}	3.5^{bc}	6.5^{ab}	0^{e}	7.5^{a}	7^{ab}	6^{abc}	4.5^{cd}	7^{a}	5^{bc}	7.5^{a}	6.5^{bc}	115.9^{ab}	73.0^{ab}	38.1^{ab}	11.5^{ab}
RCM-41-19	3^{abc}	3^{abc}	5^{abcd}	8.5^{a}	3^{cde}	3^{bc}	0^{e}	0^{e}	6.5^{ab}	7.5^{ab}	6^{abc}	6.5^{ab}	4^{c}	5^{bc}	5^{bc}	6.5^{bc}	109.1^{ab}	67.6^{bc}	32.5^{cd}	10.7^{bc}
RCM-4-19	4^{ab}	4^{ab}	8^{a}	6^{ab}	4^{abc}	3.5^{bc}	7.5^{a}	5.5^{bc}	7^{ab}	7^{ab}	6.5^{abc}	6^{ab}	7^{a}	5.5^{bc}	7^{a}	6.5^{bc}	118.2^{a}	71.1^{ab}	35.0^{bc}	10.9^{bc}
RCM-31-19	3^{abc}	2^{bc}	5^{abcd}	6^{ab}	4^{abcd}	3^{bc}	6.5^{ab}	5.5^{bc}	7^{ab}	8^{a}	6^{abc}	5^{c}	7^{a}	6^{ab}	8^{a}	8^{a}	120.8^{a}	69.8^{ab}	35.6^{bc}	10.7^{bc}
RCM-44-19	3^{abc}	4^{ab}	3.5^{f}	7^{ab}	3.5^{cde}	3.5^{bc}	0^{e}	5.5^{bc}	5^{abc}	6^{ab}	4.5^{abcd}	6^{ab}	6.5^{ab}	4.5^{cd}	5^{bc}	6^{bc}	113.6^{ab}	57.9^{cd}	33.8^{bc}	9.3^{cd}
RCM-16-19	4^{ab}	3^{abc}	6^{abc}	8^{a}	4^{abcd}	3.5^{bc}	7^{abc}	0^{e}	5^{abc}	7^{ab}	4.5^{abcd}	8^{a}	7.5^{a}	5.5^{bc}	5^{bc}	7^{ab}	123.2^{a}	73.9^{ab}	37.1^{ab}	11.8^{ab}
RCM-36-19	4^{ab}	3^{abc}	6.5^{abc}	7^{ab}	3.5^{cde}	3^{bc}	7.5^{a}	0^{e}	7^{ab}	8^{a}	5^{abcd}	6^{ab}	7.75^{a}	6^{ab}	7^{a}	8^{a}	121.2^{a}	69.1^{ab}	37.6^{ab}	11.0^{ab}
RCM-39-19	3^{abc}	4^{ab}	5.5^{abcd}	7^{ab}	5.5^{ab}	3^{bc}	0^{e}	5.5^{bc}	5^{abc}	7.5^{ab}	4^{abcd}	5^{c}	7^{a}	7^{a}	4^{d}	7.5^{ab}	103.8^{bc}	55.3^{cd}	31.0^{de}	8.8^{cd}
RCM-21-19	4^{ab}	4^{ab}	7^{ab}	8^{a}	3.5^{cde}	3^{bc}	6.5^{ab}	6.5^{ab}	6.5^{ab}	8^{a}	5.5^{abcd}	6^{ab}	7.5^{a}	7^{a}	7^{a}	7^{ab}	113.6^{ab}	60.8^{cd}	35.1^{bc}	9.5^{cd}
RCM-50-19	3^{abc}	3^{abc}	5.5^{abcd}	5^{bc}	4^{abcd}	4^{ab}	0^{e}	6^{ab}	5^{abc}	5^{bc}	5^{abcd}	5.5^{bc}	7^{a}	6^{ab}	5.5^{bc}	7^{ab}	106.5^{ab}	57.7^{cd}	31.0^{de}	9.0^{cd}
RCM-42-19	4^{ab}	4^{ab}	6^{abc}	6^{ab}	3.5^{cde}	4.5^{ab}	5.5^{abc}	6.5^{ab}	5^{abc}	7^{ab}	3.5^{def}	6^{ab}	7^{a}	6.5^{ab}	5^{bc}	5^{cd}	92.4^{cd}	60.6^{cd}	27.6^{e}	9.9^{cd}
RCM-15-19	3^{abc}	3^{abc}	7.5^{ab}	8^{a}	4.5^{abcd}	3.5^{bc}	0^{e}	0^{e}	5.5^{ab}	7^{ab}	6^{abc}	5.5^{bc}	5.5^{bc}	6^{ab}	3^{e}	7^{ab}	118.5^{a}	65.5^{bc}	34.9^{bc}	10.4^{bc}
RCM-51-19	4^{ab}	3^{abc}	5.5^{abcd}	5^{bc}	3.5^{cde}	3^{bc}	6.5^{ab}	6^{ab}	8^{a}	7.5^{ab}	4.5^{abcd}	5^{c}	7^{a}	7^{a}	7^{a}	7.5^{ab}	109.8^{ab}	55.5^{cd}	32.4^{cd}	8.7^{cd}
RCM-6-19	4^{ab}	4^{ab}	4.5^{def}	6.5^{ab}	4.5^{abcd}	3^{bc}	6.5^{ab}	6^{ab}	7^{ab}	7^{ab}	4^{abcd}	6^{ab}	7^{a}	6^{ab}	7^{a}	7^{ab}	103.5^{bc}	47.9^{d}	30.4^{de}	7.8^{c}
RCM-52-19	3^{abc}	3^{abc}	5^{abcd}	6^{ab}	5.5^{ab}	4^{ab}	0^{e}	6^{ab}	5.5^{ab}	6^{ab}	4^{abcd}	5^{c}	7^{a}	6^{ab}	5^{bc}	6^{bc}	106.8^{ab}	58.6^{cd}	32.4^{cd}	9.4^{cd}
RCM-34-19	3^{abc}	6^{a}	4.5^{def}	8^{a}	5^{ab}	6^{a}	0^{e}	7^{a}	5.5^{ab}	5.5^{bc}	4^{abcd}	4.5^{cd}	7.5^{a}	7.5^{a}	5.5^{bc}	6.5^{bc}	121.4^{a}	73.8^{ab}	37.6^{ab}	11.8^{ab}
RCM-9-19	4^{ab}	4^{ab}	3.5^{f}	7.5^{ab}	4^{abcd}	3.5^{bc}	6.5^{ab}	6.5^{ab}	6.5^{ab}	8^{a}	3^{def}	5.5^{bc}	6.5^{ab}	7^{a}	5^{bc}	8^{a}	118.2^{a}	69.8^{ab}	34.6^{bc}	11.0^{ab}
RCM-1-19	4^{ab}	2^{bc}	5.5^{abcd}	9^{a}	4^{abcd}	3.5^{bc}	6.5^{ab}	0^{e}	5.5^{ab}	8^{a}	4^{abcd}	8^{a}	7^{a}	5^{bc}	6^{ab}	8^{a}	115.0^{ab}	71.2^{ab}	33.8^{bc}	11.3^{ab}
RCM-19-19	3^{abc}	3^{abc}	5.5^{abcd}	2^{c}	4^{abcd}	4^{ab}	0^{e}	0^{e}	5^{abc}	8^{a}	5^{abcd}	6^{ab}	7^{a}	6^{ab}	5.5^{bc}	8^{a}	106.2^{ab}	61.5^{cd}	30.9^{de}	9.6^{cd}
HQPM-5	4^{ab}	3^{abc}	8.5^{a}	7.5^{ab}	4.5^{abcd}	4^{ab}	6.5^{ab}	0^{e}	7.5^{a}	8^{a}	6^{abc}	5^{c}	7^{a}	6^{ab}	7^{a}	7^{ab}	138.6^{a}	68.9^{bc}	62.6^{a}	9.0^{cd}
RCM-5-19	3^{abc}	3^{abc}	4.5^{def}	5^{bc}	4.5^{abcd}	3.5^{bc}	0^{e}	0^{e}	6^{ab}	7.5^{ab}	3.5^{def}	4.5^{cd}	6.5^{ab}	5.5^{bc}	4.5^{cd}	7.5^{ab}	99.2^{cd}	56.2^{cd}	30.1^{de}	9.0^{cd}
RCM-45-19	3^{abc}	4^{ab}	4.5^{def}	7^{ab}	4.5^{abcd}	3.5^{bc}	0^{e}	6^{ab}	6.5^{ab}	7.5^{ab}	3^{def}	5.5^{bc}	6^{ab}	7^{a}	4^{d}	7^{ab}	118.6^{a}	66.2^{bc}	40.9^{ab}	10.7^{bc}
RCM-32-19	3^{abc}	3^{abc}	2.5^{g}	7.5^{ab}	4.5^{abcd}	3^{bc}	0^{e}	0^{e}	5.5^{ab}	7.5^{ab}	2.5^{g}	5.5^{bc}	7.5^{a}	6^{ab}	6^{ab}	7^{ab}	119.5^{a}	70.6^{ab}	39.4^{ab}	11.2^{ab}
RCM-28-19	4^{ab}	4^{ab}	6^{abc}	6.5^{ab}	5^{ab}	2.5^{c}	6.5^{ab}	7^{a}	7.5^{a}	7.5^{ab}	3.5^{def}	4.5^{cd}	7^{a}	7^{a}	7^{a}	7^{ab}	118.3^{a}	65.0^{bc}	35.6^{bc}	10.4^{bc}
RCM-13-19	3^{abc}	4^{ab}	4^{def}	5.5^{bc}	4^{abcd}	3^{bc}	0^{e}	7^{a}	7^{ab}	6.5^{ab}	3.5^{def}	4.5^{cd}	6^{ab}	6^{ab}	6^{ab}	7^{ab}	114.7^{ab}	70.8^{ab}	38.1^{ab}	11.2^{ab}
RCM-3-19	3^{abc}	3^{abc}	5.5^{abcd}	7^{ab}	3.5^{cde}	3^{bc}	0^{e}	0^{e}	5.5^{ab}	6^{ab}	4^{abcd}	7^{ab}	4.5^{c}	4.5^{cd}	4^{d}	6^{bc}	103.3^{bc}	59.2^{cd}	30.9^{de}	9.1^{cd}
RCM-43-19	3^{abc}	4^{ab}	4^{def}	8^{a}	4.5^{abcd}	4.5^{ab}	0^{e}	6^{ab}	5^{abc}	7.5^{ab}	3.5^{def}	5^{c}	6.5^{ab}	6.5^{ab}	3^{e}	7^{ab}	114.5^{ab}	62.7^{cd}	35.7^{bc}	10.0^{cd}
RCM-10-19	3^{abc}	4^{ab}	4.5^{def}	7^{ab}	4.5^{abcd}	3^{bc}	0^{e}	5^{bc}	6.5^{ab}	8^{a}	3.5^{def}	5^{c}	5.5^{bc}	6.5^{ab}	5.5^{bc}	7^{ab}	118.8^{a}	65.5^{bc}	37.6^{ab}	10.6^{bc}
RCM-49-19	4^{ab}	3^{abc}	6.5^{abc}	6^{ab}	3.5^{cde}	3^{bc}	6.5^{ab}	6^{ab}	6^{ab}	6^{ab}	5.5^{abcd}	6^{ab}	7^{a}	7^{a}	7.5^{a}	7^{ab}	103.3^{bc}	57.0^{cd}	30.9^{de}	8.8^{cd}
RCM-12-19	3^{abc}	4^{ab}	5.5^{abcd}	8.5^{a}	4^{abcd}	3^{bc}	0^{e}	6^{ab}	6.5^{ab}	8^{a}	5.5^{abcd}	7^{ab}	6^{ab}	6.5^{ab}	6.5^{ab}	8^{a}	122.9^{a}	63.0^{cd}	40.1^{ab}	10.0^{cd}
RCM-26-19	3^{abc}	4^{ab}	6^{abc}	8.5^{a}	3^{cde}	3^{bc}	6^{abc}	6.5^{ab}	6^{ab}	8^{a}	5^{abcd}	7.5^{a}	5^{bc}	6.5^{ab}	6^{ab}	8^{a}	109.7^{ab}	59.1^{cd}	32.8^{cd}	9.6^{cd}
RCM-47-19	3^{abc}	4^{ab}	4^{def}	9^{a}	4^{abcd}	4^{ab}	0^{e}	6^{ab}	6^{ab}	8^{a}	3.5^{def}	5^{c}	6.5^{ab}	5.5^{bc}	3.5^{e}	8^{a}	118.0^{a}	67.4^{bc}	38.8^{ab}	10.7^{bc}

Duncan's Multiple Range Test indicated significant differences among treatments, as shown by the varying alphabetical superscripts. Genotypes with the same superscript letter are not significantly different at the 5 % level.

Table 3
Principal component analysis of different root traits of maize seedling under the control and WL condition.

Principal component		Control		WL	
		PC1	PC2	PC1	PC2
Initial eigen values	Total	2.42	1.56	2.44	1.61
	Percentage of variance	48.33	31.12	48.77	32.14
	Cumulative percentage	48.33	79.45	48.77	80.91
Rotation sums of squared loadings	Total	2.35	1.63	2.11	1.94
	Percentage of variance	46.91	32.54	42.18	38.73
	Cumulative percentage	46.91	79.45	42.18	80.91
Eigen vectors[b]		**Factor loadings**[a]			
		PC1	**PC2**	**PC1**	**PC2**
Root length ratio		0.393	−0.685	0.351	−0.531
Root mass ratio		0.987	−0.019	0.982	−0.157
Root fineness		0.052	0.688	−0.174	0.825
Root tissue density		0.496	0.823	0.125	0.973
Root: Shoot		0.984	0.083	0.988	−0.045

strong loadings for these root traits under control conditions. For the root traits, viz. root-to-shoot ratio, root mass ratio, and root length ratio, genotypes viz. RCM-38-19, RCM-11-19, RCM- 47-19, RCM-6-19, RCM-2-19, RCM-50-19, RCM-32-19, RCM-8-19, RCM-19-19, RCM-5-19 and RCM-43-19 exhibited strong positive loadings on PC1. The association of these five traits revealed by the PC1 loading further confirmed the positive correlations among them. Similarly, under WL conditions, PC1 and PC2 accounted for 80.91 % of the variability. With root-to-shoot ratio (loading = 0.988) and root mass ratio (loading = 0.982) are strongly associated with PC1 and root tissue density (loading = 0.973) and root fineness (loading = 0.825) with PC2. The loading plot (Supplementary Fig. S8) suggested that the genotypes viz. RCM-45-19, RCM-43-19, RCM-51-19, RCM-8-19, and RCM-11-19 had strong positive loadings for root-to-shoot ratio and root mass ratio whereas, for root length ratio the genotypes RCM-2-19, RCM-19-19, RCM-32-19, RCM-5-19, RCM-16-19, and RCM-44-19 have shown strong positive loadings towards PC1. For the traits root tissue density and root fineness, genotypes like RCM-34-19, RCM-10-19, RCM-23-19, RCM-42-19, and RCM-31-19 are closely associated with PC2. These results confirmed the positive correlations observed between these traits and genotypes.

The heat map analysis complemented these observations by clustering traits and genotypes based on their patterns (Supplementary Figs. S9 and S10). Under conditions, root fineness and root tissue density formed one cluster, while root length ratio, root-to-shoot

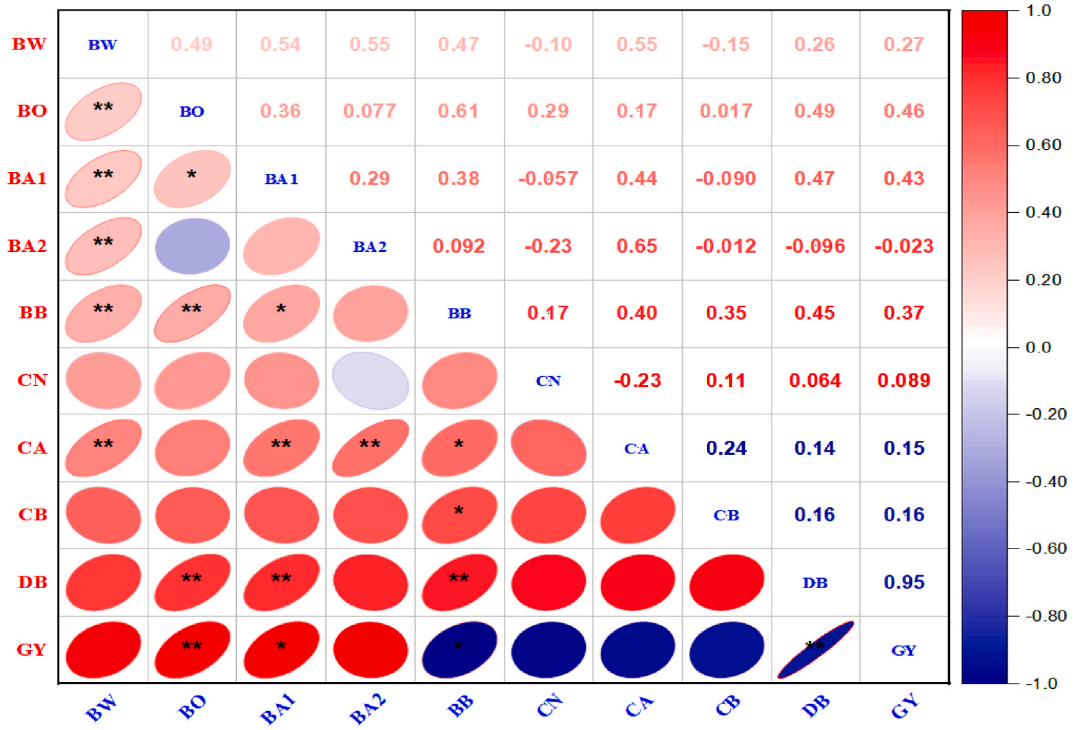

Fig. 2. Correlogram showing the correlation coefficients (r) between the root parameters in maize maturity stage under the WL condition.

ratio, and root mass ratio formed another. Furthermore, the genotypes were grouped into distinct clusters, reflecting differential root trait responses under stress and non-stress conditions. In control condition, two major cluster groups were identified, with one group consisting of 20 genotypes and the second group comprised of 15 genotypes. Similarly, under WL conditions, two main cluster groups were formed, the first one with 17 genotypes and the second group comprising 18 genotypes.

3.3.2. *Flowering stage*

The correlation matrix for major root traits *viz.*, BW, BO, BA1, BA2, BB, CN, CA, CB, dry biomass (DB), and grain yield per plant (GY) under both control (Fig. 1) and WL conditions (Fig. 2) revealed the existence of significant positive correlations. A Positive significant correlation was observed between BO and CN (0.75) under the control condition. A positive and strong significant correlation was also recorded between BA2 and CB (0.69), BW and BA2 (0.63), BB and CB (0.63), BW and CA (0.62), and BW and BO (0.55). A strong positive correlation was also found between the root parameter, BB, and DB (0.44). Under the WL condition, a strong and positive correlation was observed between BA2 and CA (0.65). A positive correlation was also observed between BO and BB (0.61), BW and BA2 (0.55), BW and CA (0.55), BW and BA1 (0.54), BW and BO (0.49), BW and BB (0.47), BA1 and CA (0.44) and BB and CA (0.40). Various root parameters also exhibited strong positive correlations with GB. For instance, BO, BA1, and BB exhibited a strong positive correlation with DB with r values viz. 0.49, 0.47, and 0.45, respectively.

PCA identified three significant components under control conditions, explaining 79.05 % of the variance, and two components under WL conditions, accounting for 74.48 % of the variance (Table 4). Under control conditions BA2 exhibited the highest loading on PC1 (0.851), followed by BW (0.789) and CB (0.784). For PC2, BA1 contributed the highest loading (0.852), with CA (0.774) and BW (0.389) also showing strong associations. PC3 was primarily influenced by BO (0.634) and CN (0.588). The loading plot (Fig. 3) highlighted that genotypes such as RCM-28-19, RCM-16-19, RCM-6-19, RCM-1-19, and RCM-42-19 demonstrated strong positive loadings on both PC1 and PC2, particularly for the traits CA and BW. Additionally, genotypes HQPM-5, RCM-36-19, RCM-21-19, RCM-51-19, RCM-4-19, RCM-49-19, RCM-31-19, and RCM-23-19 displayed significant positive associations with PC1 for root traits such as BO, BB, BA2, CB, and CN. However, PC1 was primarily influenced by BW (0.852), CA (0.773), and BA1 (0.702). PC2 was dominated by CN (0.745), BO (0.566), and BB (0.530), while PC3 showed strong loadings for CB (0.886) and CA (0.367). The loading plot (Fig. 4) revealed that genotypes RCM-26-19 and RCM-12-19 had strong positive loadings for BO and BB on both PC1 and PC2. For PC2, genotypes RCM-16-19, RCM-41-19, RCM-36-19, and RCM-3-19 were positively associated with CN. To explore the relationship between grain yield and primary root traits while eliminating redundant variables, stepwise linear multiple regression (SLMR) analysis was conducted for both control and WL conditions (Table 5). The resulting regression models used maize grain yield as the dependent variable and root architectural traits as independent variables (Eq. (4) and Eq. (5)):

Control Condition:

$$\mathrm{GY} = 8.26 + 2.11\ \mathrm{BA1} + 3.01\ \mathrm{BB} \tag{Eq. 4}$$

WL Condition:

$$\mathrm{GY} = 20.26 - 1.474\ \mathrm{BW} + 4.418\ \mathrm{BO} + 0.547\ \mathrm{BA1} + 3.002\ \mathrm{BB} - 2.841\ \mathrm{CN} - 2.274\ \mathrm{CB} \tag{Eq. 5}$$

These models indicated a positive association between grain yield and both brace root angle 1 (BA1) and brace root branching (BB) under both conditions. Under WL stress, brace root number per whorl also showed a positive correlation with grain yield, whereas the number of brace root whorls, crown root number (CN), and crown root branching (CB) negatively influenced yield.

In addition to PCA and correlation analyses, the heat map (Supplementary Figs. S11 and S12) further categorized root traits and genotypes under control and WL conditions. Under the control condition, root traits clustered into two groups: the first group included

Table 4

Principal component analysis of different root traits of maize under the control and WL conditions at the flowering stage.

Principal component		Control			Treatment		
		PC1	PC2	PC3	PC1	PC2	PC3
Initial eigen values	Total	3.58	1.63	1.11	3.07	1.67	1.22
	Percentage of variance	44.70	20.42	13.93	38.37	20.89	15.21
	Cumulative percentage	44.70	65.12	79.05	38.37	59.26	74.48
Rotation sums of squared loadings	Total	2.72	1.89	1.72	2.34	2.32	1.30
	Percentage of variance	33.95	23.65	21.45	29.26	28.99	16.23
	Cumulative percentage	33.95	57.60	79.05	29.26	58.25	74.48
Eigen vectors[b]		**Factor loadings**[a]					
		PC1	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
BW		0.588	0.364	0.544	0.621	0.621	−0.195
BO		0.211	0.916	0.175	0.882	−0.036	−0.011
BA1		−0.372	−0.105	0.804	0.567	0.458	−0.185
BA2		0.851	0.238	0.048	0.079	0.828	−0.010
BB		0.743	0.154	0.027	0.763	0.142	0.435
CN		0.221	0.896	−0.152	0.454	−0.591	0.144
CA		0.323	0.053	0.846	0.245	0.818	0.312
CB		0.871	0.154	−0.011	0.008	0.005	0.958

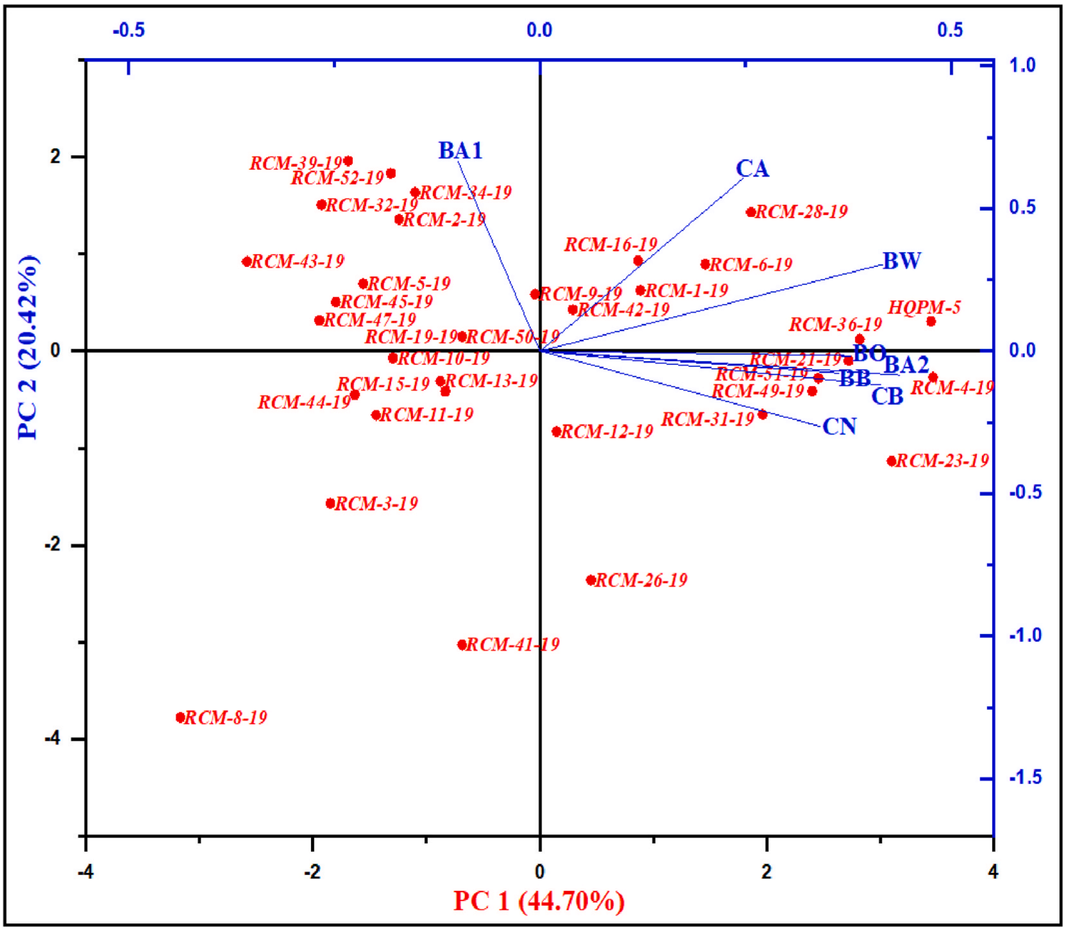

Fig. 3. Two-dimensional graphical biplot depicting the loadings and score plot formed by PC1 and PC2 of root traits and genotypes of maize under the control condition at the maturity stage.

BA1, BW, and CA, while the second group comprised BO, CN, BB, BA2, and CB. The genotypes clustered into two groups, with 16 genotypes in the first group and 19 in the second. Under WL conditions, root traits were grouped into two categories: BA2, CA, BW, and BA1 in one group, and CB, CN, BO, and BB in the other. Genotypes also clustered into two groups: 12 in the first and 23 in the second. These results complement the PCA and correlation observations, providing further insights into the relationships between root traits and grain yield.

3.4. *Dry biomass and grain yield*

The DB and GY were drastically affected in most of the genotypes due to waterlogged conditions in our study (Table 2). Among them, genotype RCM-8-19 exhibited the most severe effects, with DB yield reduced significantly by half (46.8 g plant^{-1}) and GY almost 2 times (7.9 g plant^{-1}) as compared to DB yield (90.9 g plant^{-1}) and GY (26.4 g plant^{-1}) under control conditions. This genotype was also recorded to have the lowest visual score in both control and WL conditions. Conversely, genotype RCM-11-19 was found to have the highest DB (76.7 g plant^{-1}) and GY (12.2 g plant^{-1}) under WL conditions followed by RCM-16-19 (DB: 73.9 g plant^{-1}; GY: 11.8 g plant^{-1}) and RCM-23-19 (DB: 73 g plant^{-1}; GY: 11.5 g plant^{-1}). RCM-11-19 was also found to be a promising genotype according to the visual scoring of root phenotypes as discussed earlier.

4. Discussion

The phenotypic plasticity index, measured as RC, and WTC served as a vital tool for screening maize landraces with tolerance to waterlogging (WL) at the seedling stage. Genotypes like RCM-44-19, RCM-16-19, RCM-39-19, RCM-42-19, RCM-15-19, RCM-51-19, RCM-9-19, RCM-45-19, RCM-32-19, RCM-43-19, RCM-10-19, RCM-49-19, RCM-12-19, and RCM-26-19 showed high adaptive capacity to WL, based on their RC values (RC < 1) and significant WTC scores at the seedling stage. Thus, these genotypes can be designated as WL tolerant. These findings underscore the genetic variability within maize landraces in their responses to WL stress,

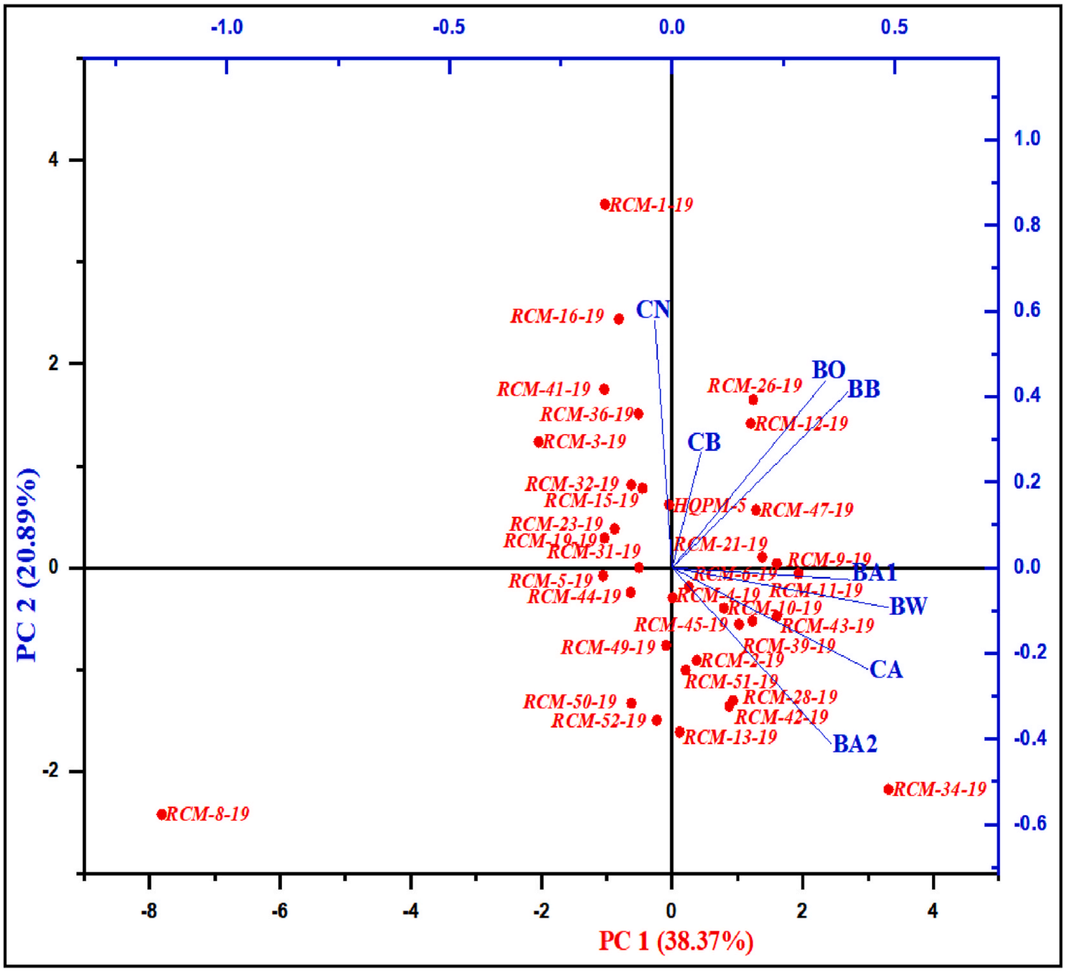

Fig. 4. Two-dimensional graphical biplot depicting the loadings and score plot formed by PC1 and PC2 of root traits and genotypes of maize under the WL condition at the maturity stage.

Table 5

Stepwise multiple regression variance analysis of maize grain yield versus primary root traits under control and WL conditions.

Control	Source	DF	Seq SS	Contribution	Adj SS	Adj MS	F-Value	P-Value	Coef	SE Coef	T-Value
	Regression	2	296.11	24.72 %	296.11	148.06	5.25	0.01	–	–	–
	BA1	1	52.37	4.37 %	73.50	73.50	2.61	0.12	8.26	8.55	0.97
	BB	1	243.74	20.34 %	243.74	243.74	8.65	0.01	2.11	1.30	1.61
	Error	32	901.96	75.28 %	901.96	28.19			3.01	1.02	2.94
	Lack-of-Fit	31	901.95	75.28 %	901.95	29.10	2690.71	0.01			
	Pure error	1	0.01	0.00 %	0.01	0.01					
	Total	34	1198.07	100.00 %							
Treatment	Regression	6	16521.4	87.85 %	16521.4	2753.5	75.9	0.000	–	–	–
	BW	1	9974.3	53.04 %	250.0	249.9	6.8	0.011	−1.44	0.56	−2.63
	BO	1	3895.8	20.72 %	1771.8	1771.7	48.8	0.000	4.41	0.63	6.99
	BA1	1	0.2	0.00 %	78.7	78.6	2.1	0.146	0.54	0.37	1.47
	BB	1	626.0	3.33 %	463.5	463.5	12.78	0.001	3.00	0.84	3.58
	CN	1	1520.9	8.09 %	332.6	332.6	9.17	0.004	−2.84	0.93	−3.03
	CB	1	504.3	2.68 %	504.3	504.3	13.91	0.000	−2.27	0.61	−3.73
	Error	63	2284.6	12.15 %	2284.6	36.2			−1.47	0.562	−2.63
	Lack-of-Fit	62	2284.6	12.15 %	2284.6	36.8	3407.7	0.014			
	Pure error	1	0.0	0.00 %	0.0	0.01					
	Total	69	18806.0	100.00 %							

Stepwise Selection of Terms: α to enter = 0.15, α to remove = 0.15.

Note: **Seq SS** = Sequential sums of squares, **Adj SS** = Adjusted sum of squares, **Adj MS** = Adjusted mean squares and **SE Coef** = Standard error of the coefficient.

which likely results from evolutionary adaptation to the heavy rainfall conditions in EHR.

Root systems played a pivotal role in conferring this tolerance [14], as WL conditions typically cause root hypoxia, inhibiting ATP synthesis and reducing root functionality [35]. This led to a decrease in root biomass and root-to-shoot ratios as observed in the current study, mirroring the stress-induced inhibition of maize growth [36]. Interestingly, certain genotypes responded to WL by increasing lateral root growth and the development of adventitious roots. The increased number of nodes is an effective mechanism that improves plant anchorage and oxygen absorption under saturated conditions [37–39]. The Current investigation also revealed that the WL condition significantly reduced both shoot and root biomass, with a more pronounced effect observed on shoots compared to roots during the mature stage. This finding aligns with the previous research by Salah et al. [40]. This evolutionary adaptation, particularly observed in maize landraces from the heavy-rainfall regions of Northeastern India, underscores the plants' resilience to harsh environments. Contrary to this, Li et al. [31], Zaidi et al. [41], and Liu et al. [37] reported that WL conditions inhibited root growth and lateral root development thereby reducing the root length, root surface area, and root volume. They also reported that biomass reduction was more pronounced in roots than in shoots.

Correlation coefficients are used to measure the strength and degree of the relationship between two variables, and through this breeder can decide which traits to focus on for breeding programs. It can also help to identify how changes in one trait/character can affect other traits. For instance, a positive correlation between root traits under WL conditions indicates that the two traits are linked and one can focus on such traits. The Phenotyping of root traits BW, BO, BA1, BA2, BB, CN, CA, and CB did not show any significant reduction during the WL condition when compared to the control. Excessive moisture conditions resulted in robust root growth and branching for certain genotypes such as RCM-12-19, RCM-32-19, RCM-16-19, and RCM-23-19 (Table 2). This adaptability was further confirmed by the significant positive correlation between root traits. This correlation between CA and BA2 under the WL condition during flowering stage aligns with findings from Trachsel et al. [19], who reported a similar relationship in maize studies conducted using shovelomics. PCA is a multivariate statistical tool used to reduce the dimensionality of large data sets by transforming a large set of variables into a smaller one that retains the majority of the information [42]. The Eigen value of the principal component (PC) represents its relative contributions to total variance (characteristic values or latent roots). The application of PCA revealed that root traits such as root mass ratio, root length ratio, and brace root characteristics contributed substantially to the total variance under WL conditions, indicating their importance in stress resilience. In contrast, BO, BB, CB, BA1, BA2, BW, and CA root traits had a strong correlation with PC1 in WL condition during flowering stage. On average, all of these root traits contributed in the same magnitude and direction, indicating that these root traits responded to the WL condition. Similarly, Li et al. [43] found that the majority of the traits were highly correlated with PC1.

Moreover, regression analysis highlighted that key root traits like brace root angle and branching were strong predictors of grain yield (GY) under WL conditions. In maize, brace roots and crown roots, both nodal/postembryonic root types, take over the tasks of anchorage and nutrient supply from embryonic roots during the late vegetative phase until maturity, [44]. Brace roots, in particular, provide crucial structural support and have been linked to resistance to root lodging [45,46]. Lodging reduces maize yield by 5–20 % due to impaired photosynthetic efficiency, ear damage, and challenges during mechanical harvesting [47]. Higher brace root number and greater brace root expansion have been associated with increased resistance to root lodging, which explains the current study findings that maize entries with shallow brace root angles (BA1) and extensive brace root branching (BB) exhibited higher GY in both control and WL stress conditions [48,49]. Nitrogen, phosphorus, and potassium are the major nutrients limiting plant growth [50]. Due to the accumulation of plant residue over time, limited P leaching, and higher topsoil microbial activity, phosphorus is concentrated in the topsoil [51]. The root growth angle plays a significant role in determining root foraging depth, which strongly correlates with the soil resource acquisition depth [52,53]. Shallow root angles, higher lateral root density, lower metabolic cost, and longer root hairs along with enhanced brace root branching, improve topsoil foraging and phosphorus acquisition, which may explain the GY increase in maize inbred lines with these traits [54–56]. Additionally, under WL stress, a high number of brace roots per whorl were associated with increased GY. This is likely because plants allocate carbon to brace roots in lower whorls, reducing the metabolic cost of topsoil exploration.

Crown root number (CN) also influences nutrient acquisition [57], and previous studies have shown that genotypic variation in maize CN ranged from 5 to 75 under normal conditions [58,59]. Lynch [57] proposed that an intermediate crown root number (CN) is ideal, as a low CN may lead to insufficient resource capture and increase the risk of lodging, especially in low-input systems [60]. Conversely, under stress or nutrient-limiting conditions, a high CN can cause intra-root competition, limiting root elongation and leading to energy inefficiency [57]. The optimal CN depends on variables like soil type and stress severity [61]. When combined with a steep root angle and reduced lateral branching, an intermediate CN may synergistically improve resource acquisition under drought and nutrient stress, particularly for nitrogen [57,62]. The mean value of CN in our study under WL conditions was low. In our study, regression analysis showed that maize with low CN, reduced branching of crown root laterals, and steep crown root angles were associated with increased yield under WL stress, implying that the combination of these three crown root traits can be synergistic for mobile nutrient acquisition under WL. This could be an adaptive response to reduce the carbon cost for root maintenance and growth, allowing a more efficient resource acquisition. As a result, maize entries that can acquire limiting soil resources with minimal metabolic costs tend to have superior yields, as more metabolic resources are available for growth and reproduction [63].

Furthermore, a decrease in CN due to a restriction in transportable nutrients, particularly nitrogen, caused by hypoxia may be attributed to fewer crown root nodes and roots per node [58], which will increase root exploration for water and nutrient uptake in deep soil strata [64]. This study supports the "steep, cheap, and deep" (SCD) root ideotype proposed by Lynch [57], suggesting that reduced CN and branching improve nutrient uptake from deeper soil layers, lower metabolic costs, and ultimately increase yield under WL stress [65]. Reduced CN and CB, according to our hypothesis, would improve nutrient uptake from deeper soil layers, lower metabolic expenses, and increase crop output under WL stress. As a result, when screening maize for WL tolerance, the observed traits (brace- and crown roots) can be taken into account. These findings provide practical insights for breeding programs targeting water-logging tolerance in maize. Positive correlations among traits like brace root branching (BB), brace root orientation (BO), and crown root angle (CA) suggest that improving one trait may simultaneously enhance others, facilitating efficient trait selection. Genotypes with fewer crown roots (CN), greater brace root branching (BB), and shallow brace root angles (BA1) demonstrated higher grain yields under waterlogged conditions, making these traits key targets for developing stress-resilient varieties. Metrics such as relative change (RC), waterlogging tolerance coefficient (WTC), and principal component analysis (PCA)-derived trait prioritization can streamline the screening process, reducing reliance on extensive field trials. Additionally, the ability of certain genotypes to promote lateral root growth and adventitious root development under stress conditions highlights the significance of structural root traits in conferring adaptability. Together, these insights pave the way for breeding maize ideotypes optimized for waterlogging resilience.

5. Conclusions

This study highlights the significant potential of diverse maize landraces to tolerate WL stress, particularly through root system adaptations. The use of phenotypic tools such as shovelomics and metrics like waterlogging tolerance coefficients (WTC) proved effective for identifying adaptive genotypes, underscoring the importance of structural root traits in breeding stress-resilient maize. Key findings indicate that brace root traits such as angle (BA1), branching (BB), and orientation (BO) enhance phosphorus uptake from topsoil under WL stress, while crown root traits like reduced number (CN) and branching (CB) facilitate efficient nitrogen acquisition from deeper soil layers. These traits align with the “steep, cheap, and deep” (SCD) ideotype, promoting resource efficiency under stress. Landraces like RCM-12-19, RCM-32-19, RCM-16-19, and RCM-23-19 demonstrated exceptional root growth and branching post-WL, making them prime candidates for breeding programs targeting WL resilience. Four landraces (RCM-12-19, RCM-32-19, RCM-16-19, and RCM-23-19) demonstrated to have rapid root growth and branching after WL at the flowering stage which would be leveraged for future maize breeding for WL environments of EHR under changing climate. These findings provide actionable insights for developing maize varieties optimized for the challenging agroecological conditions of the Eastern Himalayan Region (EHR). Further research integrating genotyping and molecular techniques is needed to strengthen these breeding strategies.

CRediT authorship contribution statement

E. Lamalakshmi Devi: Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Krishnappa Rangappa:** Writing – review & editing, Supervision, Resources, Investigation, Conceptualization. **Ayam Gangarani Devi:** Resources, Investigation, Formal analysis, Data curation. **S.K. Chongtham:** Software, Resources, Formal analysis, Data curation. **Ingudam Bhupenchandra:** Writing – review & editing, Software, Data curation. **Konsam Sarika:** Writing – review & editing, Investigation, Data curation. **Harendra Verma:** Resources, Investigation, Data curation. **Rumi Narzari:** Writing – review & editing, Data curation. **Samarendra Hazarika:** Writing – review & editing, Project administration. **Sankar Prasad Das:** Writing – review & editing, Supervision, Resources. **B.U. Choudhury:** Supervision, Formal analysis. **Anil Kumar Choudhury:** Software, Data curation. **T.L. Bhutia:** Writing – review & editing, Resources, Formal analysis. **V.K. Mishra:** Supervision, Project administration.

Consent to participate

Not applicable.

Consent to publish

All authors approved and consented to publish this work.

Ethics approval

Not applicable.

Data availability statement

The datasets presented in this study will be provided on request.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Krishnappa Rangappa reports financial support and administrative support were provided by ICAR Research Complex for North Eastern Hill Region. Krishnappa Rangappa reports a relationship with ICAR Research Complex for North Eastern Hill Region that includes: employment. Krishnappa Rangappa has patent Not Applicable(NA) pending to NA. Authors declare no conflict of Interest If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2025.e42340.

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