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RESEARCH ARTICLE

Response of transient soil waterlogging on shoot growth pattern and root architecture of finger millet and barnyard millet seedlings

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Abstract

Millets, as key crops in semi-arid and arid tropical regions, are gaining recognition for their nutritional benefits and resilience to challenging conditions. Finger millet and barnyard millet, in particular, stand out for their nutrient profiles and adaptability. However, research on their response to waterlogging, a major abiotic stress, remains limited. This study aimed to examine the immediate response of finger millet and barnyard millet seedlings to transient waterlogging conditions, focusing on their growth patterns and changes in root architecture to understand their morpho-physiological adaptive strategy. Seedlings were subjected to varying durations of waterlogging: control, 48, 74 and 120 hours to assess parameters such as shoot and root characteristics, leaf growth and tolerance indices. Results showed a decrease in root length and an increase in shoot length with prolonged waterlogging. Root and shoot biomass, along with seedling dry weight, rose as waterlogging durations increased. Significant increases were observed in root surface area, volume and the number of root tips and forks. Leaf area initially expanded but declined after 72 hours of waterlogging, accompanied by changes in specific leaf area and chlorophyll concentration. Tolerance indices, such as root-to-shoot ratio, decreased under waterlogging conditions, with finger millet exhibiting higher tolerance than barnyard millet. These findings provide insights into the adaptive strategies of millets under waterlogging, which is valuable for crop management and breeding for enhanced stress tolerance.

Keywords

Finger millet; barnyard millet; root architecture; leaf area; root shoot ratio; tolerance indices

Introduction

Millets, vital crops grown mostly in semiarid, tropical, and subtropical areas of Asia and Africa, are gaining recognition for their nutritional advantages and extensive stress resilience, with production anticipated to increase by 40%(1-3). Finger millet, or Ragi, is notable for its superior nutrient profile and resilience to environmental stresses compared to staples like wheat and rice (3-6). Among millet varieties, finger millet contains higher levels of essential amino acids, such as valine, threonine and lysine (7). Similarly, barnyard millet, known for its ability to thrive in marginal soils, offers greater nutritional value than rice, making it especially suitable for individuals with dietary restrictions (8-10). India leads in barnyard millet production, particularly in adverse conditions like drought or flooding (11). While drought stress effects on millet are well-documented, research on waterlogging impacts remains limited, underscoring the need for further exploration in this area (12).

Waterlogging, a situation wherein plants are submerged, or soil gets saturated with water, presents a significant obstacle to plant growth and development. This stress affects crucial processes such as seed germination, vegetative growth and reproductive success by hindering the plant's ability to conduct aerobic respiration and efficiently manage energy metabolism. The lack of oxygen in waterlogged soils disrupts normal metabolic functions, ultimately reducing plant growth and yield (13). As climate change intensifies, the frequency and severity of abiotic stresses like waterlogging are expected to rise. This is particularly concerning for agricultural systems as extreme weather events, including heavy rainfall and flooding, become more common. To ensure sustainable agriculture and adapt to a changing climate, it is crucial to understand how various plant species, exceptionally resilient crops like millets, respond to such adverse conditions (14).

This study aims to elucidate the processes underlying the tolerance of finger millet and barnyard millet seedlings to transient waterlogging stress by analyzing the effects of waterlogging on their growth patterns and root architecture. Understanding these morpho-physiological adaptations will provide valuable insights into how millets cope with waterlogging stress and guide breeding or agronomic strategies to improve their resilience in waterlogged environments.

Materials and Methods

The research was conducted in August 2023 at the Department of Botany, Plant Physiology and Biochemistry, Dr. Rajendra Prasad Central Agricultural University, Pusa, Samastipur. Pre-screened genotypes of finger millet (ST-5) and barnyard millet (RAU-9) were sourced from the Department of Plant Breeding and Genetics of Tirhut College of Agriculture, Dholi. Soil were obtained from the Department of Horticulture at Dr. Rajendra Prasad Central Agricultural University, Pusa, Samastipur, Bihar. Soil and meteorological data are provided in Table 1.

Healthy seeds of both finger millet and barnyard millet were selected and sown on August 5, 2023 in plastic pots (75mm x 115mm) containing finely pulverized soil (370 g) and arranged according to the different treatment conditions. 18 days after sowing, the pots were subjected to varying durations of waterlogging (48, 74 and 120 hours), along with a control group. Waterlogging was induced by fully submerging the seedlings up to the crown region, with the water level maintained above the crown through manual watering at regular intervals. Data for all parameters were collected following the waterlogging period on the 25th day after sowing.

Shoot and root length (in cm) and shoot and root dry weight (in g) were assessed. Leaf area was measured using leaves of different sizes (large, medium and small) and calculated using graph paper. Soil and Plant Analyzer Development (SPAD) units were measured at the center of the leaves using a portable Minolta SPAD-502 chlorophyll meter (Minolta Camera Co., Ltd., Osaka, Japan).

Table 1. Details of soil and meteorological data of August-2023.

Properties of soil	Data
Soil electrical conductivity (dSm^{-1}) at ambient temperature (25^0C)	0.36
At ambient temperature (25^0C), the electrical conductivity of saturation extract (dSm^{-1})	1.97
Soil pH	7.1
Sand (%)	18.5
Silt (%)	40.71
Clay (%)	37.53
Organic Carbon (%)	1.08
Available Nitrogen (kg ha^{-1})	217
Available P_2O_5 (kg ha^{-1})	61.98
Available K_2O (kg ha^{-1})	225
Zn (ppm)	0.97
Cu (ppm)	0.79
Fe (ppm)	2.73
Mn (ppm)	3.57
B (ppm)	0.32
S (ppm)	71.02
Meteorological parameters of Aug-2023	
Average maximum temperature (^0C)	32.2±5
Average minimum temperature (^0C)	24.7±5
Relative humidity (%) morning	93±5
Relative humidity (%) evening	77±5
Wind speed (km/hr)	11.68
Evaporation (mm)	3.5

Root architectural analysis involved extracting roots by carefully cutting the plastic pots along one side and gently washing away the soil with water. After air drying the roots in the shade for 30 to 40 minutes, the turgid roots were spread on a transparent fiber tray (25 x 25 cm) without overlapping. The roots were then scanned to create 2-D root images at 300 dpi resolution using an Epson Perfection scanner from Regent Instruments. The images were analyzed using WinRHIZO software to retrieve data on root surface area (cm^2), root volume (cm^3), number of root forks and number of root tips. Ratios of root-to-shoot length (root length [cm]/shoot length [cm]) and root-to-shoot dry weight (root dry weight [g]/shoot dry weight [g]) were calculated (15), as well as the waterlogging tolerance Coefficient (WTC), which was determined as the ratio of biomass under waterlogged conditions to biomass under control conditions (16).

Statistical analyses included a one-way ANOVA for Table 2 and a two-way factorial ANOVA for Fig. 1, conducted in a completely randomized design. A post hoc analysis using Duncan's Multiple Range Test (DMRT) identified significant differences within treatments for Table 2 and among interactions (crop x treatment) in Fig.1, with a significance level set at 5%. Additionally, principal component analysis and correlation analysis at a 0.05 significance level were conducted separately for finger millet and barnyard millet using KAU Grape software (17).

Table 2. Effect of different duration of waterlogging treatment (T) on shoot length (S.L), Shoot weight (S.W), Seedling dry weight (SD. W), leaf area (L.A), Root length (R.L), Root weight (RW), Root surface area (RSA), Root volume (RV), No of root tips (NRT) and no of root forks (NRF) in finger millet and barnyard millet seedlings.

Crops	T (In hours)	S.L (cm)	SD. L (cm)	S.W (g)	SD. W (g)	L.A (cm^2)	R.L (cm)	R.W (g)	RSA (cm^2)	R.V (cm^3)	NRT	NRF
Finger millet	Control	25.3^{b}	41.6^{a}	0.17^{d}	0.45^{d}	10.69^{b}	16.27^{a}	0.28^{b}	21.98^{c}	0.32^{c}	418.0^{c}	823.3^{b}
	48.0	29.3^{a}	44.83^{a}	0.20^{c}	0.50^{c}	12.02^{b}	15.50^{ab}	0.30^{b}	31.07^{c}	0.50^{bc}	406.3^{c}	1444^{ab}
	72.0	31.0^{a}	45.57^{a}	0.26^{b}	0.61^{b}	16.70^{a}	14.57^{bc}	0.34^{a}	34.22^{b}	0.71^{b}	557.7^{b}	1354^{b}
	120	30.0^{a}	43.47^{b}	0.30^{a}	0.66^{a}	NA	13.47^{c}	0.36^{a}	42.61^{a}	0.85^{a}	683.7^{a}	2133^{a}
Barnyard millet	Control	34.0^{b}	53.77^{a}	0.40^{c}	0.78^{b}	23.69^{b}	19.77^{a}	0.34^{b}	54.41^{b}	1.34^{b}	643.0^{b}	2133^{a}
	48.0	40.7^{a}	58.34^{a}	0.45^{b}	0.80^{a}	29.67^{b}	17.672^{b}	0.34^{b}	57.26^{b}	1.68^{b}	716.7^{a}	1700^{a}
	72.0	39.7^{a}	55.50^{a}	0.49^{a}	0.85^{a}	34.38^{a}	15.83^{bc}	0.36^{a}	72.01^{a}	2.68^{a}	757.7^{a}	2144^{a}
	120	41.3^{a}	57.10^{a}	0.49^{a}	0.87^{a}	NA	15.77^{c}	0.37^{a}	68.00^{a}	1.78^{a}	728.7^{a}	1906^{a}

Results represented are the averages of three replicates (n=3) and distinct superscript letters for each treatment are used to indicate statistically significant variations ($p \leq 0.05$) between treatments.

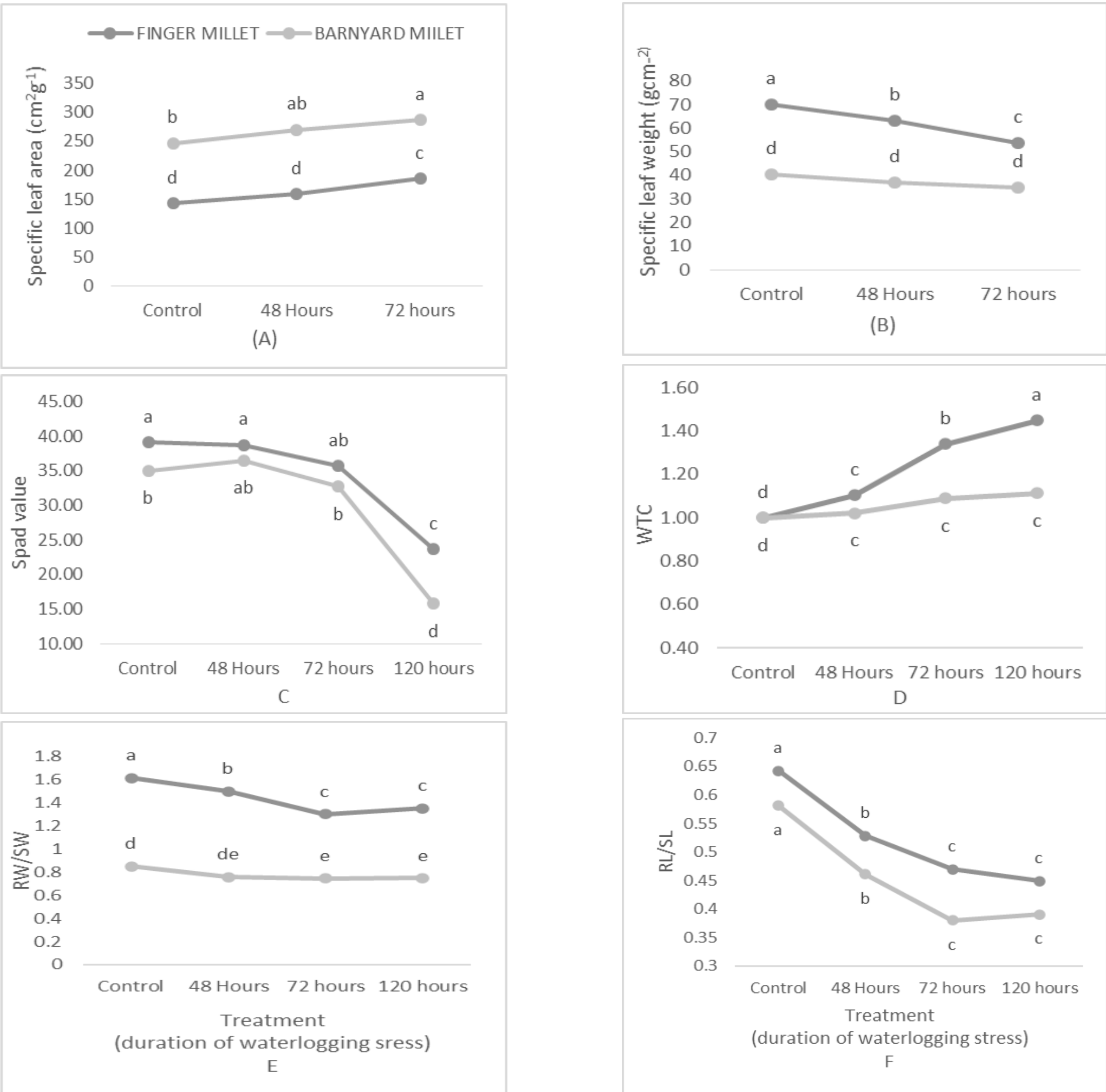

Fig. 1. Comparative analysis on the effect of different duration of waterlogging treatment on A: specific leaf area, B: specific leaf weight, C: chlorophyll content (SPAD value), D: waterlogging tolerance coefficient (WTC), E: root to shoot biomass ratio (RW/SW) and F: Root to shoot length ratio (RL/SL) between finger millet and barnyard millet seedlings. Results represented in the figure are the averages of three replicates (n=3), and distinct superscript letters for each interaction are used to indicate statistically significant variations ($p \leq 0.05$) between different interactions (Crop x treatment).

Results

Growth pattern of seedlings and root architectural adaptation (Table 2; Fig. 5 & 6)

Under waterlogging conditions, root length decreased progressively with increased exposure: from the reduction of 4.17% and 10.62% at 48 hours to 17% and 20.23% at 120 hours in finger millet and barnyard millet, respectively. In contrast, shoot length consistently increased across all durations, peaking at 72 hours with increases of 22.36% and 22.54% in finger and barnyard millet, respectively. Total seedling length remained largely unaffected, although barnyard millet seedlings were generally longer than finger millet.

Root biomass (RW) and shoot biomass (SW) rose with extended waterlogging duration for both millets. Compared to controls, RW and SW exhibited changes of RW by 7.14% and 0.98% (not significant); SW by 15.78% and 12.74% (at 48 hours) to 28.57% and 7.84% and 53.46% and 22.5% (at 120 hours) for finger millet and barnyard millet, respectively. Finger millet demonstrated significant variations in response to different waterlogging durations, whereas barnyard millet's response remained consistent.

Seedling dry weight increased with prolonged waterlogging, from 10.29% and 2.136% at 48 hours to 38.08% and 9.12% at 120 hours in finger and barnyard millet, respectively. Root surface area (RSA) and root volume (RV) increased markedly with waterlogging. After 120 hours, RSA rose 93.87% in finger millet and 24.97% in barnyard millet, while RV increased by 165% and 100%, respectively.

Root tip number (NRT) and root fork number (NRF) in finger millet saw the most significant changes at 120 hours, with NRT increasing by 63.55% and NRF by 159%. In barnyard millet, NRT showed an increase of up to 17.833% at 72 hours compared to controls, while NRF remained unaffected.

Leaf growth pattern

The leaf area of finger millet and barnyard millet significantly increased under waterlogged conditions, peaking at 72 hours before wilting at 120 hours. Leaf area expanded by 12.44% and 25.41% at 48 hours, reaching 56.26% and 45.21% at 72 hours for finger and barnyard millet, respectively (Table 2). Specific leaf area (SLA) showed no significant change at 48 hours but rose by 30.22% and 16.09% at 72 hours in finger millet and barnyard millet, respectively (Fig- 1 A). In contrast, specific leaf weight (SLW) significantly declined by 23.26% in finger millet and showed a non-significant decrease of 13.86% in barnyard millet at 72 hours (Fig-1 B). Leaf chlorophyll concentration, measured with a SPAD meter, only significantly reduced under 120 hours of waterlogging, decreasing by 39.47% in finger millet and 54.88% in barnyard millet (Figure 1C).

Tolerance indices

The root-to-shoot biomass ratio (RW/SW) and root-to-shoot length ratio (RL/SL) of both crops were significantly affected by waterlogging. After 120 hours of waterlogging, RW/SW decreased by 16.91% in finger millet and 11.96% in barnyard millet, while RL/SL declined by 30.69% and 32.76%, respectively. Under these conditions, finger millet exhibited higher RW/SW (44.70%), RL/SL (44.70%) and waterlogging tolerance coefficient (19.48%) compared to barnyard millet (Fig-1 D, E, & F). Additionally, finger millet demonstrated better chlorophyll content, with a 10.48% increase under control conditions and a 33.28% increase after 120 hours of waterlogging, compared to barnyard millet (Figure 1C).

Principal component analysis

Principal component analysis (PCA) revealed that three major principal components (PCs) contributed to finger and barnyard millet seedling traits. The first two principal components, PC1 and PC2, exhibited the highest eigenvalues: 13.327 and 2.226 for finger millet and 12.802 and 1.918 for barnyard millet. PC1 accounted for 83.2964% of the variance in finger millets and 74.288% in barnyard millet, while PC2 accounted for 14.165% and 11.99%, respectively. Together, they contributed to 97.462% of the variation in finger millet and 92% in barnyard millet data [Table 3].

For both millets, PC1 primarily included root length (RL), shoot length (SL), root weight (RW), shoot weight (SW), root surface area (RSA), root volume (RV), SPAD value, root-to-shoot length ratio (RL/SL), root-to-shoot biomass ratio (RW/SW), SLA, SLW and waterlogging tolerance coefficient (WTC). PC2 included the SPAD value, while in finger millet, the NRF contributed to PC1 but was associated with PC3 [Fig- 2 & 3].

Correlation analysis demonstrated that seedling weight was positively correlated with shoot length, shoot weight, root weight, root surface area, root volume and specific leaf area and strongly correlated with the WTC. Conversely, seedling weight was negatively correlated with root length, root-to-shoot length ratio, root-to-shoot biomass ratio and specific leaf weight [Fig- 4]. Additional data related to

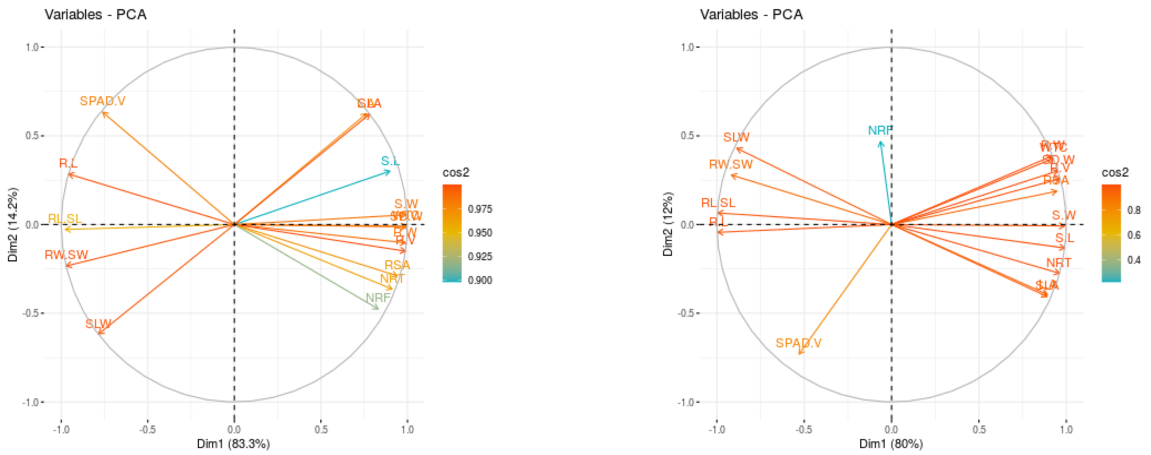

Fig. 2. Principal component analysis of finger millet and barnyard millet seedling parameters with the depiction of first two principal components (Dim stands for PC)

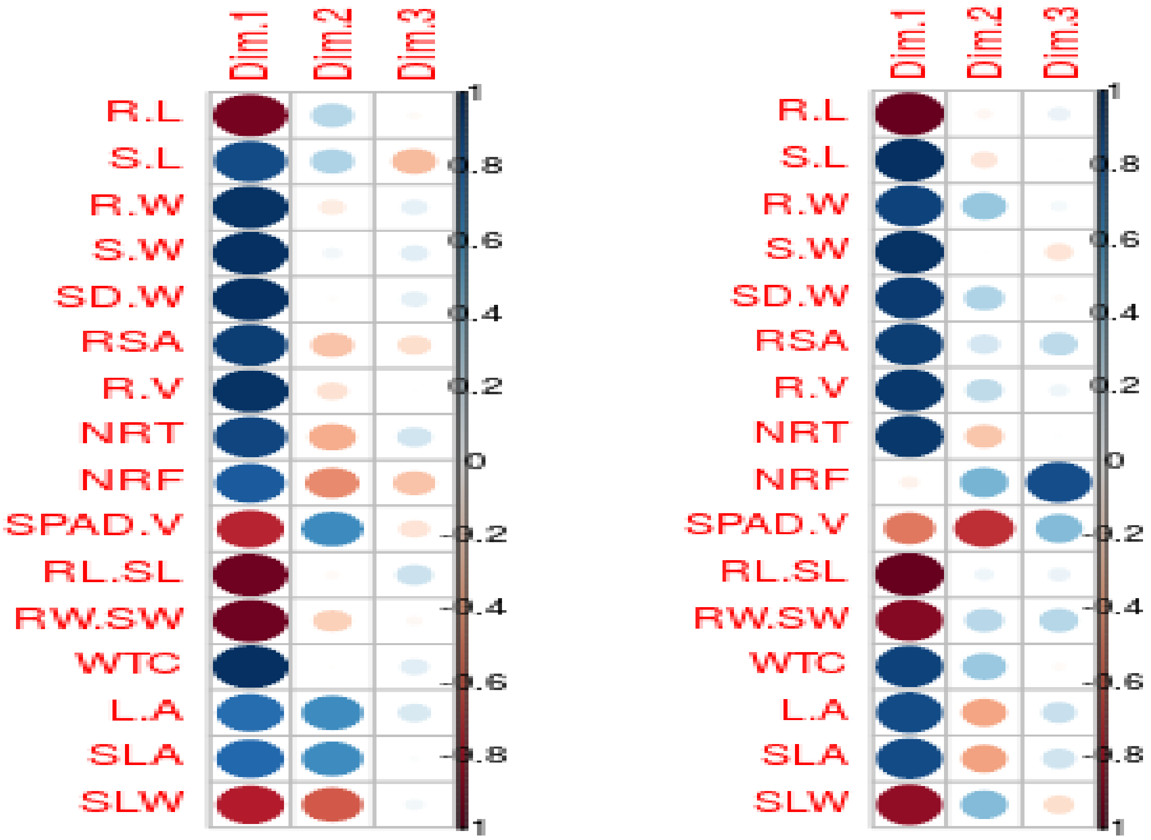

Fig. 3. Correlation between seedling parameters and principal component of finger millet and barnyard millet seedlings (Dim stands for PC) - correlation value ranges from -1 (strong negative correlation to +1 (strong positive correlation).

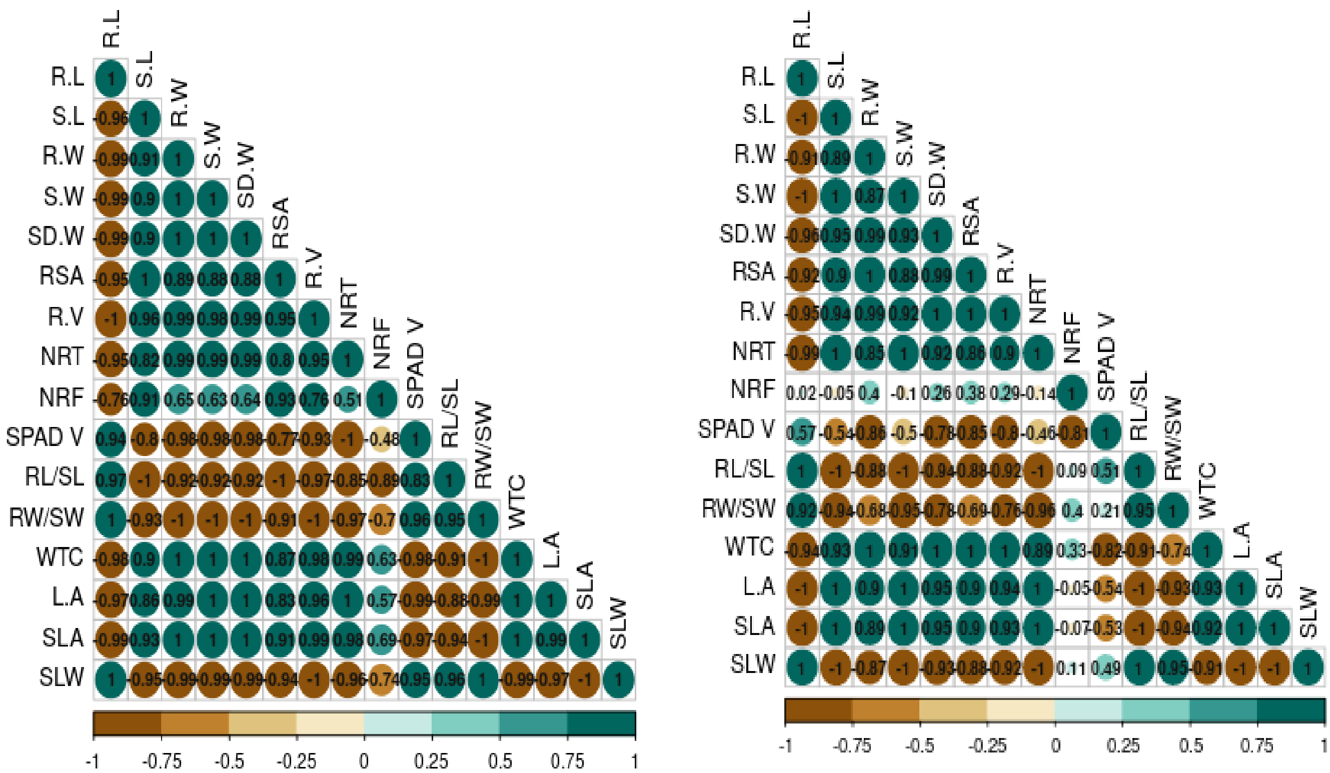

Fig. 4. Correlation among seedlings parameters of finger millet and barnyard millet seedlings- correlation value ranges from -1(strong negative correlation to +1 (strong positive correlation)

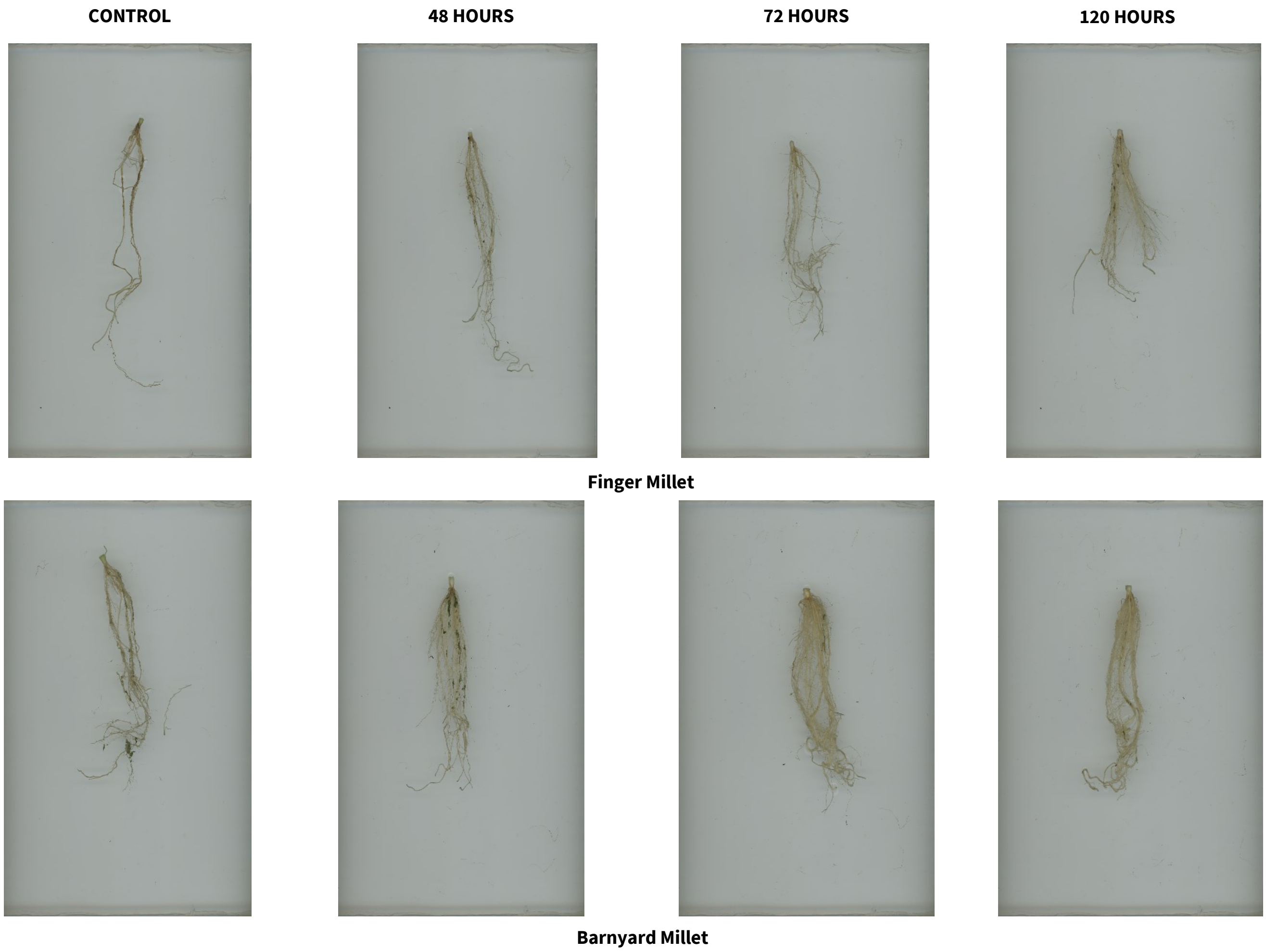

Fig. 5. Effect of different durations of waterlogging on root growth in finger millet and barnyard millet seedlings

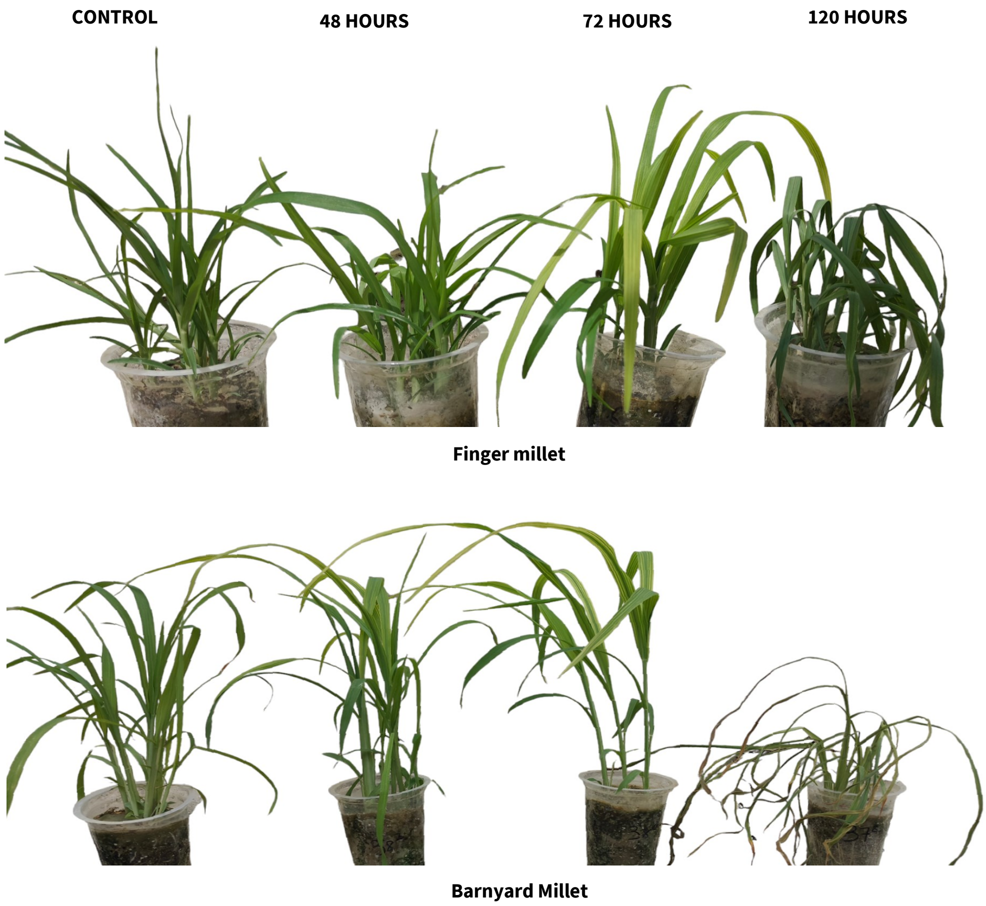

Fig. 6. Effect of different durations of water logging treatment on shoot growth and leaf area pattern in finger millet and barnyard millet seedlings.

Table 3. Eigenvalue and percentage contribution of variable on principal components

Principal component (PC)	Finger millet			Barnyard millet		
	PC1	PC2	PC3	PC1	PC2	PC3
Eigenvalue	13.327	2.266	0.406	12.802	1.918	1.28
Percentage of variance	83.296	14.165	2.538	80.009	11.99	8
Cumulative percentage of variance	83.296	97.462	100	80.009	92	100
Percentage contribution of variable on PCs						
Seedling parameters	PC1	PC2	PC3	PC1	PC2	PC3
R. L	6.89	3.585	0.119	7.735	0.099	0.614
S. L	6.057	4.007	25.113	7.675	0.912	0.002
R. W	7.333	0.471	2.969	6.621	7.828	0.171
S. W	7.373	0.132	3.546	7.652	0.003	1.594
SD. W	7.41	0.007	3.019	7.092	4.782	0.034
RSA	6.647	3.688	7.514	6.985	1.837	5.51
R. V	7.334	0.996	0.001	7.254	3.476	0.369
NRT	6.233	5.836	9.115	7.221	3.937	0.006
NRF	5.181	9.996	20.41	0.031	11.413	60.705
SPAD.V	4.341	17.694	5.017	2.191	27.816	14.523
RL.SL	7.159	0.033	11.129	7.717	0.222	0.611
RW. SW	7.083	2.405	0.364	6.572	4.066	6.302
W.T.C	7.383	0.004	3.919	6.717	7.262	0.063
L.A	4.363	17.222	6.927	6.213	8.107	3.834
SLA	4.59	17.123	0.055	6.192	8.593	3.319
SLW	4.622	16.801	0.784	6.132	9.645	2.344

PCA, including the scree plot, individual PCA and PCA biplot, are presented in the supplementary data [Figure 8].

Discussion

Waterlogging conditions resulted in increases in shoot length, shoot dry weight, leaf area and specific leaf area in both finger millet and barnyard millet, consistent with findings in little millet and other millet species (18-20). The increase in shoot length and dry weight is ascribed to an expanded leaf area, an improved plant growth rate, endogenous hormonal modulation and diminished water usage efficiency in waterlogged conditions, resulting in a reallocation of resources towards shoot development (20, 21). Some species elongate their shoots to access more air when submerged; however, this strategy can result in plant death if energy reserves are depleted. This was evident in our study, where plants began to wilt with prolonged waterlogging (22, 23).

Waterlogging conditions reduced root length while increasing root dry weight. Roots are key in managing hypoxic soil conditions, typically growing longer to access water and nutrients. However, in waterlogged soils, fully saturated pores inhibit root length growth (24). In contrast, root dry weight increased, as also observed in little millet (18). The development of adventitious roots in wet conditions depends on the frequency of flooding and shows a correlation between waterlogging tolerance and root length density (24, 25). An increase in root dry biomass is associated with vigorous root growth and enhanced carbohydrate metabolism under waterlogged conditions (18, 23). The presence of more root tips and forks in finger millet may contribute to greater root volume. Additionally, the increases in root volume and surface area can also be attributed to the formation of lysigenous aerenchyma under waterlogged conditions (18, 26).

Waterlogging prompts plants to absorb more water and transpire it through their leaves to alleviate stress. Leaf area increased significantly for up to 72 hours under waterlogged conditions, as energy is redirected towards leaf elongation. This results in thinner cell walls and cuticles, leading to an increase in specific leaf area (SLA) in both finger millet and barnyard millet, while specific leaf weight (SLW) in finger millet decreased (27, 28). Both crops exhibited some tolerance to waterlogging, with finger millet demonstrating more remarkable leaf plasticity, indicating a higher tolerance than barnyard millet. There was no significant difference in SPAD values under mild waterlogging, likely due to chloroplast reorientation that enhances photosynthesis and dry biomass production during mild stress up to 72 hours. However, with increased waterlogging extending to 120 hours, SPAD values significantly decreased due to chloroplast degradation triggered by severe stress (29, 30).

The root-to-shoot length ratio and root-to-shoot biomass ratio decrease significantly under waterlogging conditions due to increased energy allocation towards shoot growth. This occurs because oxygen depletion, or hypoxia, primarily impacts non-photosynthesizing components like roots (31). The increase in the tolerance coefficient during waterlogging may result from the downregulation of respiration and limited fermentation stimulation, leading to a positive energy balance and enhanced plant growth, including increased leaf area, shoot dry weight and root dry weight. Finger millet exhibits higher RL/SL, RW/SW and Tolerance Index than barnyard millet under waterlogging stress, indicating greater tolerance at the same growth stage. This higher tolerance is attributed to finger millet's enhanced morphological plasticity, including significant differences in SLA and SLW, as well as a greater number of root forks compared to barnyard millet.

Conclusion

Finger and barnyard millet may endure light waterlogging for a maximum duration of 72 hours; however, extended waterlogging lasting up to 120 hours is detrimental. Both crops adapt to waterlogging by increasing shoot length, shoot dry weight, leaf area and specific leaf area. This growth is attributed to leaf elongation, an enhanced plant growth rate and the redirected of energy towards shoot development. While root length decreases, root dry weight increases due to inhibited normal growth in saturated soils. The increased root dry biomass indicates vigorous lateral root growth, with more root tips and forks forming adventitious roots and root hairs. Leaf area increases significantly up to 72 hours, resulting in reduced leaf thickness. There is no significant difference in SPAD values up to 72 hours; however, a decrease occurs after 120 hours of waterlogging. Finger millet demonstrates more remarkable leaf plasticity and tolerance than barnyard millet, with a significant change in SLW. Root-to-shoot length and biomass ratios decrease under stress, with finger millet displaying higher tolerance indices due to enhanced morphological plasticity.

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Authors' contributions

Dayanji Sherpa and Shailesh Kumar conceptualized, conducted formal analysis, investigated and composed the original draft. Shailesh Kumar and Sweta Mishra curated, supervised, reviewed and validated the data. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

In the drafting of this manuscript, the writers utilized [CHAT GPT] to enhance the language and readability. Subsequent to utilizing this tool/service, the writers assessed and refined the text as necessary and assume complete responsibility for the publication's content.

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