scientific reports

OPEN

Root growth, yield and stress tolerance of soybean to transient waterlogging under different climatic regimes

Vinay M. Gangana Gowdra[1,2]✉, B. S. Lalitha[1], Hanamant M. Halli[2]✉, E. Senthamil[2,3], Priyanka Negi[2], H. M. Jayadeva[1], P. S. Basavaraj[2], C. B. Harisha[2], K. M. Boraiah[2], Sandeep B. Adavi[4], P. G. Suresha[5], Raghavendra Nargund[6], Ganesh Mohite[2] & K. Sammi Reddy[2]

Global warming-induced abiotic stresses, such as waterlogging, significantly threaten crop yields. Increased rainfall intensity in recent years has exacerbated waterlogging severity, especially in lowlands and heavy soils. Its intensity is projected to increase by 14–35% in the future, posing a serious risk to crop production and the achievement of sustainable development goals. Soybean, a major global commercial crop cultivated across diverse climates, is highly sensitive to waterlogging, with yield losses of up to 83% due to impaired root morphology and growth. Therefore, understanding the stage-specific response of soybean to varying intensities of waterlogging under different climate regimes is crucial to mitigate the impact of climate change. This study evaluated two climate regimes (Summer: C_S and Rainy: C_R), four growth stages (S_{15}: 15 days after emergence, S_{30}, S_{45}, and S_{60}), and five waterlogging durations (D_2: 2 days, D_4, D_6, D_8, and D_{10}) using a randomized complete block design (RCBD) with seven replications in 2023. Results revealed that waterlogging adversely affected soybean root morphology (reducing root volume by 8.6% and dry weight by 5.3%) and growth (decreasing leaf area by ~6% and dry matter by 48.2%), with more severe effects observed during the summer compared to the rainy season. Among growth stages, soybean was most sensitive at S_{45}, showing greater reductions in growth attributes and seed yield (~64.9%) across climate regimes. Prolonged waterlogging (2–10 days) had a pronounced negative impact on root and shoot parameters, resulting in yield reductions of 25.4–47.8% during summer and 47.0–68.2% during the rainy season, compared to the control. Yield stability was highest at D_2 (yield stability index: 0.53) with minimal yield reductions, while D_{10} caused the greatest yield loss (~58%). Interestingly, the summer climate regime, characterized by bright sunshine hours and higher temperatures, supported better post-stress recovery, leading to higher grain yields. In conclusion, waterlogging during $C_R \times S_{45} \times D_{10}$ caused the most substantial yield reduction (~91%).

Keywords Climate regimes, Root morphology, Dry matter partitioning, Stress tolerance, Waterlogging, Growth stages, Soybean yield

Global warming, a key driver of climate change, contributes to extreme weather events by raising the Earth's temperature. By 2100, it is projected that global temperatures could increase by 1.4 to 4.4 °C, leading to an up to 40% rise in the annual wettest days across almost all continents[1]. A single-degree rise in temperature can increase atmospheric moisture content by 6–7%, potentially triggering extreme rainfall events and more severe wet extremes in regions that already receive high rainfall[2,3]. In India, the frequency of extreme wet years could increase eightfold between 2050 and 2100, compared to an average of five wet years between 1965 and 2015, with expected rainfall increases of 9.7 to 24.3%[4]. Additionally, seasonal mean precipitation is predicted to

[1]University of Agricultural Sciences, GKVK, Bangalore, Karnataka 560065, India. [2]ICAR–National Institute of Abiotic Stress Management, Pune, Maharashtra 413115, India. [3]University of Agricultural Sciences, Dharwad, Karnataka 580005, India. [4]ICAR–National Institute of Biotic Stress Management, Raipur, Chhattisgarh 493225, India. [5]MACS–Agharkar Research Institute, Soratewadi, Pune, Maharashtra 412306, India. [6]ICAR–Indian Institute of Soybean Research, Indore, Madhya Pradesh 452001, India. ✉email: vinaymg.581@gmail.com; hmhalli4700@gmail.com

rise from 6.2 to 7.3 mm/day, reflecting an intensification of rainfall by 14 to 35% by the end of 2050 and 2100, respectively[1,4]. Currently, 16% of global cultivated areas are prone to waterlogging, resulting in approximately $1.5 billion in economic losses annually. In the future, high-intensity rainfall is likely to expand the areas affected by waterlogging, including irrigated regions in India, causing significant economic losses for farmers[5,6].

Waterlogging occurs when the soil remains saturated for an extended period, exceeding 20% of its field capacity[7]. This condition significantly hinders oxygen diffusion resulting in rapid decreases in soil redox potential[8–10]. In such energy-deficient conditions, plants temporarily rely on glycolysis and ethanol fermentation for energy[11]. However, prolonged waterlogging can lead to the accumulation of toxic compounds such as lactate, which severely impairs respiration[12]. Additionally, soil carbon can be lost via ethanol production and the generation of reactive oxygen species (ROS)[11,12]. This energy deficit reduces the phosphorylation of aquaporins, thereby lowering the hydraulic conductivity of plant roots and hindering water and nutrient absorption[13]. The impaired root function triggers partial stomatal closure, reduced CO_2 influx and photosynthesis results in reduced plant growth, ultimately causing significant yield losses[14,15]. Some plants have developed adaptive mechanisms to cope with waterlogging, such as forming adventitious roots and aerenchyma cells, which facilitate oxygen and nutrient transport to aerial parts with wider variations among species or varieties[5,16]. However, waterlogging-induced imbalances in assimilate accumulation and translocation can reduce shoot and root dry matter by 75–77% and 64–75%, respectively, in soybeans[15]. Therefore, studying the impact of waterlogging on major crops is crucial to understanding their responses to changing weather patterns and developing strategies to mitigate yield losses under such conditions.

Soybean, a vital crop, known for its diverse uses in food, feed, industrial applications, and as a future bio-diesel crop[17,18]. It accounts for approximately half of the global edible oil production and about two-thirds of the world's protein concentrate for livestock feed[19]. Globally, soybean is cultivated on 133.8 million hectares, with an annual production of 348.9 mt[20]. In India, soybean is primarily grown in the central and western states on vertisols, which are prone to waterlogging due to excessive rainfall and low infiltration rates, significantly impacting yields[18]. Studies reveal that waterlogging is the second most damaging abiotic stress affecting soybean after drought, with potential yield losses of up to 80%, depending on the crop's phenology[19,21,22]. Yield reductions are typically ranges from 17 to 43% during the vegetative stage and 50–56% at the reproductive stage depending on the duration and timing of waterlogging in soybean[23]. Additionally, one of the key factors contributing to yield reduction is a decrease in the number of pods per plant, which can drop by as much as 37% under waterlogged conditions[24].

Several studies have explored the response of soybean to waterlogging by examining fixed durations during different crop growth stages or vice versa[24–27]. However, there is limited information on the combined impact of variable waterlogging durations across different growth stages in soybean. Additionally, research has shown that a combination of elevated temperature and waterlogging can enhance photosynthesis and dry matter allocation in crops like tomato compared to ambient temperature conditions[28]. Similarly, elevated temperatures in conjunction with waterlogging have been reported to alleviate adverse effects following stress relief in rice[29]. Similarly, the adverse impact of elevated temperature, growth stages and waterlogging on maize has been reported by Shao et al.[30]. Despite these findings in tomato, rice and maize, studies investigating the combined influence of elevated temperature and waterlogging is lacking in one of the important crops like soybean. Moreover, the response of soybean to variable waterlogging durations at different growth stages, particularly under diverse climate conditions, is poorly understood. These interactions encompassing climate regimes, growth stages, and waterlogging durations play a critical role in determining root morphology, growth dynamics, and ultimately crop yield. Therefore, detailed investigations on the combined effects of these factors to mitigate stress impacts and address knowledge gaps for both current and future scenarios are required. In this context, we hypothesize that the impact of waterlogging on soybean is differentially regulated by varying climate regimes, which include changes in temperature, relative humidity, and sunshine hours. To test this hypothesis, the present study was designed for two growing seasons in a pot culture experiment with the following objectives: (i) To investigate the combined effects of climate regimes, growth stages, and waterlogging durations on growth, dry matter partitioning, and root surface architecture and (ii) To estimate yield losses and evaluate stress tolerance indices resulting from the interactions between climate regimes, growth stages, and waterlogging durations in soybean (Fig. 1).

Material and methods

Study location

The study was conducted at the ICAR-National Institute of Abiotic Stress Management, Baramati, Maharashtra, India (18° 09′ 30.62″ N; 74° 30′ 03.08″ E; mean sea level: 570 m). This location experiences semi-arid climatic conditions typical of the Deccan Plateau region, with an average annual rainfall of 560 mm. The majority of rainfall (70%) occurs during the southwest monsoon season (June–September), followed by 21% during the post-monsoon period (October–December)[31]. Weather parameters recorded at fortnightly intervals during the crop growth period are presented in Table S1. The average maximum and minimum temperatures during the summer season (C_S) were 34.9 °C and 18.5 °C, respectively, whereas during the rainy season (C_R), the average maximum and minimum temperatures were 31.2 °C and 20.5 °C, respectively. Bright sunshine hours were also higher during C_S (8.3 h day^{-1}) compared to C_R (4.6 h day^{-1}). Conversely, C_R recorded greater cumulative rainfall (311 mm) and higher average relative humidity, with maximum and minimum values of 86.4% and 53.0%, respectively, compared to C_S.

Experimental details and crop management

The study was conducted through two separate pot experiments during 2023: one in the summer season (C_S, February to June) and the other in the rainy season (C_R, July to November). The experiments were designed

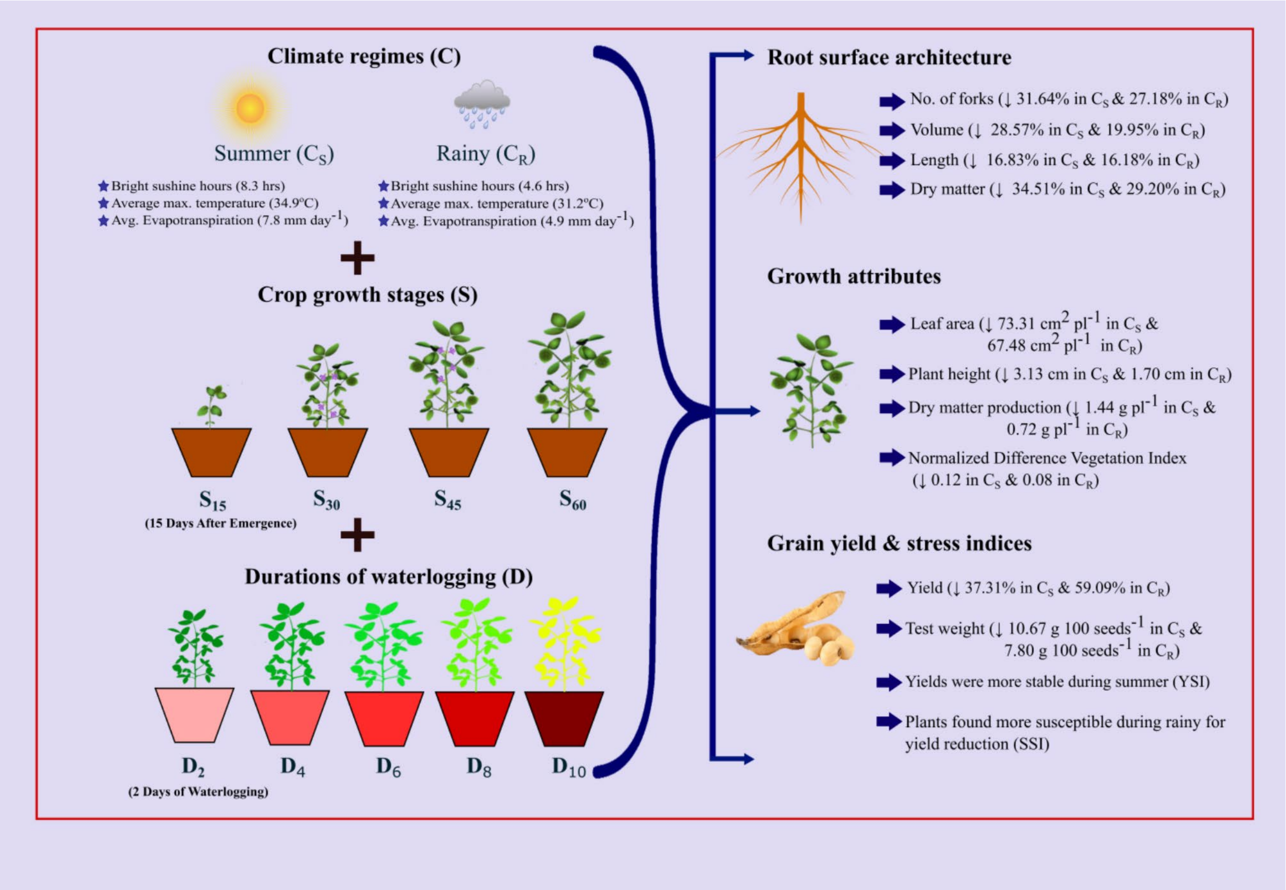

Fig. 1. Response of soybean to waterlogging stress at different growth stages under climatic regimes.

to analyze soybean responses to varied durations of waterlogging across different crop growth stages under distinct climatic regimes. The experiment followed a factorial randomized complete block design (FRCBD) with three factors, each replicated seven times (three replications for growth and yield observations, two for destructive sampling viz., dry matter accumulation, root attributes and biochemical and another two as non-treated control; one for destructive sampling and another for recording growth and yield observations). Thus, each replication consists of 21 pots with two plants in each pot (total 42 plants per replication). The first factor comprised two seasons with differing climatic regimes (C_S and C_R), the second factor included four growth stages (S_{15}: 15 Days After Emergence (DAE), S_{30}: 30 DAE, S_{45}: 45 DAE, and S_{60}: 60 DAE), and the third factor involved five waterlogging durations (D_2: 2 days, D_4: 4 days, D_6: 6 days, D_8: 8 days, and D_{10}: 10 days), compared against a control treatment with no waterlogging. The soybean variety NRC-136 (procured from the Indian Institute of Soybean Research, Indore-452 001, Madhya Pradesh) which can withstand higher temperatures and susceptible to waterlogging conditions, suited to both rainy and summer conditions. The seeds were manually sown in pots of 8452 cm^3 capacity (calculated using the hollow cone formula; Eq. 1). Each pot was filled with 14 kg of soil, up to 90% of its capacity, and four seeds were dibbled per pot. Regular irrigation at 60% of field capacity was provided to ensure better germination and seedling establishment[16]. In case of excessive rainfall, the extra water from the pots was immediately drained after cessation of rainfall. The recommended nutrient dose (40:80:25 kg N: P_2O_5: K_2O ha^{-1}) was applied to each pot based on weight. The nutrients were supplied through urea $CO(NH_2)_2$, diammonium phosphate $(NH_4)_2HPO_4$, and potassium chloride (KCl) and thoroughly mixed with the soil before sowing. Thinning was performed 7 DAE, and two healthy plants were retained per pot. To address iron deficiency, a foliar spray of 0.1% chelated iron (12% Fe as Fe–EDTA) was applied at 12 DAE.

$$\text{Soil volume of pot } \left(\mathrm{cm}^3\right) = \frac{1}{3} \times \pi \text{ h } \left[\mathrm{R}^2 + \mathrm{Rr} + \mathrm{h}^2\right] \tag{1}$$

where ‘R’ is the radius of topsoil surface, ‘r’ is the radius of a bottom surface, ‘h’ is the height of the filled soil in the pot.

Imposition of waterlogging

Waterlogging was imposed on the plants by placing the filled pots in a constructed concrete tank with a capacity of 38.08 m^3 (5.43 m × 5.48 m × 1.28 m) for the specified durations as per the experimental treatments. The water level in the tank was maintained at approximately 2.5 cm above the soil surface. After the designated waterlogging period, the pots were removed from the tank to record various morphological observations at each growth stage.

Root sampling

Destructive root sampling was carried out at each growth stage to study root morphology during both C_S and C_R. Pots were carefully depotted, and the roots were thoroughly washed to remove adhered soil particles as depicted in Fig. S1. Immediately after root removal, the number and length of aerial roots were recorded. The roots were then cut at the crown portion and stored in polythene bags at − 20 °C in a deep freezer for further analysis. Subsequently, the roots were analyzed using a WinRHIZO root scanner (Regent–STD 1600 + WINRHIZOTM 2013, Regent Instruments, Canada, Quebec). Before scanning, the roots were defrosted and stained with a pinch of potassium permanganate ($KMnO_4$) for 30 min. The stained roots were spread uniformly in a tray filled with clear water to prevent overlapping. Various root morphological traits were measured by analysing the root images, as described by Halli et al.[32,33]. After scanning, the roots were shade-dried and then oven-dried at 65 °C in a hot air oven to determine their dry weight.

Growth, physiology and yield parameters

Growth parameters, such as plant height, number of trifoliate leaves, leaf area, number of branches, and normalized difference vegetation index (NDVI), were recorded within 30 min of removing the pots from waterlogging stress to minimize the influence of microclimatic changes on the observations. The NDVI was measured 0.5 m above the plant canopy using a handheld GreenSeeker® device (Trimble, USA) as described by Verhulst and Govaerts[34] in Eq. (2). Similarly, photosystem-II activity during the post-stress period (10 days after relieving stress) was measured using a high-sensitivity charge-coupled device (CCD) camera, as described by Basavaraj et al.[16]. The images were analyzed using the FluoroCam software package (FluoroCam 7), and PSII efficiency was calculated using Eq. (3).

$$\mathrm{NDVI} = \frac{(\mathrm{NIR} - \mathrm{IR})}{(\mathrm{NIR} + \mathrm{IR})} \tag{2}$$

NIR and IR indicate the light reflections at near infra-red and red spectrum regions, respectively.

$$\mathrm{Qmax} = \frac{(\mathrm{Fm} - \mathrm{F0})}{\mathrm{Fm}} \tag{3}$$

where Qmax is quantum efficiency of PSII, F0 and Fm are minimum and maximum fluorescence of dark adapted leaves. Fm–F0 indicates the variable fluorescence.

Leaf area and dry matter partitioning were recorded treatment wise from destructive sampling. The leaves were separated from the shoots, and the leaf area was measured using leaf area meter (a LI-COR Li3100C). Subsequently, the separated leaves and stem parts were oven-dried at 65 °C for 72 h to determine the dry weight. Matured pods were harvested by plucking 10 days after physiological maturity, and the yield per plant was recorded. The general growth of soybean plants at 90 DAS is presented in Fig. S2.

Stress indices

To determine the impact of climate regimes and waterlogging stress at different growth stages of soybean, few selected stress indices were calculated such as, Yield Stability Index; (YSI)[35], Stress Susceptibility Index (SSI)[36], and Tolerance Index (TOL)[37]. These indices were calculated using the equations listed below.

$$\mathrm{YSI} = \frac{\mathrm{Y_{si}}}{\mathrm{Y_{ci}}} \tag{4}$$

$$\mathrm{SSI} = \frac{1 - (\mathrm{Y_{si}} - \mathrm{Y_{ci}})}{1 - (\mathrm{Ys} - \mathrm{Yc})} \times 100 \tag{5}$$

$$\mathrm{TOL} = \mathrm{Yci} - \mathrm{Ysi} \tag{6}$$

where Y_{si} and Y_{ci} are the yield of ith treatment under stress and control conditions, respectively. The Y_s and Y_c are the average yields of all treatments under stress and control conditions respectively.

Data analysis

The data recorded on various parameters of soybean, such as growth, root morphology, yield, and stress indices, were subjected to a normality test. Since the dataset was found to be normally distributed, no transformation was necessary. The data were then analyzed using analysis of variance (ANOVA), considering climate regime or growing season, growth stages, and durations of waterlogging as fixed effects, and replications as random effects in a factorial randomized complete block design (FRCBD) with three replications, using the F-test. Significant differences between treatments were tested using the Duncan Multiple Range Test ($\alpha = 0.05$). Furthermore, Principal Component Analysis (PCA) and biplots were analyzed using an open access software "GRAPES" to interpret the relationships between key traits, such as root morphology, grain yield, and stress indices, across different treatments to discriminate the associated variability[38].

Results

Modifications in root morphology due to waterlogging stress under different climates

The root morphological features of soybean were significantly affected by transient waterlogging stress under both climatic conditions (Tables 1, S2 and Fig. 2). Regardless of crop stages (S) and durations (D), the reduction in root parameters was greater during the summer (C_S) compared to the rainy season (C_R). The reduction in root length ranged from 5.0–32.6% in summer to 8.9–24.3% in the rainy season. Similarly, reductions in root surface area (2.7–44.0% in C_S & 8.4–28.5% in C_R), average root diameter (0.7–20.8% in C_S & 0.3–23.0% in C_R), root volume (2.2–69.7% in C_S & 1.8–33.4% in C_R), and root dry weight (5.6–57.5% in C_S & 0–51.8% in C_R)

Treatments	Root length (%)		Root surface area (%)		Average root diameter (%)		Root volume (%)	
	Summer	Rainy	Summer	Rainy	Summer	Rainy	Summer	Rainy
Seasons/climate (C)								
Summer (C_S)	16.83^{a}		20.80^{a}		8.74^{a}		28.57^{a}	
Rainy (C_R)	16.18^{b}		19.88^{b}		8.22^{b}		19.95^{b}	
S.Em. ±	0.13		0.19		0.08		0.24	
Stages of waterlogging (S)								
S_{15}	14.0^{c}	14.3^{c}	19.1^{c}	18.1^{c}	6.7^{b}	6.9^{c}	21.1^{b}	16.6^{c}
S_{30}	12.0^{d}	12.4^{d}	7.1^{d}	14.3^{d}	4.6^{d}	5.0^{d}	15.8^{c}	15.5^{d}
S_{45}	17.8^{b}	18.4^{b}	20.6^{b}	22.5^{b}	6.0^{c}	7.4^{b}	19.6^{b}	22.0^{b}
S_{60}	23.4^{a}	19.6^{a}	36.5^{a}	24.7^{a}	17.7^{a}	13.5^{a}	57.7^{a}	25.7^{a}
S.Em. ±	0.28	0.25	0.43	0.32	0.18	0.16	0.58	0.33
Durations of waterlogging (D)								
D_2	9.5^{e}	12.9^{e}	8.9^{e}	14.0^{e}	4.8^{d}	2.4^{e}	15.5^{d}	10.1^{e}
D_4	13.6^{d}	13.9^{d}	13.4^{d}	16.7^{d}	4.8^{c}	4.3^{d}	19.7^{c}	15.6^{d}
D_6	17.5^{c}	16.2^{c}	20.7^{c}	21.1^{c}	6.1^{b}	8.6^{c}	34.3^{b}	20.3^{c}
D_8	20.8^{b}	17.7^{b}	27.0^{b}	23.3^{b}	10.1^{b}	12.3^{b}	35.4^{b}	24.5^{b}
D_{10}	22.9^{a}	20.2^{a}	34.0^{a}	24.3^{a}	10.6^{a}	13.6^{a}	38.0^{a}	29.3^{a}
S.Em. ±	0.31	0.28	0.48	0.35	0.20	0.18	0.65	0.37
Interactions (S × D)								
$S_{15}D_2$	5.0^{l}	12.2^{i}	2.7^{i}	8.6^{l}	0.7^{k}	2.4^{k}	2.2^{j}	6.5^{i}
$S_{15}D_4$	10.5^{j}	13.1^{hi}	9.8^{g}	13.8^{j}	1.4^{jk}	5.6^{ij}	3.5^{j}	12.9^{h}
$S_{15}D_6$	17.0^{ef}	14.4^{gh}	12.7f.	20.1^{gh}	9.2^{ef}	7.0^{gh}	30.6^{ef}	13.7^{h}
$S_{15}D_8$	17.4^{ef}	14.8^{fg}	26.7^{cd}	22.9^{ef}	9.5^{e}	7.5^{fg}	33.3^{de}	21.0^{de}
$S_{15}D_{10}$	20.2^{d}	17.0^{de}	43.4^{a}	24.8^{c-e}	12.7^{d}	12.0^{d}	36.0^{cd}	28.9^{b}
$S_{30}D_2$	7.9^{k}	8.9^{j}	0.8^{i}	8.4^{l}	2.1^{j}	0.3^{l}	9.9^{i}	1.8^{j}
$S_{30}D_4$	9.8^{j}	8.9^{j}	6.2^{h}	11.4^{k}	2.2^{j}	0.3^{l}	16.1^{h}	12.8^{h}
$S_{30}D_6$	11.3^{ij}	12.0^{i}	7.5^{gh}	14.7^{ij}	5.6^{h}	6.2^{hi}	17.6^{gh}	16.7^{g}
$S_{30}D_8$	14.1^{gh}	14.3^{gh}	8.3^{gh}	16.7^{i}	6.0^{gh}	8.5f.	17.8^{gh}	19.8^{e}
$S_{30}D_{10}$	17.1^{ef}	18.0^{cd}	12.6f.	20.2^{gh}	7.0^{g}	9.7^{e}	17.8^{gh}	26.4^{c}
$S_{45}D_2$	12.8^{hi}	16.3^{ef}	6.1^{h}	19.2^{h}	3.6^{i}	2.3^{k}	10.5^{i}	17.6^{fg}
$S_{45}D_4$	15.9^{fg}	16.7^{de}	13.0f.	20.0^{gh}	5.0^{h}	6.5^{hi}	18.7^{gh}	16.9^{g}
$S_{45}D_6$	18.0^{e}	18.7^{c}	18.8^{e}	23.3^{d-f}	6.0^{gh}	6.5^{hi}	19.6^{gh}	22.0^{d}
$S_{45}D_8$	20.8^{d}	18.9^{c}	28.9^{c}	25.1^{cd}	6.9^{g}	10.1^{e}	21.0^{g}	25.0^{c}
$S_{45}D_{10}$	21.5^{d}	21.5^{b}	36.0^{b}	25.0^{cd}	8.3f.	11.6^{d}	28.4f.	28.5^{b}
$S_{60}D_2$	12.4^{hi}	14.3^{gh}	26.1^{d}	19.7^{gh}	12.8^{d}	4.6^{j}	39.4^{bc}	14.3^{h}
$S_{60}D_4$	18.0^{e}	16.9^{de}	24.7^{d}	21.6^{fg}	15.8^{c}	4.6^{j}	40.7^{b}	19.7^{ef}
$S_{60}D_6$	23.5^{c}	19.5^{c}	43.8^{a}	26.1^{bc}	19.4^{b}	14.5^{c}	69.3^{a}	28.8^{b}
$S_{60}D_8$	30.7^{b}	23.0^{ab}	43.9^{a}	28.5^{a}	19.9^{ab}	23.0^{a}	69.4^{a}	32.4^{a}
$S_{60}D_{10}$	32.6^{a}	24.3^{a}	44.0^{a}	27.4^{ab}	20.8^{a}	20.9^{b}	69.7^{a}	33.4^{a}
S.Em. ±	0.62	0.55	0.95	0.71	0.40	0.36	1.31	0.7

Table 1. Percent reduction in root morphological traits of soybean to transient waterlogging under different climatic regimes. *S_{15}: 15 DAE; Days after emergence, S_{30}: 30 DAE, S_{45}: 45 DAE, S_{60}: 60 DAE, D_2: 2 DWL; Days of waterlogging, D_4: 4 DWL, D_6: 6 DWL, D_8: 8 DWL, D_{10}: 10 DWL. Means followed by the same letter (s) within the column are not significant ($p < 0.05$).

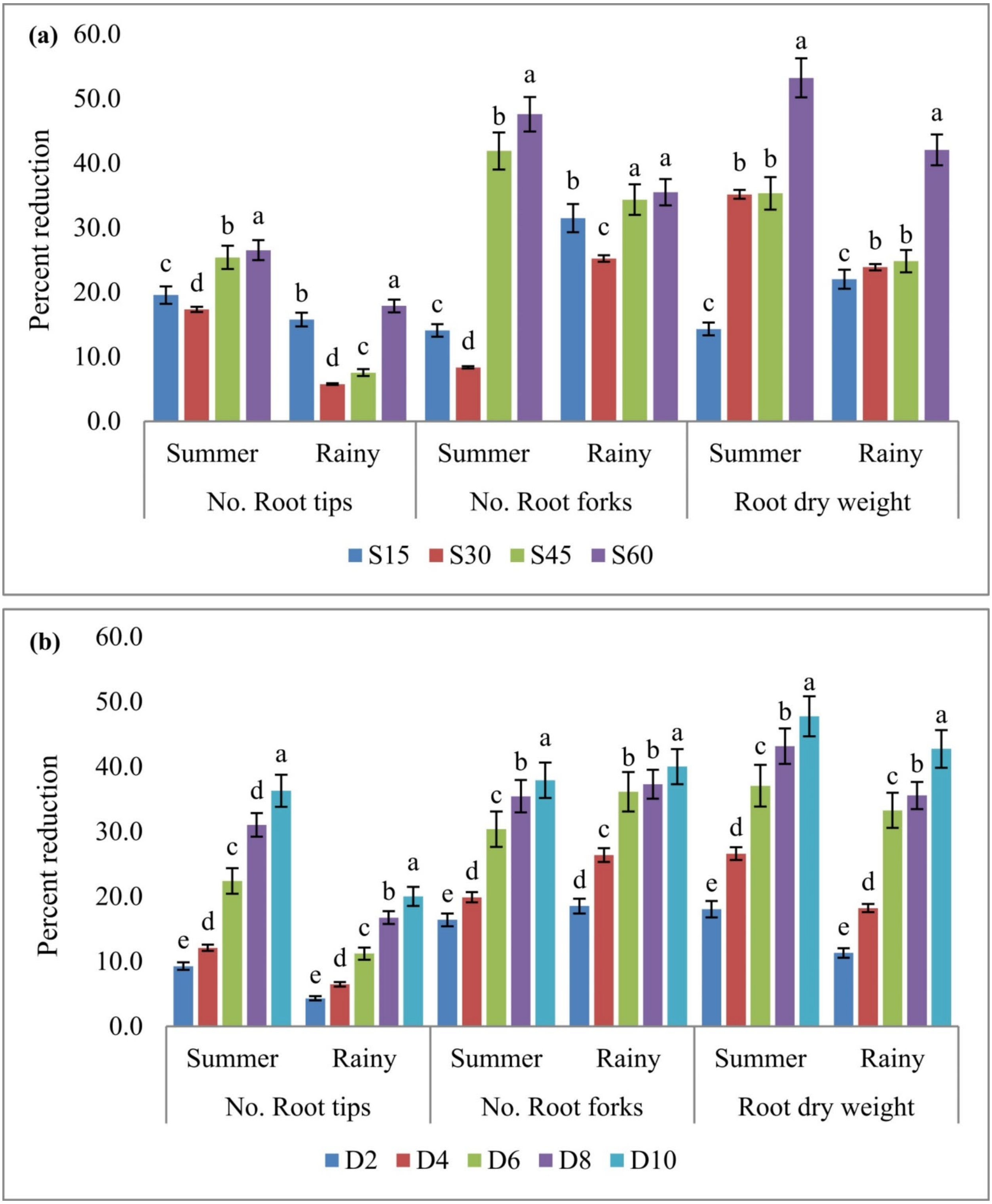

Fig. 2. Percent reductions in root morphological features under waterlogging (**a**) at different crop stages, (**b**) for different durations of waterlogging. *S_{15}: 15 DAE; Days after emergence, S_{30}: 30 DAE, S_{45}: 45 DAE, S_{60}: 60 DAE, D_2: 2 DWL; Days of waterlogging, D_4: 4 DWL, D_6: 6 DWL, D_8: 8 DWL, D_{10}: 10 DWL.

were observed. Furthermore, the soybean plants exhibited greater reductions in root morphological features when subjected to waterlogging at 60 DAE (S_{60}) compared to other stages in both climates (Table 1 and Fig. 2a). Similarly, longer waterlogging durations (D_2 to D_{10}) consistently reduced root growth in both C_S and C_R (Table 1 and Fig. 2b). The maximum reduction in root length was recorded after 10 days of waterlogging (D_{10}) under C_S climate (22.9%), compared to C_R (20.2%). Additionally, the highest reductions in root surface area (34.0%), root volume (38.0%), root tips (36.3%), and root dry weight (47.7%) occurred in C_S. Regarding the interaction effect, growth stages and duration of waterlogging (S × D) significantly influenced root growth in both climates (Tables 1 and S2). The treatment combination $S_{60} \times D_{10}$ resulted in the maximum reduction in root surface area (44% in C_S and 27.4% in C_R), root tips (42% in C_S and 27.2% in C_R), root forks (60.9% in C_S and 41.3% in C_R), and root volume (69.7% in C_S and 33.4% in C_R). Meanwhile, the greatest reduction in average root diameter was observed in the combination $S_{60} \times D_{8-10}$.

Soybean plants formed adventitious or aerial roots as an adaptive strategy to waterlogging stress (Table 2). Regardless of the stages and durations of waterlogging, plants grown in summer produced a higher number of longer aerial roots (2.38 and 0.98 cm for the number and length of aerial roots, respectively) compared to those grown in rainy season (C_R). Waterlogging at 15 DAE (S_{15}) resulted in a higher number of adventitious roots (6.2 in C_S and 5.3 in C_R) with greater length (2.5 cm in C_S and 1.9 cm in C_R), followed by waterlogging at 30 DAE

Treatments	Number of adventitious roots		Adventitious root length (cm)	
	Summer	Rainy	Summer	Rainy
Seasons/climate (C)				
Summer (C_S)	2.38^a		0.983^a	
Rainy (C_R)	1.75^b		0.603^b	
S.Em. ±	0.03		0.012	
Stages of waterlogging (S)				
S_{15}	6.2^a	5.3^a	2.5^a	1.9^a
S_{30}	3.3^b	1.7^b	1.4^b	0.5^b
S_{45}	0.0^c	0.0^c	0.0^c	0.0^c
S_{60}	0.0^c	0.0^c	0.0^c	0.0^c
S.Em. ±	0.07	0.05	0.03	0.02
Durations of waterlogging (D)				
D_2	0.7^e	0.4^e	0.2^e	0.2^e
D_4	1.2^d	0.9^d	0.4^d	0.3^d
D_6	1.5^c	1.2^c	0.6^c	0.5^c
D_8	3.5^b	1.9^b	1.7^b	0.7^b
D_{10}	5.1^a	4.3^a	2.1^a	1.5^a
S.Em. ±	0.07	0.06	0.03	0.02
Interactions (S × D)				
$S_{15}D_2$	2.7^f	1.8^e	1.0^f	0.7^e
$S_{15}D_4$	4.7^e	3.6^d	1.5^e	1.1^d
$S_{15}D_6$	6.0^d	4.9^c	2.2^d	1.8^c
$S_{15}D_8$	7.3^b	7.6^b	3.4^c	2.6^b
$S_{15}D_{10}$	10.3^a	8.5^a	4.5^a	3.2^a
$S_{30}D_2$	0.0^g	0.0^f	0.0^g	0.0f.
$S_{30}D_4$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{30}D_6$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{30}D_8$	6.5^c	0.0^f	3.2^c	0.0^f
$S_{30}D_{10}$	10.0^a	8.7^a	3.9^b	2.7^b
$S_{45}D_2$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{45}D_4$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{45}D_6$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{45}D_8$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{45}D_{10}$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{60}D_2$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{60}D_4$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{60}D_6$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{60}D_8$	0.0^g	0.0^f	0.0^g	0.0^f
$S_{60}D_{10}$	0.0^g	0.0^f	0.0^g	0.0^f
S.Em. ±	0.15	0.11	0.06	0.04

Table 2. Number of adventitious roots and adventitious root length of soybean to transient waterlogging stress under different climatic regimes. *S_{15}: 15 DAE; Days after emergence, S_{30}: 30 DAE, S_{45}: 45 DAE, S_{60}: 60 DAE, D_2: 2 DWL; Days of waterlogging, D_4: 4 DWL, D_6: 6 DWL, D_8: 8 DWL, D_{10}: 10 DWL. Means followed by the same letter (s) within the column are not significant ($p < 0.05$).

(S_{30}). However, no adventitious roots were formed when plants were exposed to waterlogging at 45 (S_{45}) and 60 DAE (S_{60}) (Table 2). Regarding waterlogging duration, significantly more (5.1 in C_S and 4.3 in C_R) and longer aerial roots (2.1 cm during.

C_S and 1.5 cm during C_R) were formed at 10 days (D_{10}) in both C_S and C_R. Furthermore, the interaction between the stage and duration (S × D) influenced adventitious root formation in soybean. The combination of $S_{15} \times D_{10}$ during the summer (C_S) produced the highest number of roots with the greatest length compared to other treatments.

Waterlogging induced changes in plant growth attributes

The soybean growth attributes were significantly influenced by climate regimes, growth stages, durations, and their interactions (Table 3). Across growth stages and durations, the reduction in growth parameters compared to the respective control plants was greatest in C_S (summer) compared to C_R. Specifically, plant height was

Treatments	Plant height (cm)		Number of leaves pl^{-1}		Leaf area (cm^2 pl^{-1})		Number of branches pl^{-1}		NDVI	
	Summer	Rainy	Summer	Rainy	Summer	Rainy	Summer	Rainy	Summer	Rainy
Seasons/climate (C)										
Summer (C_S)	3.13^{a}		5.30^{a}		73.31^{a}		1.44^{a}		0.12^{a}	
Rainy (C_R)	1.70^{b}		3.11^{b}		67.48^{b}		0.72^{b}		0.08^{b}	
S.Em. ±	0.030		0.054		0.762		0.014		0.001	
Stages of waterlogging (S)										
S_{15}	0.33^{c}	0.85^{d}	0.49^{d}	0.27^{d}	13.42^{d}	11.96^{d}	0.0^{d}	0.0^{d}	0.03^{c}	0.05^{c}
S_{30}	3.20^{b}	2.08^{b}	3.08^{c}	1.20^{c}	39.92^{c}	79.15^{c}	0.8^{c}	0.7^{c}	0.13^{b}	0.10^{b}
S_{45}	5.61^{a}	2.78^{a}	5.32^{b}	3.93^{b}	103.39^{b}	93.23^{b}	2.2^{b}	0.7^{b}	0.17^{a}	0.14^{a}
S_{60}	3.38^{b}	1.10^{c}	12.33^{a}	7.05^{a}	113.20^{a}	108.93^{a}	2.8^{a}	1.5^{a}	0.13^{b}	0.05^{c}
S.Em. ±	0.08	0.03	0.13	0.08	1.52	1.57	0.45	0.02	0.002	0.002
Durations of waterlogging (D)										
D_2	1.63^{c}	1.08^{e}	2.97^{e}	1.79^{d}	30.23^{e}	27.53^{e}	1.0^{c}	0.5^{e}	0.08^{e}	0.04^{e}
D_4	1.86^{c}	1.37^{d}	3.97^{d}	2.67^{c}	51.53^{d}	46.57^{d}	1.5^{b}	0.6^{d}	0.10^{d}	0.06^{d}
D_6	3.38^{b}	1.69^{c}	5.50^{c}	3.46^{b}	72.87^{c}	79.86^{c}	1.5^{b}	0.7^{c}	0.12^{c}	0.09^{c}
D_8	3.62^{b}	1.95^{b}	6.53^{b}	3.50^{b}	87.68^{b}	96.89^{b}	1.5^{b}	0.7^{b}	0.13^{b}	0.11^{b}
D_{10}	5.16^{a}	2.43^{a}	7.55^{a}	4.14^{a}	95.12^{a}	115.72^{a}	1.7^{a}	1.1^{a}	0.15^{a}	0.13^{a}
S.Em. ±	0.09	0.04	0.15	0.09	1.70	1.75	1.69	0.02	0.002	0.002
Interactions (S × D)										
$S_{15}D_2$	0.03^{k}	0.45^{mm}	0.00^{k}	0.0^{j}	3.35^{j}	3.32^{k}	0.0^{h}	0.0^{g}	0.01^{h}	0.02^{j}
$S_{15}D_4$	0.10^{k}	0.48^{lm}	0.22^{k}	0.17^{ij}	7.01^{ij}	5.34^{k}	0.0^{h}	0.0^{g}	0.02^{gh}	0.03^{ij}
$S_{15}D_6$	0.28^{k}	0.68^{l}	0.33^{jk}	0.17^{ij}	15.22^{hi}	11.89^{jk}	0.0^{h}	0.0^{g}	0.03^{fg}	0.05^{gh}
$S_{15}D_8$	0.45^{jk}	1.08^{jk}	0.78$^{i–k}$	0.33$^{h–j}$	19.50^{h}	17.44^{ij}	0.0^{h}	0.0^{g}	0.04f.	0.06^{fg}
$S_{15}D_{10}$	0.80^{ij}	1.55^{h}	1.11^{ij}	0.67^{hi}	22.01^{h}	21.78^{ij}	0.0^{h}	0.0^{g}	0.06^{e}	0.07^{e}
$S_{30}D_2$	1.23^{hi}	1.15^{ij}	0.78$^{i–k}$	0.50$^{h–j}$	15.79^{hi}	31.94^{i}	0.3^{g}	0.2f.	0.07^{e}	0.05^{gh}
$S_{30}D_4$	1.44^{gh}	1.92^{fg}	1.17^{ij}	0.83^{gh}	23.38^{h}	41.92^{h}	0.5^{g}	0.2f.	0.10^{d}	0.09^{d}
$S_{30}D_6$	3.29^{e}	2.18^{e}	2.89^{h}	1.33^{fg}	39.95^{g}	82.18f.	0.5^{g}	0.5^{d}	0.13^{c}	0.10^{d}
$S_{30}D_8$	4.00^{d}	2.45^{d}	4.56^{g}	1.33^{fg}	56.43f.	112.11^{de}	1.0f.	1.3^{b}	0.16^{b}	0.14^{c}
$S_{30}D_{10}$	6.03^{c}	2.70^{c}	6.00f.	2.00^{de}	64.07f.	127.57^{b}	1.6^{e}	1.3^{b}	0.20^{a}	0.13^{c}
$S_{45}D_2$	1.92^{g}	1.78^{g}	1.56^{i}	1.50^{ef}	41.33^{g}	29.98^{h}	1.6^{e}	0.3^{e}	0.14^{bc}	0.07^{ef}
$S_{45}D_4$	2.53f.	2.05^{ef}	3.06^{h}	2.33^{d}	80.38^{e}	72.24^{fg}	2.1^{d}	0.7^{c}	0.15^{bc}	0.09^{d}
$S_{45}D_6$	6.61^{b}	2.82^{c}	5.67f.	4.83^{c}	93.25^{d}	122.91^{bc}	2.6^{c}	0.7^{c}	0.19^{a}	0.14^{c}
$S_{45}D_8$	6.67^{b}	3.07^{b}	7.33^{e}	4.83^{c}	129.72^{c}	127.37^{b}	2.2^{d}	0.1^{fg}	0.19^{a}	0.19^{b}
$S_{45}D_{10}$	10.34^{a}	4.17^{a}	8.97^{d}	6.17^{b}	172.26^{a}	113.62^{cd}	2.6^{c}	1.5^{a}	0.19^{a}	0.24^{a}
$S_{60}D_2$	3.34^{e}	0.92^{k}	9.56^{d}	5.17^{c}	60.44f.	44.89^{h}	2.1^{d}	1.5^{a}	0.11^{d}	0.03^{ij}
$S_{60}D_4$	3.38^{e}	1.03^{jk}	11.44^{c}	7.33^{a}	95.33^{d}	66.79^{g}	3.2^{a}	1.5^{a}	0.11^{d}	0.04^{hi}
$S_{60}D_6$	3.36^{e}	1.07^{jk}	13.11^{b}	7.50^{a}	143.05^{b}	102.44^{e}	3.0^{b}	1.5^{a}	0.13^{c}	0.06^{fg}
$S_{60}D_8$	3.36^{e}	1.20^{jk}	13.44^{ab}	7.50^{a}	145.06^{b}	130.63^{b}	2.9^{b}	1.5^{a}	0.14^{c}	0.06^{fg}
$S_{60}D_{10}$	3.44^{e}	1.30^{i}	14.11^{a}	7.73^{a}	122.13^{c}	199.91^{a}	2.7^{c}	1.5^{a}	0.14^{c}	0.06^{fg}
S.Em. ±	0.17	0.07	0.29	0.18	3.40	3.50	1.01	0.04	0.005	0.004

Table 3. Reduction in growth attributes of soybean to transient waterlogging under different climatic regimes. *S_{15}: 15 DAE; Days after emergence, S_{30}: 30 DAE, S_{45}: 45 DAE, S_{60}: 60 DAE, D_2: 2 DWL; Days of waterlogging, D_4: 4 DWL, D_6: 6 DWL, D_8: 8 DWL, D_{10}: 10 DWL. Means followed by the same letter (s) within the column are not significant ($p < 0.05$).

reduced by 3.13 cm, the number of trifoliate leaves by 5.30, leaf area by 73.31 cm^2 pl^{-1}, the number of branches by 1.44, and NDVI values by 0.12. Among the growth stages, S_{60} recorded the greatest reduction in the number of trifoliate leaves (12.33 in C_S and 7.0 in C_R), leaf area (113.20 cm^2 pl^{-1} in C_S and 108.9 cm^2 pl^{-1} in C_R), and the number of branches (2.8 in C_S and 1.5 in C_R), followed by 45 DAE (S_{45}). However, the highest reduction in plant height (5.61 cm in C_S and 2.78 cm in C_R) and NDVI (0.17 in C_S and 0.14 in C_R) was observed at 45 DAE (S_{45}). The least effect of waterlogging on growth attributes was observed at the initial stage (S_{15}). Similarly, the greatest reduction in growth parameters occurred at D_{10}, while the least reduction was observed at D_2. Furthermore, the interaction of $S_{45} \times D_{10}$ significantly decreased plant height and NDVI (Table 3), whereas the reduction in the number of leaves and branches was greatest with $S_{60} \times D_{10}$.

Dry matter accumulation in waterlogging stress under different climatic conditions

Waterlogging stress significantly reduced the dry matter accumulation in various parts of the soybean plants in both climates (Table 4). The maximum reduction in leaf weight (0.76 g pl^{-1}), stem weight (0.34 g pl^{-1}), pod weight (0.54 g pl^{-1}), and total dry matter (1.68 g pl^{-1}) immediately after relieving waterlogging stress was observed during summer (C_S), compared to rainy season (C_R), over their respective controls. The reduction in dry matter accumulation progressively increased up to S_{45}, with the maximum reduction in leaf weight, stem weight, and total dry matter. A declining trend was observed at S_{60}. Meanwhile, waterlogging at later growth stages drastically reduced pod weight compared to the control. Similarly, longer waterlogging durations intensified the negative impact on total dry matter production, due to cumulative reductions in leaf and stem weight, with the highest reduction observed at D_{10} (Table 4). The interaction of $S \times D$ had a significant negative effect on the allocation of dry matter to different parts of the plant. The greatest reductions in leaf weight (3.51 g pl^{-1} in C_S and 1.53 g pl^{-1} in C_R), stem weight (1.39 g pl^{-1} in C_S and 0.44 g pl^{-1} in C_R), and total dry matter (6.37 g pl^{-1} in C_S and 2.22 g pl^{-1} in C_R) occurred at $S_{45} \times D_{10}$. Meanwhile, the highest reduction in pod weight (1.22 g pl^{-1}) was observed at $S_{60} \times D_2$.

Similarly, dry matter partitioning in different parts of the soybean plant at the harvest stage was significantly influenced by waterlogging stress (Figs. 3a and 4b, and Table 5). Despite a greater reduction in growth attributes, higher dry matter accumulation at the harvest stage was observed in C_S compared to C_R across all growth stages and durations (Table 5). Regarding growth stages, stem dry weight, pod weight, and total dry matter accumulation were highest in S_{15} compared to other growth stages across both climate regimes (Figs. 3a and 4a). Similarly, increasing waterlogging durations consistently decreased dry matter accumulation in the leaf, stem, pod, and total dry matter of the plant (Figs. 3b and 4b). Waterlogging for 10 days (D_{10}) resulted in significantly the lowest dry matter in all parts of the plant, while the least reduction in dry matter accumulation was observed with D_2 under both C_S and C_R. Furthermore, the interaction of $S_{15} \times D_2$ resulted in higher total dry matter accumulation in C_S, while $S_{60} \times D_2$ was superior for total dry matter accumulation in C_R (Table 5).

Combined effect of climate, growing stages, and waterlogging on yield and tolerance indices of soybean

Climatic regimes influenced the yield attributes and stress indices of soybean across growth stages and waterlogging durations (Tables 6, S3 and Figs. 5a,b). The reduction in yield ranged from 13 to 56% during summer (C_S) compared to 19–91% in the rainy season (C_R) (Table 6). The crop was found to be more sensitive to waterlogging stress in the C_R, with lower average seed yield (35.71%) and fewer pods per plant (5.95%) compared to the control. As a result, the crop showed a lower yield stability index (YSI) (0.41), higher stress susceptibility index (SSI) (1.00), and tolerance index (TOL) (3.92) compared to C_S (Table S3). The least influence of waterlogging on 100-seed weight and seed yield was recorded at S_{15} in C_S, while the maximum yield reduction was observed at S_{45}. Among the waterlogging durations, an increase in duration (D_{10}) exacerbated soybean yield loss, with a maximum reduction of 68.18% in C_R and 47.61% in C_S. The least reduction in yield and yield-contributing traits was observed at D_2 (Table 6). A similar trend was observed for yield attributes, YSI, and stress tolerance indices (SSI and TOL), indicating that prolonged waterlogging durations negatively impacted soybean performance (Table 6 and Fig. 5b). Regarding the interaction effect, $S_{45} \times D_{10}$ caused the maximum reduction in grain yield (90.90% in C_R and 55.22% in C_S), number of pods per plant (88.30% in C_R and 64.89% in C_S), and number of seeds per pod (35.0% in C_R and 22.22% in C_S).

Association between root, growth and yield attributes

The relationship between the reduction in root and growth attributes with yield and stress indices under different factors (C, S, and D) was analyzed using Pearson correlation coefficient analysis. The results revealed that the reduction in root attributes was negatively correlated with seed yield and the yield stability index (YSI) in both climates (data not presented). Additionally, Principal Component Analysis (PCA) showed that among the 10 principal components (PCs), PC1 (50.5%), PC2 (26.9%), and PC3 (10.9%) cumulatively accounted for 88.3% of the total variability (Fig. 6a). The PCA biplot indicated that total dry matter (TDA), number of pods (NP), stress susceptibility index (SSI), and leaf area (LA) made the greatest contribution to PC1, as evidenced by the angle and length of the vector. Meanwhile, the highest contribution to the variability in PC2 came from the reduction in root attributes, including root length, root volume, and root dry weight. The contributions of seed yield (SY) and yield stability index (YSI) to PC1 and PC2 were nearly equal, as displayed by the ~45° angle between their vectors (Fig. 6b–c). Notably, SY, NP, and YSI were closely associated with combinations of summer climate during later growth stages and shorter durations of waterlogging ($C_S S_{60} D_{2-4}$). In contrast, reductions in root length, root volume, and root dry weight were strongly associated with summer during later growth stages and longer durations of waterlogging ($C_S S_{60} D_{8-10}$). Leaf area reduction, however, was associated with $C_S S_{45} D_{8-10}$ (Fig. 6c). SSI had a strong negative relationship with the number of pods, seed yield, and YSI, as indicated by the angle between the vectors. Additionally, reductions in root length, root volume, and root dry weight showed a moderate negative association with the production of aerial roots and yield attributes (Fig. 6b–c).

Treatments	Leaf weight (g pl^{-1})		Stem weight (g pl^{-1})		Pod weight (g pl^{-1})		Total dry matter (g pl^{-1})	
	Summer	Rainy	Summer	Rainy	Summer	Rainy	Summer	Rainy
Seasons/climate (C)								
Summer (C_S)	0.76^{a}		0.34^{a}		0.54^{a}		1.68^{a}	
Rainy (C_R)	0.49^{b}		0.21^{b}		0.17^{b}		0.87^{b}	
S.Em. ±	0.008		0.004		0.007		0.018	
Stages of waterlogging (S)								
S_{15}	0.14^{d}	0.06^{c}	0.02^{c}	0.02^{d}	0^{c}	0.00^{c}	0.16^{d}	0.08^{d}
S_{30}	0.54^{c}	0.44^{b}	0.18^{b}	0.16^{c}	0^{c}	0.00^{c}	0.79^{c}	0.60^{c}
S_{45}	1.38^{a}	1.03^{a}	0.57^{a}	0.35^{a}	1.46^{a}	0.18^{b}	3.49^{a}	1.55^{a}
S_{60}	0.95^{b}	0.44^{b}	0.58^{a}	0.29^{b}	0.68^{b}	0.50^{a}	2.27^{b}	1.23^{b}
S.Em. ±	0.020	0.012	0.009	0.005	0.018	0.006	0.045	0.021
Durations of waterlogging (D)								
D_2	0.25^{e}	0.23^{e}	0.23^{d}	0.18^{c}	0.71^{a}	0.25^{a}	1.22^{d}	0.66^{d}
D_4	0.45^{d}	0.39^{d}	0.24^{d}	0.19^{c}	0.62^{b}	0.14^{b}	1.33^{cd}	0.71^{d}
D_6	0.58^{c}	0.44^{c}	0.29^{c}	0.19^{c}	0.47^{c}	0.16^{b}	1.40^{c}	0.79^{c}
D_8	0.99^{b}	0.63^{b}	0.38^{b}	0.24^{a}	0.44^{c}	0.15^{b}	1.86^{b}	1.02^{b}
D_{10}	1.51^{a}	0.76^{a}	0.55^{a}	0.22^{b}	0.44^{c}	0.15^{b}	2.58^{a}	1.13^{a}
S.Em. ±	0.023	0.013	0.010	0.006	0.020	0.007	0.050	0.023
Interactions (S × D)								
$S_{15}D_2$	0.03^{l}	0.01^{j}	0.02^{k}	0.01^{j}	0^{e}	0.00^{g}	0.05^{k}	0.02^{i}
$S_{15}D_4$	0.07^{kl}	0.03^{j}	0.02^{k}	0.01^{j}	0^{e}	0.00^{g}	0.09^{k}	0.04^{i}
$S_{15}D_6$	0.14^{j-l}	0.04^{j}	0.02^{k}	0.03^{ij}	0^{e}	0.00^{g}	0.16^{k}	0.06^{hi}
$S_{15}D_8$	0.18^{i-k}	0.09^{ij}	0.02^{k}	0.04^{h-j}	0^{e}	0.00^{g}	0.20^{jk}	0.12^{hi}
$S_{15}D_{10}$	0.28^{hi}	0.12^{i}	0.03^{k}	0.05^{hi}	0^{e}	0.00^{g}	0.31^{i-k}	0.17^{h}
$S_{30}D_2$	0.10^{kl}	0.07^{ij}	0.07^{jk}	0.07^{gh}	0^{e}	0.00^{g}	0.17^{k}	0.14^{hi}
$S_{30}D_4$	0.26^{h-j}	0.21^{h}	0.12^{ij}	0.09^{g}	0^{e}	0.00^{g}	0.48^{ij}	0.30^{g}
$S_{30}D_6$	0.34^{h}	0.29^{g}	0.18^{hi}	0.12f.	0^{e}	0.00^{g}	0.52^{i}	0.41^{g}
$S_{30}D_8$	0.72f.	0.71^{e}	0.21^{h}	0.25^{cd}	0^{e}	0.00^{g}	1.14^{h}	0.96f.
$S_{30}D_{10}$	1.30^{c}	0.91^{c}	0.31^{g}	0.28^{c}	0^{e}	0.00^{g}	1.65^{g}	1.18^{e}
$S_{45}D_2$	0.24^{h-j}	0.70^{e}	0.10^{j}	0.22^{e}	1.29^{b}	0.09f.	1.80^{fg}	1.01f.
$S_{45}D_4$	0.58^{g}	0.80^{d}	0.21^{h}	0.27^{c}	1.48^{a}	0.09f.	2.27^{de}	1.17^{e}
$S_{45}D_6$	0.67^{fg}	0.93^{c}	0.39f.	0.37^{b}	1.56^{a}	0.20^{e}	2.89^{c}	1.49^{c}
$S_{45}D_8$	1.91^{b}	1.19^{b}	0.74^{b}	0.44^{a}	1.48^{a}	0.24^{de}	4.14^{b}	1.87^{b}
$S_{45}D_{10}$	3.51^{a}	1.53^{a}	1.39^{a}	0.44^{a}	1.47^{a}	0.25^{d}	6.37^{a}	2.22^{a}
$S_{60}D_2$	0.62^{fg}	0.14^{hi}	0.72^{b}	0.45^{a}	1.53^{a}	0.90^{a}	2.87^{c}	1.49^{c}
$S_{60}D_4$	0.87^{e}	0.51f.	0.60^{c}	0.38^{b}	1.00^{c}	0.46^{b}	2.47^{d}	1.34^{d}
$S_{60}D_6$	1.16^{d}	0.53f.	0.56^{cd}	0.26^{cd}	0.32^{d}	0.43^{b}	2.04^{ef}	1.22^{de}
$S_{60}D_8$	1.16^{d}	0.53f.	0.54^{de}	0.24^{de}	0.28^{d}	0.38^{c}	1.98f.	1.14^{e}
$S_{60}D_{10}$	0.97^{e}	0.50f.	0.49^{e}	0.13f.	0.27^{d}	0.35^{c}	1.98f.	0.97f.
S.Em. ±	0.045	0.026	0.021	0.011	0.041	0.014	0.100	0.046

Table 4. Effect of transient waterlogging on dry matter accumulation of soybean under different climatic regimes. *S_{15}: 15 DAE; Days after emergence, S_{30}: 30 DAE, S_{45}: 45 DAE, S_{60}: 60 DAE, D_2: 2 DWL; Days of waterlogging, D_4: 4 DWL, D_6: 6 DWL, D_8: 8 DWL, D_{10}: 10 DWL. Means followed by the same letter (s) within the column are not significant ($p < 0.05$).

Discussion

Waterlogging is the second most important abiotic stress affecting soybean, causing yield losses of 40–80%. Furthermore, approximately 1700 mha of agricultural land are affected by waterlogging due to excessive rainfall and poor soil drainage. This intensive rainfall events is expected to increase by 35% by 2050, driven by rising global temperatures[39,40]. In this context, a well-planned, visionary study was conducted on the globally important soybean crop to understand the combined impact of climate regimes, growth stages, and durations of waterlogging on root morphology, stress recovery, and yield attributes in order to plan mitigation measures.

Root morphology of soybean vs waterlogging stress

Roots are the first plant organs that come into contact with edaphic stress factors and respond by modifying their surface architecture, including length, surface area, volume, number of forks, average diameter, and dry

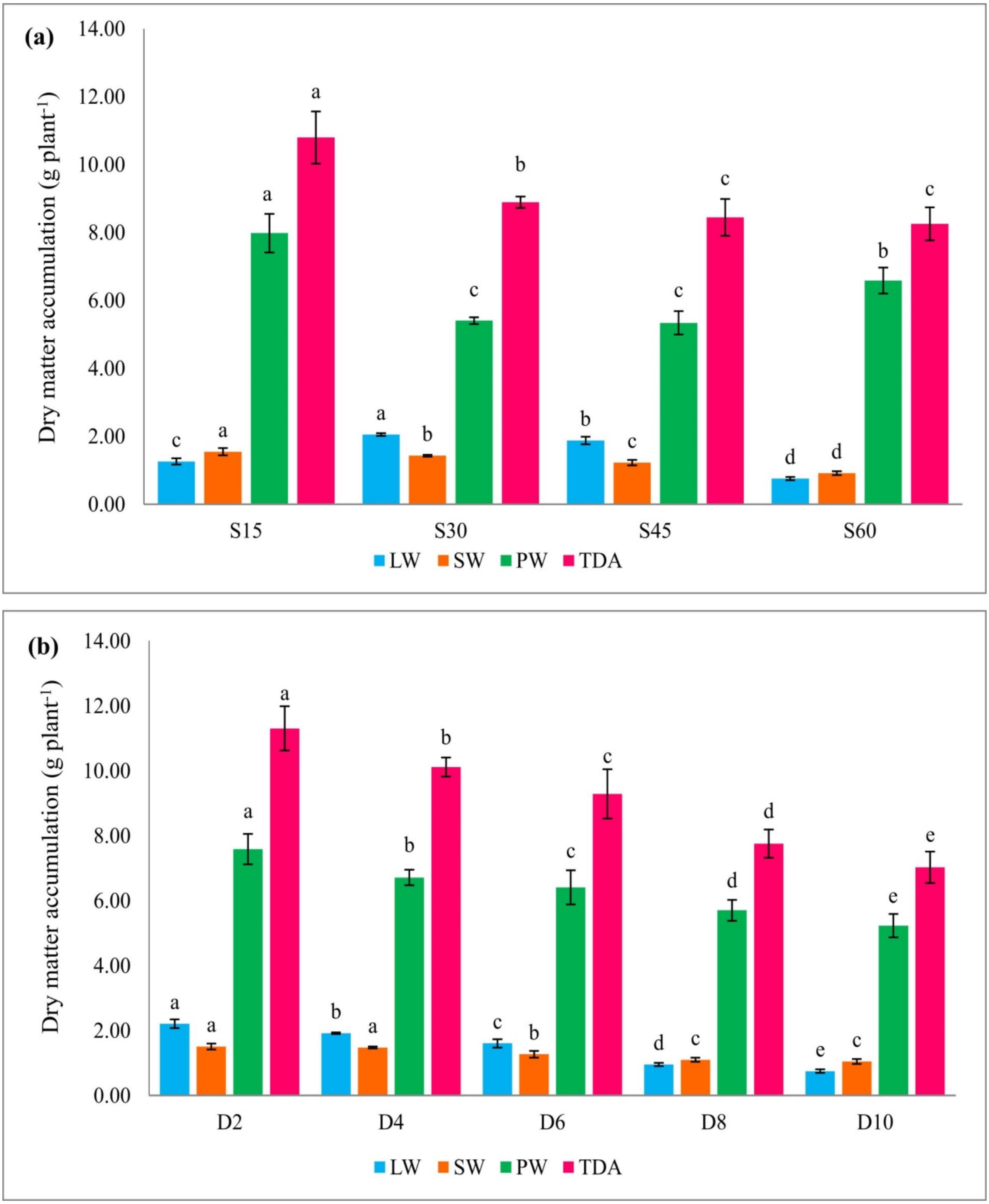

Fig. 3. (**a**) Soybean dry matter accumulation at different growth stages and (**b**) soybean dry matter accumulation at different durations of waterlogging at harvest during summer. $^{*}S_{15}$: 15 DAE; Days after emergence, S_{30}: 30 DAE, S_{45}: 45 DAE, S_{60}: 60 DAE, D_2: 2 DWL; Days of waterlogging, D_4: 4 DWL, D_6: 6 DWL, D_8: 8 DWL, D_{10}: 10 DWL, LW: Leaf weight (g pl^{-1}), SW: Stem weight (g pl^{-1}), PW; Pod weight (g pl^{-1}), TDA; Total drymatter accumulation (g pl^{-1}).

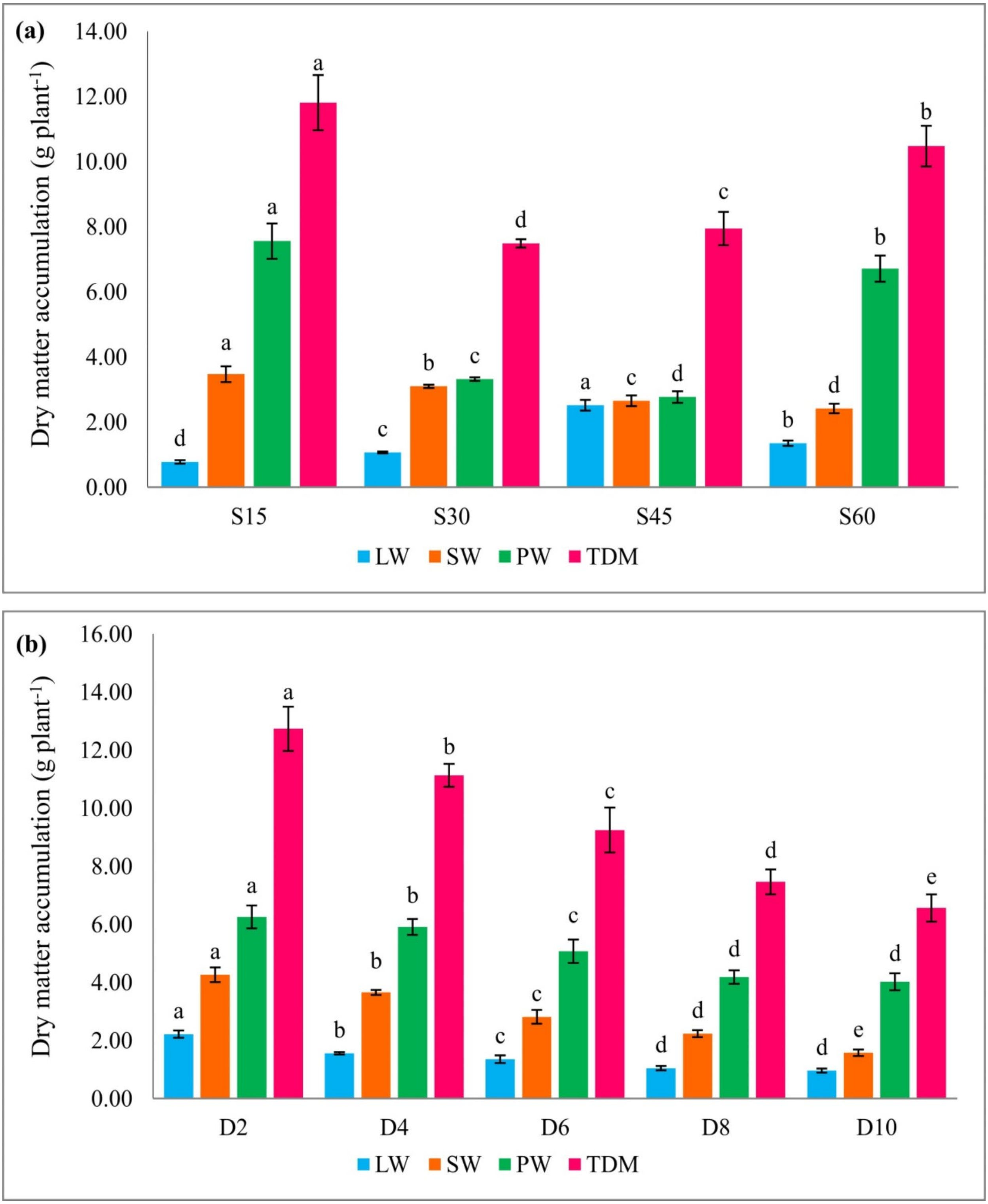

Fig. 4. (**a**) Soybean dry matter accumulation at different crop growth stages and (**b**) Soybean dry matter accumulation at harvest under different durations of waterlogging, in rainy season. *S_{15}: 15 DAE; Days after emergence, S_{30}: 30 DAE, S_{45}: 45 DAE, S_{60}: 60 DAE, D_2: 2 DWL; Days of waterlogging, D_4: 4 DWL, D_6: 6 DWL, D_8: 8 DWL, D_{10}: 10 DWL, LW: Leaf weight (g plant^{-1}), SW: Stem weight (g plant^{-1}), PW; Pod weight (g plant^{-1}), TDA; Total drymatter accumulation (g plant^{-1}).

Treatments	Leaf weight (g pl^{-1})		Stem weight (g pl^{-1})		Pod weight (g pl^{-1})		Total dry matter (g pl^{-1})	
	Summer	Rainy	Summer	Rainy	Summer	Rainy	Summer	Rainy
Seasons/climate (C)								
Summer	1.49^{a}		2.91^{a}		8.72^{a}		9.43^{a}	
Rainy	1.43^{b}		1.28^{b}		6.33^{b}		9.10^{b}	
S.Em. ±	0.014		0.018		0.060		0.069	
Interactions (S × D)								
$S_{15}D_2$	1.38f.	1.18^{d}	1.73^{b}	4.07^{c}	9.48^{b}	8.20^{b}	12.58^{b}	13.4^{c}
$S_{15}D_4$	1.34^{fg}	1.15^{d}	1.60^{c}	3.89^{cd}	7.88^{c}	8.37^{b}	10.84^{c}	13.4^{c}
$S_{15}D_6$	1.22f.$^{-h}$	0.66^{fg}	1.52^{cd}	3.51^{e}	7.69^{cd}	7.35^{c}	10.43^{cd}	11.5^{de}
$S_{15}D_8$	1.17^{h-j}	0.48^{gh}	1.51^{cd}	3.73^{de}	7.69^{cd}	6.44^{d}	10.38^{cd}	10.7^{ef}
$S_{15}D_{10}$	1.19^{g-i}	0.42^{h}	1.38^{e}	2.16^{hi}	7.19^{de}	7.43^{c}	9.76^{d}	10.0f.
$S_{30}D_2$	2.75^{b}	2.27^{c}	2.11^{a}	5.38^{a}	5.99^{g-i}	4.73^{fg}	10.85^{c}	12.4^{d}
$S_{30}D_4$	2.52^{c}	1.20^{d}	2.01^{a}	4.37^{b}	5.78^{g-i}	4.23^{gh}	10.31^{cd}	9.8f.
$S_{30}D_6$	2.83^{e}	1.01^{de}	1.41^{de}	2.38^{gh}	5.62^{hi}	2.71^{j}	9.86^{d}	6.1^{i}
$S_{30}D_8$	1.58^{e}	0.47^{gh}	0.85^{k-m}	2.04^{ij}	4.78^{kl}	2.66^{j}	7.21^{g}	5.2^{ij}
$S_{30}D_{10}$	0.59^{l}	0.40^{h}	0.79^{m}	1.34^{l}	4.86^{k}	2.26^{jk}	6.24^{h}	4.0^{k}
$S_{45}D_2$	3.69^{a}	2.81^{a}	1.30^{ef}	3.94^{cd}	6.78^{ef}	3.98^{hi}	11.78^{b}	10.7^{ef}
$S_{45}D_4$	2.76^{b}	2.68^{ab}	1.38^{e}	3.71^{de}	6.28^{fg}	3.61^{i}	10.42^{cd}	10.0f.
$S_{45}D_6$	1.55^{e}	2.61^{b}	1.15^{gh}	2.91f.	5.47^{ij}	2.79^{j}	8.17^{ef}	8.3^{g}
$S_{45}D_8$	0.59^{l}	2.32^{c}	1.23^{fg}	1.42^{l}	4.21^{lm}	1.87^{kl}	6.03^{h}	5.6^{ij}
$S_{45}D_{10}$	0.80^{k}	2.18^{c}	1.08^{hi}	1.30^{l}	3.96^{m}	1.59^{l}	5.84^{h}	5.1^{j}
$S_{60}D_2$	1.01^{j}	2.60^{b}	0.89^{j-m}	3.67^{de}	8.11^{c}	8.10^{b}	10.01^{cd}	14.4^{b}
$S_{60}D_4$	1.06^{ij}	1.20^{d}	0.92^{j-l}	2.66^{fg}	6.91^{e}	7.45^{c}	8.89^{e}	11.3^{e}
$S_{60}D_6$	0.82^{k}	1.17^{d}	1.00^{ij}	2.47^{g}	6.87^{ef}	7.44^{c}	8.69^{e}	11.1^{e}
$S_{60}D_8$	0.48^{lm}	0.93^{e}	0.82^{lm}	1.76^{jk}	6.12^{gh}	5.75^{e}	7.41^{fg}	8.4^{g}
$S_{60}D_{10}$	0.41^{m}	0.84^{ef}	0.94^{jk}	1.51^{kl}	4.92^{jk}	4.83f.	6.27^{h}	7.2^{h}
Control	1.69^{d}	0.44^{h}	1.50^{cd}	4.56^{b}	10.08^{a}	9.97^{a}	13.27^{a}	15.0^{a}
S.Em. ±	0.06	0.07	0.04	0.10	0.21	0.19	0.30	0.33

Table 5. Interaction effect of stages and durations of waterlogging on soybean dry matter accumulation at harvest under different climatic conditions. *S_{15}: 15 DAE; Days after emergence, S_{30}: 30 DAE, S_{45}: 45 DAE, S_{60}: 60 DAE, D_2: 2 DWL; Days of waterlogging, D_4: 4 DWL, D_6: 6 DWL, D_8: 8 DWL, D_{10}: 10 DWL. Means followed by the same letter (s) within the column are not significant ($p < 0.05$).

matter. In our study, the combined effect of $C_S \times S_{60} \times D_{8\text{-}10}$ drastically reduced root growth attributes (Tables 1 and S2). The faster depletion of O_2 in warm water (~ average temperature 34.9 °C) due to its higher solubility compared to cold water (~ temperature 31.2 °C) during the summer climate regime (C_S) possibly reduced root the morphological parameters over C_R (Tables 1 and S2). As a result, oxygen-deficit conditions may have led to a higher accumulation of ethylene and a reduced biosynthesis of auxin (*ANTHRANILATE SYNTHASE* α1; ASA1, *ANTHRANILATE SYNTHASE β1*; ABS) and transport (*PIN1, PIN2, PIN4, AUX1*) during C_S. This likely limited the primary root growth, possibly through jasmonic acid signaling, and diverted more energy toward the formation of aerial roots as a survival mechanism[41–43]. The present findings highlight the augmenting effect of higher temperatures combined with waterlogging in reducing root growth attributes. Our results align with those of Zhen et al.[29], who found that higher temperatures (35–38 °C) reduced root diameter and outer root thickness in waterlogged conditions compared to moderate temperatures (30–34 °C) in rice.

The response of roots to hypoxic conditions varies with factors such as stress intensity, crop growth stage, and internal adjustments[44]. In our study, the greatest reductions in root attributes at $S_{60} > S_{45}$ (Tables 1 and Fig. 2a) were related to the plant's prioritization of completing its life cycle, thereby redirecting more resources toward reproductive parts, such as flowers and seeds, at the expense of root growth. This is supported by the reduced number of days to harvest at S_{60} (94 days during C_S and 104 days in C_R) and lower stem weight (Table 6, Figs. 3a and 4a). Consequently, no aerial roots were produced during later growth stages of soybean, which may have reduced the O_2 supply, increased ROS activity, and resulted in greater root damage. In contrast, the lower reductions in root attributes during the earlier stages (S_{15} and S_{30}) are likely due to the formation of adventitious roots, which may have supplied necessary O_2 and facilitated the absorption of water and nutrients for maintaining growth (Table 2). These results align with the findings of Basavaraj et al.[16], who indicated that varieties producing a higher number of aerial roots experienced less reduction in root attributes in cowpea.

The progressive reduction in root morphological features with increased waterlogging durations from 2 to 10 days was attributed to the reduced diffusion of oxygen under hypoxic conditions. Waterlogging for 5 days was found to create anoxic (absence of O_2) conditions, leading to the formation of aerial roots to meet the plant's oxygen demands for survival[45,46]. Further, hypoxia-induced ROS production and autophagy in root cells

Treatments	Seed yield (g pl^{-1})		Number of pods pl^{-1}		Number of seeds pod^{-1}		100 seed weight		Days to harvest	
	Summer	Rainy	Summer	Rainy	Summer	Rainy	Summer	Rainy	Summer	Rainy
Seasons/climate (C)										
Summer (C_S)	4.2 ^{a}		23.7 ^{a}		1.6^{a}		10.67 ^{a}		105.01^{b}	
Rainy (C_R)	2.7 ^{b}		25.2 ^{b}		1.7^{a}		7.80 ^{b}		115.76^{a}	
S.Em. ±	0.029		0.198		NS		0.303		0.68	
Stages of waterlogging (S)										
S_{15}	5.1^{a}	3.8^{b}	32.2^{a}	37.7^{a}	1.8^{a}	1.8^{a}	8.8^{c}	6.3^{c}	108^{ab}	128^{a}
S_{30}	3.6^{c}	1.6^{c}	21.4^{b}	14.3^{b}	1.6^{b}	1.7^{b}	10.1^{b}	7.6^{b}	111^{a}	128^{a}
S_{45}	3.8^{b}	0.9^{d}	19.9^{c}	11.5^{c}	1.5^{c}	1.5^{c}	11.8^{a}	7.8^{b}	107^{b}	103^{b}
S_{60}	4.4^{b}	4.4^{a}	21.5^{b}	37.3^{a}	1.5^{c}	1.6^{d}	11.9^{a}	9.4^{a}	94^{c}	104^{b}
S.Em. ±	0.06	0.05	0.35	0.43	0.02	0.02	0.2	0.2	1.5	1.3
Durations of waterlogging (D)										
D_2	5.0^{a}	3.5^{a}	29.2^{a}	31.5^{a}	1.7^{a}	1.8^{a}	10.7^{b}	7.8^{b}	109^{a}	113^{c}
D_4	4.6^{b}	2.9^{b}	25.4^{b}	26.1^{b}	1.8^{a}	1.7^{b}	9.9^{c}	7.0^{c}	107^{ab}	113^{c}
D_6	4.1^{c}	2.5^{c}	23.5^{c}	24.6^{c}	1.7^{a}	1.7^{ab}	10.3^{bc}	7.4^{bc}	105^{ab}	115^{bc}
D_8	3.9^{d}	2.4^{c}	21.6^{d}	22.9^{d}	1.6^{b}	1.6^{c}	10.8^{b}	7.9^{b}	103^{b}	118^{a}
D_{10}	3.5^{e}	2.1^{d}	19.0^{e}	21.0^{e}	1.4^{c}	1.4^{d}	11.6^{a}	8.8^{a}	102^{b}	120^{a}
S.Em. ±	0.07	0.06	0.39	0.49	0.03	0.03	0.2	0.2	1.7	1.4
Interactions (S × D)										
$S_{15}D_2$	5.9^{b}	4.3^{cd}	35.5^{b}	41.5^{bc}	1.7^{b-d}	2.0^{a}	9.5^{g-i}	7.0$^{f.-h}$	103^{d-f}	124^{c}
$S_{15}D_4$	5.2^{c}	3.9^{ef}	33.6^{b}	38.5^{d}	1.8^{ab}	2.0^{a}	8.5^{j}	6.0^{i}	106^{b-f}	123^{c}
$S_{15}D_6$	4.9^{cd}	3.7^{fg}	30.5^{c}	38.0^{de}	2.0^{b-d}	1.9^{ab}	8.3^{j}	5.8^{i}	107^{b-f}	124^{c}
$S_{15}D_8$	4.8^{cd}	3.6^{gh}	31.3^{c}	35.0^{fg}	1.8^{bc}	1.9^{b-d}	8.6^{ij}	6.1^{hi}	109^{b-e}	131^{bc}
$S_{15}D_{10}$	4.6^{de}	3.3^{h}	29.8^{c}	35.7^{ef}	1.7^{c-e}	1.4^{h}	9.2^{h-j}	6.7^{g-i}	114^{a-c}	140^{a}
$S_{30}D_2$	4.1^{fg}	2.9^{i}	27.3^{d}	23.8^{h}	1.8^{bc}	2.0^{ab}	10.3^{e-g}	7.8^{d-f}	120^{a}	123^{c}
$S_{30}D_4$	4.0$^{f.-h}$	1.6^{j}	22.0^{e-g}	13.2^{j}	1.8^{b-d}	1.6^{e-g}	8.3^{j}	5.8^{i}	112^{a-d}	124^{c}
$S_{30}D_6$	3.5^{i-k}	1.3^{j-l}	22.8^{ef}	12.7^{j}	1.6^{ef}	1.5^{g}	9.6^{gh}	7.1^{fg}	111^{a-d}	128^{c}
$S_{30}D_8$	3.4^{j-l}	1.1^{k-m}	20.5^{gh}	12.2^{j-l}	1.7^{b-d}	1.6^{fg}	10.0$^{f.-h}$	7.5^{e-g}	109^{b-e}	130^{bc}
$S_{30}D_{10}$	3.1^{l}	1.1^{l}	14.3^{j}	9.7^{kl}	1.3^{gh}	1.9^{a-c}	12.3^{ab}	9.8^{a}	104^{c-f}	136^{ab}
$S_{45}D_2$	4.3^{ef}	1.4^{jk}	24.7^{e}	16.5^{i}	1.5^{fg}	1.7^{e-g}	11.7^{b-d}	7.7^{e-g}	115^{ab}	104^{d}
$S_{45}D_4$	4.1^{fg}	1.4^{j-l}	22.7^{e-g}	13.5^{j}	1.7^{c-e}	1.6^{g}	10.8^{a-c}	6.8^{g-i}	111^{a-d}	103^{d}
$S_{45}D_6$	3.8^{g-j}	0.7^{m}	20.0^{h}	12.3^{jk}	1.7^{b-d}	1.7^{d-f}	11.1^{c-e}	7.1^{fg}	111^{a-d}	104^{d}
$S_{45}D_8$	3.6^{h-k}	0.6^{m}	17.7^{i}	9.3^{l}	1.4$^{f.-h}$	1.3^{h}	12.4^{ab}	8.4^{c-e}	100^{e-g}	104^{d}
$S_{45}D_{10}$	3.0^{l}	0.6^{m}	14.5^{j}	6.0^{m}	1.4$^{f.-h}$	1.1^{i}	13.0^{a}	9.0^{a-c}	99^{fg}	101^{d}
$S_{60}D_2$	5.6^{b}	5.3^{b}	29.2^{cd}	44.3^{b}	1.7^{b-d}	1.6^{e-g}	11.3^{c-e}	8.8^{b-d}	97^{fg}	102^{d}
$S_{60}D_4$	4.9^{cd}	4.6^{c}	23.2^{ef}	39.2^{cd}	1.8^{b-d}	1.6^{fg}	12.1^{a-c}	9.6^{ab}	98^{fg}	102^{d}
$S_{60}D_6$	4.3^{ef}	4.3^{cd}	20.5^{gh}	35.5^{ef}	1.6^{de}	1.8^{c-e}	12.1^{a-c}	9.6^{ab}	92^{g}	104^{d}
$S_{60}D_8$	3.8^{g-i}	4.1^{de}	17.0^{i}	35.0^{fg}	1.3^{h}	1.7^{d-f}	12.1^{a-c}	9.6^{ab}	92^{g}	107^{d}
$S_{60}D_{10}$	3.2^{kl}	3.6^{fg}	17.5^{i}	32.5^{g}	1.3^{h}	1.3^{h}	12.1^{a-c}	9.6^{ab}	92^{g}	103^{d}
Control	6.7^{a}	6.6^{a}	41.3^{a}	51.3^{a}	1.8^{ab}	2.0^{a}	10.3^{e-g}	8.9^{b-d}	95^{g}	102^{d}
S.Em. ±	0.14	0.11	0.8	1.0	0.05	0.05	0.4	0.4	3.3	2.9

Table 6. Transient waterlogging effect on soybean yield under different climatic regimes. *S_{15}: 15 DAE; Days after emergence, S_{30}: 30 DAE, S_{45}: 45 DAE, S_{60}: 60 DAE, D_2: 2 DWL; Days of waterlogging, D_4: 4 DWL, D_6: 6 DWL, D_8: 8 DWL, D_{10}: 10 DWL. Means followed by the same letter (s) within the column are not significant ($p < 0.05$).

may result in accelerated root death and decay. Similar findings in soybean showed increased reductions in primary root length, diameter, volume, and surface area with longer waterlogging durations[47,48]. Additionally, a reduction in the quantum efficiency of PSII likely lowered photosynthesis and subsequent growth while increasing the activity of energy-driven processes, which might have negatively affected root attributes. As a result, soybean produced a greater number of longer adventitious roots (Table 2), likely due to the expression of 1-aminocyclopropane-1-carboxylic acid[49,50]. Despite the formation of adventitious roots, the reduction in primary root growth was due to the adventitious roots' inability to supply sufficient oxygen for the plant's shoot and root growth. Therefore, root morphology in soybean was found to be more sensitive to increased waterlogging durations, particularly at later growth stages, especially under summer climate conditions.

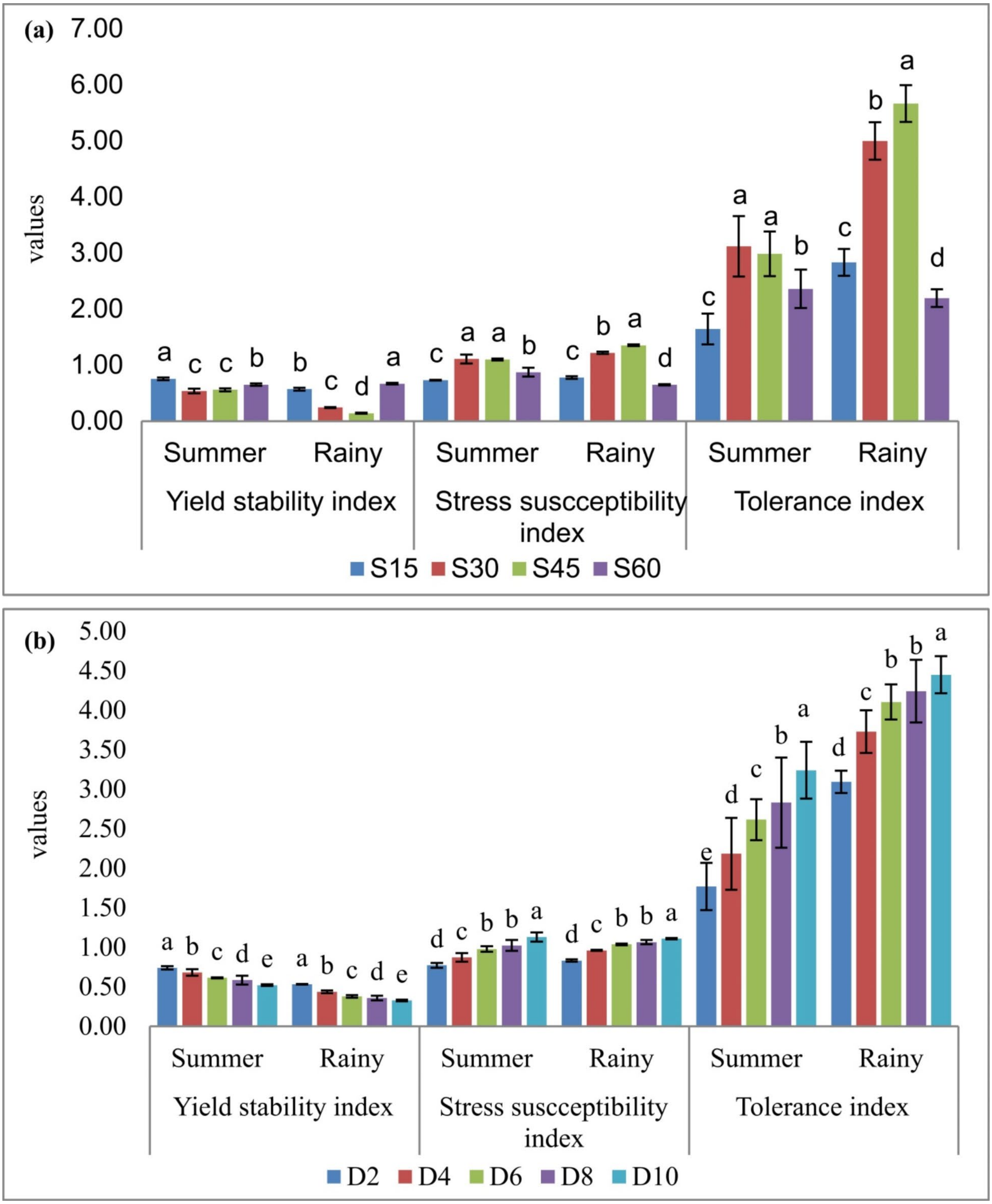

Fig. 5. Different climatic regimes influenced changes in yield stability, susceptibility and tolerance indices of soybean to waterlogging (**a**) at different crop growth stages, (**b**) under varied durations of waterlogging. *S_{15}: 15 DAE; Days after emergence, S_{30}: 30 DAE, S_{45}: 45 DAE, S_{60}: 60 DAE, D_2: 2 DWL; Days of waterlogging, D_4: 4 DWL, D_6: 6 DWL, D_8: 8 DWL, D_{10}: 10 DWL.

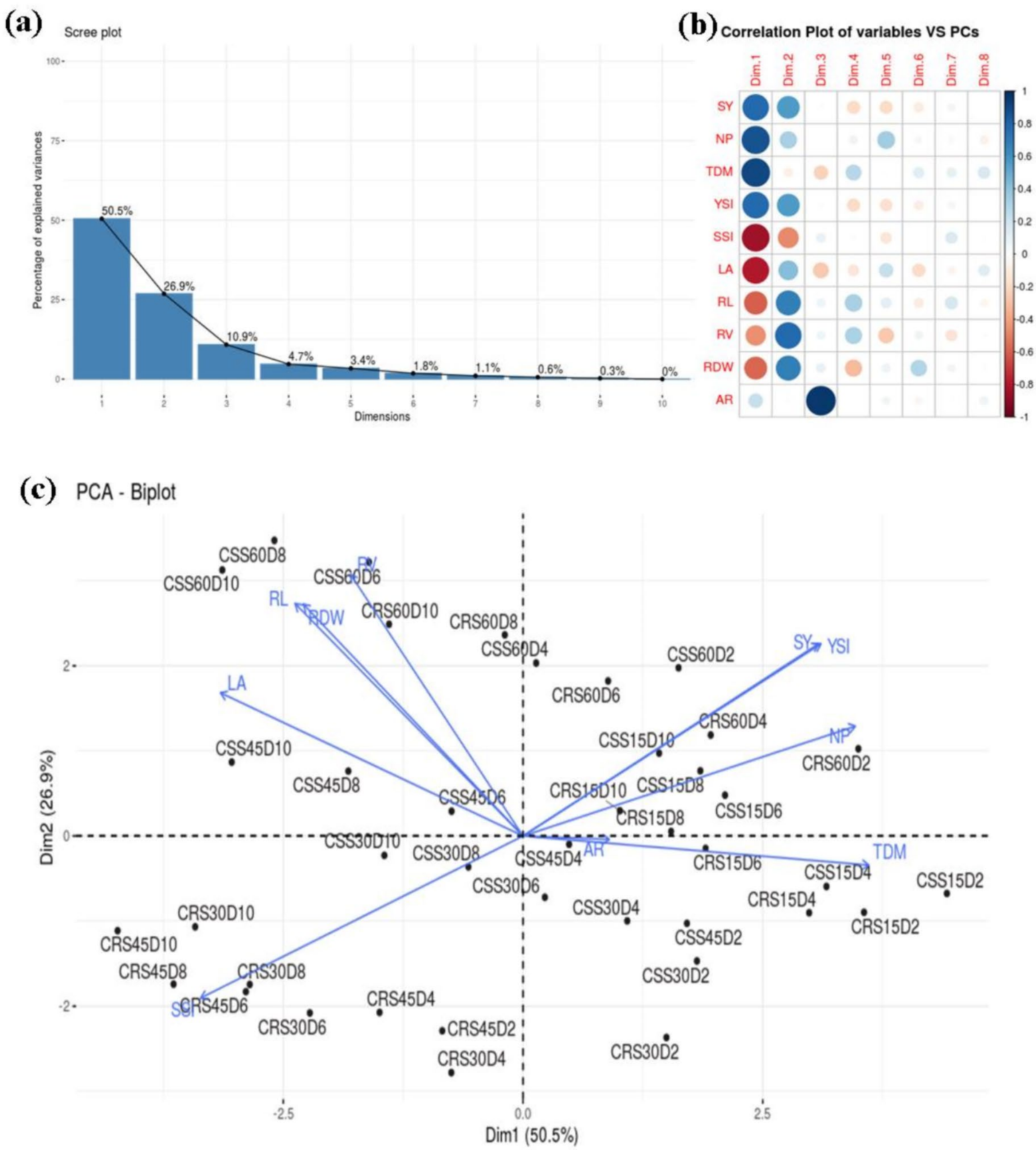

Fig. 6. Principle component analysis of root, shoot and yield attributes of waterlogged plants indicated in (**a**) Scree plot, (**b**) variables vs pc and (**c**) biplot in summer season. *SY; Seed yield, NP; Number of pods plant^{-1}, TDM; Total dry matter, YSI; Yield stability index, SSI; Stress susceptibility index, LA; Leaf area, RL; Root length, RV; Root volume, RDW; Root dry weight, AR; Adventitious roots.

Growth attributes v/s waterlogging

The amplified negative effect of the summer climate (C_S) on the growth attributes of soybean (Table 3) was associated with the combined stresses of waterlogging and higher temperatures. These stresses likely affected lignin biosynthesis, leading to reduced cell elongation and cell wall formation, which in turn hindered plant growth, as observed in maize[30]. Additionally, higher canopy temperatures during C_S may have led to the generation of ROS, causing lipid peroxidation of chloroplasts, which subsequently damaged PSII and reduced NDVI values (0.12). Moreover, poor root development due to waterlogging combined with higher temperatures impaired the transport of endogenous hormones (auxin and cytokinin) to the shoot system and the absorption of nutrients, especially nitrogen, which collectively resulted in poor soybean growth. As a result, the accumulation of dry matter in the leaf, stem, pod and total dry matter immediately after relief from stress was significantly lower (Table 4). It is further speculated that the increased canopy temperature, due to stomatal closure, might have induced ethanol fermentation and accelerated carbohydrate depletion, leading to higher respiration and reduced dry matter accumulation[51,52]. In this context, similar results have been found in maize, where elevated temperatures combined with waterlogging led to greater reductions in plant height, stem girth, and dry matter accumulation[30,53].

Across seasons, the considerable reduction in plant height, NDVI, and other growth attributes due to waterlogging at S_{45} (Table 3) was primarily attributed to poor root growth, reduced photosynthesis, and nutrient deficiencies, particularly nitrogen (N)[19,54]. Moreover, S_{45} coincides with the peak growth stages of soybean, specifically the early reproductive stage (flower development and pod initiation stages) which is an energy-intensive process. Therefore, waterlogging stress severely affected dry matter accumulation and growth attributes at this stage[5,26,46]. Hypoxic conditions may exacerbate nitrogen loss and reduce its uptake, leading to leaf chlorosis and a decline in overall plant growth, as reflected in the reduction of NDVI and dry matter accumulation in leaves and stems (Tables 3 and 4). In contrast, the least impact of waterlogging on growth and dry matter accumulation at the initial stage (S_{15}) may be due to the lag phase (slow growth) and the formation of aerial roots, which likely helped supply oxygen, nitrogen, and water to the growing plants, in comparison to the later stages of S_{45} and S_{60} (Tables 3 and 4).

Increased reductions in growth and dry matter accumulation due to waterlogging durations ranging from 2 to 10 days at different growth stages and climatic regimes in soybean are primarily attributed to reduced root morphological attributes (Tables 1 and Fig. 2b). The poor root characteristics, such as reduced length, area, volume, and dry weight, were unable to meet the increasing water and nutrient demands of the crop, leading to poor dry matter accumulation. It is believed that prolonged stress (8–10 days) increased ROS activity due to higher canopy temperatures, which further exacerbated leaf chlorosis, as evidenced by the reduced NDVI values (Table 3). In addition, the reduced PS II activity (data not presented) and increased energy consumption for growth maintenance collectively decreased the accumulation of photosynthates in the leaf (68.15% during C_S and 30.56% during C_R) and stem (68.81% during C_S and 22.45% during C_R) (Table 4). Previous studies have shown that reductions in photosynthesis, stomatal conductance, and chlorophyll content hindered overall growth in soybean[23,49]. Similar reductions in plant height, number of trifoliate leaves, and shoot dry mass were observed in mung bean with increased waterlogging durations[45]. Therefore, the maximum reductions in soybean growth attributes were observed with 8 to 10 days of waterlogging at S_{45} under the summer climate ($C_S \times S_{45} \times D_{8\text{-}10}$).

Yield and dry matter at harvest versus waterlogging

The crop's growth during stress and the subsequent post-stress recovery phase collectively determine the final yield. The present study demonstrates the contrasting reductions in yield parameters and seed yield of soybean under the rainy climate regime (C_R). Despite less severe reductions in root and shoot growth attributes under C_R, seed yield was significantly lower in this climate regime (35.7% lower than under the summer climate, C_S), which may be due to slow post-stress recovery. The relatively poor growth recovery during the rainy climate was attributed to fewer bright sunshine hours (BSH; 4.6 h), which affected PSII activity, crop growth recovery, and yield contributing parameters (Tables 6, S1 and Fig. S3a). As a result, plants allocated more dry matter to vegetative parts, such as the stem (15.71% more than in C_S), leading to a lower yield (Table 5). The plants were also found to be more susceptible to stress, as indicated by the higher stress susceptibility index (SSI; 1.00) and tolerance index (TOL; 3.92) (Table S3). Similarly, Henshaw et al.[47] reported reduced soybean yield due to lower BSH under both waterlogged and control plants. In contrast, the higher number of BSH (8.3 h) and higher temperature (35.3 °C) during the post-stress period in summer likely influenced crop recovery by accelerating growth (105 days) and remobilization of photosynthates to the grains (27.4% higher in C_S compared to C_R) rather than to vegetative parts. Consequently, the higher evapotranspiration demand, coupled with lower relative humidity, might have enhanced stomatal conductance and photosynthesis, thus improving recovery during the post-stress period. This is evident from greater PSII activity and dry matter accumulation during summer which facilitated better seed filling during summer (Tables 5, S1, 5, and Fig. S3a). Therefore, plants exhibited higher test weight (10.67 g per 100 seeds) and seed yield (4.2 g per plant) under C_S (Table 6). A previous study by Matsunami et al.[55] emphasized the importance of crop growth rate during the post-stress period in determining soybean yield under waterlogging.

Regarding growth stages, the greater seed yield observed with waterlogging during the post-reproductive phase (S_{60}) was attributed to the effective remobilization of accumulated photosynthates from leaves and stems to the pods, rather than spending extra energy on repairing waterlogging damage. Thus, soybean plants quickly redirected stored photosynthates toward grain filling, as evidenced by the higher reduction in root attributes (Table 1 and Fig. 2a). Meanwhile, the higher yield at the initial stage (S_{15}) is due to the formation of aerial roots, which helped the crop survive during waterlogging. Additionally, the longer recovery period allowed for better formation and filling of reproductive parts (Table 6). Therefore, both the S_{60} and S_{15} stages showed a close association with seed yield and its stability index across both climate regimes (Fig. 6c). Notably, the lower seed yields observed during waterlogging at S_{30} can be attributed to the coincidence of flower initiation, which resulted in higher flower drop and poor pollination, thereby reducing the number of pods per plant. Similarly, the lower yield observed during waterlogging at S_{45} was likely due to the overlap with the peak flowering to pod formation stage, which reduced pod formation (Table 6). Furthermore, the importance of the number of pods per plant in determining final yield and its stability is reflected in the Principal Component Analysis (PCA), as depicted in Fig. 6c. Additionally, the higher biomass accumulation in vegetative parts, even at harvest, evidently led to lower yields (Figs. 3a and 4a). These results are consistent with the findings of Linkemar et al.[24] and report of Ploschuk et al.[19].

Regardless of climate regimes and growth stages, increased waterlogging intensity (10 days) exacerbated yield reductions by negatively affecting root architecture, crop physiology, and growth attributes. As a result, plants allocated more energy toward forming aerial roots and combating ROS through antioxidant production (data not presented). Consequently, lower leaf PSII activity (0.082 during C_S and 0.085 during C_R) was observed even during the post-stress period (Fig. S3c), leading to reduced dry matter accumulation and a lower number of seeds in soybean across both climates (Table 6 and Figs. 3b, 4b). As a result, plants exhibited lower YSI and tolerance across waterlogging durations (D_2 to D_{10}) (Fig. 5b). Our findings align with the results of Ploschuk et al.[19], who reported that increased waterlogging for 13 days caused yield reductions of 37% to 47% compared to the control. Overall, the interaction of $C_R \times S_{45} \times D_{8\text{-}10}$ amplified the adverse effects of waterlogging, resulting in greater reductions in yield and attributes in soybean.

Conclusion

The present study highlights the sensitivity of soybean growth stages to waterlogging intensity under two different climate regimes. Flower initiation to pod development stages (S_{30} and S_{45}) exhibited higher sensitivity to waterlogging. Meanwhile, the formation of aerial roots and the reallocation of reserved dry matter toward grain production resulted in better yields when waterlogging occurred at the early (S_{15}) and later stages (S_{60}), respectively. Additionally, increased waterlogging intensity beyond 6 days adversely reduced grain yield by 50%, due to poor below-ground and above-ground growth of soybean. Notably, the combination of a summer climate regime and waterlogging (above 6 days) amplified reductions in root morphology and growth in soybean, but favoured post-stress recovery and yield due to higher sunshine hours and temperatures compared to the rainy climate. The present findings are in compliance with current climatic conditions as well as projected future conditions (~4 °C increase in temperature by 2080–2100). This information could be useful for planning proactive mitigation strategies (e.g., developing climate-smart varieties and agronomic management practices) to counter the detrimental effects of waterlogging. Additionally, it could help farm managers effectively manage waterlogging and assist policymakers in estimating yield losses under increasing temperatures. However, authors suggest that further intensive studies should focus on understanding the post-stress recovery of the crop, as well as management strategies for faster recovery from waterlogging.

Data availability

Data is available on request to corresponding author.

Received: 23 December 2024; Accepted: 24 February 2025
Published online: 26 February 2025

References

1. Lee, H., Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P., Trisos, C., Romero, J., Aldunce, P., Barret, K. & Blanco, G. IPCC, 2023: Climate Change 2023: Synthesis report, summary for policymakers. Contribution of working Groups I, II and III to the sixth assessment report of the intergovernmental panel on climate change [Core writing team, H. Lee and J. Romero (eds.)]. (IPCC, 2023).
2. Tabari, H. Climate change impact on flood and extreme precipitation increases with water availability. *Sci. Rep.* **10**(1), 13768. https://doi.org/10.1038/s41598-020-70816-2 (2020).
3. Bezdan, J. et al. Impact of climate change on extreme rainfall events and pluvial flooding risk in the Vojvodina region (North Serbia). *Atm.* **15**(4), 488. https://doi.org/10.3390/atmos15040488 (2024).
4. Katzenberger, A., Levermann, A., Schewe, J. & Pongratz, J. Intensification of very wet monsoon seasons in India under global warming. *Geophys. Res. Lett.* **49**(15), e2022GL098856. https://doi.org/10.1029/2022GL098856 (2022).
5. Ploschuk, R. A., Miralles, D. J., Colmer, T. D., Ploschuk, E. L. & Striker, G. G. Waterlogging of winter crops at early and late stages: Impacts on leaf physiology, growth and yield. *Front. Plant Sci.* **9**, 1863. https://doi.org/10.3389/fpls.2018.01863 (2018).
6. Wu, C. et al. Genome-wide association mapping of flooding tolerance in soybean. *Mol. Breed.* **40**, 1–14. https://doi.org/10.1007/s11032-019-1086-0 (2020).
7. Aggarwal, P. K., Kalra, N., Chander, S. & Pathak, H. Info- Crop: a dynamic simulation model for the assessment of crop yields, losses due to pests, and environmental impact of agro-ecosystems in tropical environments. I. Model description. *Agric. Syst.* **89**, 1–25. https://doi.org/10.1016/j.agsy.2005.08.001 (2006).
8. Jackson, M. B. & Armstrong, W. Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. *Plant Biol.* **1**, 274–287. https://doi.org/10.1055/s-2007-978516 (1999).
9. Ponnamperuma, F. N. The chemistry of submerged soils. In *Advances in Agronomy* Vol. 24 (ed. Sparks, D.) 29–96 (Academic Press, 1972).
10. Visser, E. J. & Voesenek, L. A. C. J. Acclimation to soil flooding–sensing and signal-transduction. *Plant Soil* **274**, 197–214. https://doi.org/10.1007/s11104-004-1650-0 (2005).
11. Xu, X., Wang, H., Qi, X., Xu, Q. & Chen, X. Waterlogging-induced increase in fermentation and related gene expression in the root of cucumber (*Cucumis sativus* L.). *Sci. Hortic.* **179**, 388–395. https://doi.org/10.1016/j.scienta.2014.10.001 (2014).
12. Zhang, P., Lyu, D., Jia, L., He, J. & Qin, S. Physiological and de novo transcriptome analysis of the fermentation mechanism of *Cerasus sachalinensis* roots in response to short-term waterlogging. *BMC Genom.* **18**, 649. https://doi.org/10.1186/s12864-017-4055-1 (2017).
13. Walne, C. H. & Reddy, K. R. Developing functional relationships between soil waterlogging and corn shoot and root growth and development. *Plants* **10**(10), 2095. https://doi.org/10.3390/plants10102095 (2021).
14. Striker, G. G., Insausti, P., Grimoldi, A. A., Ploschuk, E. L. & Vasellati, V. Physiological and anatomical basis of differential tolerance to soil flooding of *Lotus corniculatus* L. and *Lotus glaber* Mill. *Plant Soil* **276**, 301–311. https://doi.org/10.1007/s11104-005-5084-0 (2005).

15. Hasanuzzaman, M. et al. Soybean production and environmental stresses. In *Environmental Stresses in Soybean Production* (ed. Miransari, M.) 61–102 (Academia press, 2016).
16. Basavaraj, P. S. et al. Adventitious root formation confers waterlogging tolerance in cowpea (*Vigna unguiculata* (L.) Walp.). *Front. Sustain. Food Syst.* **8**, 1373183. https://doi.org/10.3389/fsufs.2024.1373183 (2024).
17. Sun, J. et al. Importing food damages domestic environment: Evidence from global soybean trade. *Proc. Natl. Acad. Sci.* **115**(21), 5415–5419. https://doi.org/10.1073/pnas.1718153115 (2018).
18. Anthony, S. C. & Singh, M. K. A Study of water logging tolerance on soybean (*Glycine max* L.) yielding and quality in Vindhyan region of Madhya Pradesh. *J. Emerg. Technol. Innov. Res.* **7**(11), 147–156 (2020).
19. Ploschuk, R. A., Miralles, D. J. & Striker, G. G. A quantitative review of soybean responses to waterlogging: Agronomical, morpho-physiological and anatomical traits of tolerance. *Plant Soil* **475**(1), 237–252. https://doi.org/10.1007/s11104-022-05364-x (2022).
20. Food and Agricultural Organization https://www.fao.org/faostat/en/#data/QCL. Accessed on 20/09/2024
21. Phukan, U. J., Mishra, S. & Shukla, R. K. Waterlogging and submergence stress: affects and acclimation. *Crit. Rev. Biotechnol.* **36**, 956–966. https://doi.org/10.3109/07388551.2015.1064856 (2016).
22. Valliyodan, B. et al. Genetic diversity and genomic strategies for improving drought and waterlogging tolerance in soybeans. *J. Exp. Bot.* **68**, 1835–1849. https://doi.org/10.1093/jxb/erw433 (2017).
23. Oosterhuis, D. M., Scott, H. D., Hampton, R. E. & Wullschleger, S. D. Physiological responses of two soybean [*Glycine max* (L.) Merr.] cultivars to short-term flooding. *Environ. Exp. Bot.* **30**(1), 85–92. https://doi.org/10.1016/0098-8472(90)90012-S (1990).
24. Linkemer, G., Board, J. E. & Musgrave, M. E. Waterlogging effects on growth and yield components in late-planted soybean. *Crop Sci.* **38**(6), 1576–1584. https://doi.org/10.2135/cropsci1998.0011183X003800060028x (1998).
25. Bacanamwo, M. & Purcell, L. C. Soybean root morphological and anatomical traits associated with acclimation to flooding. *Crop Sci.* **39**, 143–149. https://doi.org/10.2135/cropsci1999.0011183X003900010023x (1999).
26. Garcia, N. et al. Waterlogging tolerance of five soybean genotypes through different physiological and biochemical mechanisms. *Environ. Exp. Bot.* **172**, 103975 (2020).
27. Fletcher, E., Patterson, R., Dunne, J., Saski, C. & Fallen, B. Evaluating the effects of flooding stress during multiple growth stages in soybean. *Agron.* **13**(5), 1243. https://doi.org/10.3390/agronomy13051243 (2023).
28. Wen, J. et al. Moderately elevated temperature offsets the adverse effects of waterlogging stress on tomato. *Plants* **13**(14), 1924. https://doi.org/10.3390/plants13141924 (2024).
29. Zhen, B. et al. Effects of combined high temperature and waterlogging stress at booting stage on root anatomy of rice (*Oryza sativa* L.). *Water* **12**(9), 2524. https://doi.org/10.3390/w12092524 (2020).
30. Shao, J. et al. Combined effects of high temperature and waterlogging on yield and stem development of summer maize. *Crop J.* **11**(2), 651–660. https://doi.org/10.1016/j.cj.2022.08.005 (2023).
31. Harisha, C. B. et al. Promising bioregulators for higher water productivity and oil quality of chia under deficit irrigation in semiarid regions. *Plants* **12**(3), 662. https://doi.org/10.3390/plants12030662 (2023).
32. Halli, H. M. et al. Influence of planting and irrigation levels as physical methods on maize root morphological traits, grain yield and water productivity in semi-arid region. *Agron.* **11**(2), 294. https://doi.org/10.3390/agronomy11020294 (2021).
33. Halli, H. M. et al. Range grasses to improve soil properties, carbon sustainability, and fodder security in degraded lands of semi-arid regions. *Sci. Total Environ.* **851**, 158211. https://doi.org/10.1016/j.scitotenv.2022.158211 (2022).
34. Verhulst, N. & Govaerts, B. The normalized difference vegetation index (NDVI) GreenSeeker^{TM} handheld sensor: toward the integrated evaluation of crop management. Part A: concepts and case studies. CIMMYT, Mexico, 13 (2010).
35. Simane, B. & Struik, P. C. Agroclimatic analysis: a tool for planning sustainable durum wheat (*Triticum turgidum* var. durum) production in Ethiopia. *Agric. ecosysts. & environ.* **47**(1), 31–46. https://doi.org/10.1016/0167-8809(93)90134-B (1993).
36. Basavaraj, P. S. et al. Stress tolerance indices for the identification of low phosphorus tolerant introgression lines derived from *Oryza rufipogon* Griff. *Plant Gent. Resources* **19**(4), 328–338. https://doi.org/10.1017/S147926212100038 (2021).
37. Rosielle, A. A. & Hamblin, J. Theoretical aspect of selection for yield in stress and non-stress environment. *Crop Sci.* **21**, 943–946. https://doi.org/10.2135/cropsci1981.0011183X002100060033x (1981).
38. Gopinath, P. P., Parsad, R., Joseph, B. & Adarsh, V. S. GrapesAgri1: Collection of shiny apps for data analysis in agriculture. *J. Open Source Softw.* **6**(63), 3437. https://doi.org/10.21105/joss.03437 (2021).
39. Konnerup, D., Toro, G., Pedersen, O. & Colmer, T. D. Waterlogging tolerance, tissue nitrogen and oxygen transport in the forage legume *Melilotus siculus*: A comparison of nodulated and nitrate-fed plants. *Ann. Bot.* **121**, 699–709. https://doi.org/10.1093/aob/mcx202 (2018).
40. Voesenek, L. A. C. J. & Sasidharan, R. Ethylene–and oxygen signalling–drive plant survival during flooding. *Plant Biol* **15**, 426–435. https://doi.org/10.1111/plb.12014 (2013).
41. Jackson, M. B. Ethylene and responses of plants to soil waterlogging and submergence. *Annu. Rev. Plant Physiol.* **35**, 145–174. https://doi.org/10.5555/19850330973 (1985).
42. Labandera, A. M. et al. The PRT6 N-degron pathway restricts VERNALIZATION 2 to endogenous hypoxic niches to modulate plant development. *New Phytol.* **229**(1), 126–139. https://doi.org/10.1111/nph.16477 (2021).
43. Liu, Z. et al. Ethylene augments root hypoxia tolerance via growth cessation and reactive oxygen species amelioration. *Plant Physiol.* **190**(2), 1365–1383. https://doi.org/10.1093/plphys/kiac245 (2022).
44. Daniel, K. & Hartman, S. How plant roots respond to waterlogging. *J. Exp. Bot.* **75**(2), 511–525. https://doi.org/10.1093/jxb/erad332 (2024).
45. Kyu, K. L., Malik, A. I., Colmer, T. D., Siddique, K. H. & Erskine, W. Response of mungbean (cvs. Celera II-AU and Jade-AU) and blackgram (cv. Onyx-AU) to transient waterlogging. *Front. Plant Sci.* **12**, 709102. https://doi.org/10.3389/fpls.2021.709102 (2021).
46. Adegoye, G. A. et al. Waterlogging effects on soybean physiology and hyperspectral reflectance during the reproductive stage. *Agric.* **13**(4), 844. https://doi.org/10.3390/agriculture13040844 (2023).
47. Henshaw, T. L., Gilbert, R. A., Scholberg, J. M. S. & Sinclair, T. R. Soya bean (*Glycine max* L. Merr.) genotype response to early-season flooding: I. Root and nodule development. *J. Agron. Crop Sci.* **193**, 177–188. https://doi.org/10.1111/j.1439-037X.2007.00257.x (2007).
48. Senthamil, E. et al. Waterlogging effects on root morphology, yield, and stress tolerance in cowpea (*Vigna unguiculata* L. Walp) grown on semi-arid Vertisols. *J. Agric. Crop Sci.* **211**, e70014. https://doi.org/10.1111/jac.70014 (2025).
49. Kim, Y. H. et al. Comparative analysis of endogenous hormones level in two soybean (*Glycine max* L.) lines differing in waterlogging tolerance. *Front. Plant Sci.* **6**, 714. https://doi.org/10.3389/fpls.2015.00714 (2015).
50. Zhang, Y., Liu, G., Dong, H. & Li, C. Waterlogging stress in cotton: Damage, adaptability, alleviation strategies, and mechanisms. *Crop J.* **9**(2), 257–270. https://doi.org/10.1016/j.cj.2020.08.005 (2021).
51. Van Eck, W. H. J. M., Lenssen, J. P. M., Rengelink, R. H. J., Blom, C. W. P. M. & De Kroon, H. Water temperature instead of acclimation stage and oxygen concentration determines responses to winter floods. *Aquatic Bot.* **81**(3), 253–264. https://doi.org/10.1016/j.aquabot.2004.10.006 (2005).
52. Vartapetian, B. B. Plant anaerobic stress as a novel trend in ecological physiology, biochemistry, and molecular biology: 2. Further development of the problem. *Russian J. Plant Physiol.* **53**, 711–738. https://doi.org/10.1134/S102144370606001X (2006).
53. Xu, L., Pan, R., Shabala, L., Shabala, S. & Zhang, W. Y. Temperature influences waterlogging stress-induced damage in *Arabidopsis* through the regulation of photosynthesis and hypoxia-related genes. *Plant Growth Regul.* **89**, 143–152. https://doi.org/10.1007/s10725-019-00518-x (2019).

54. Shaw, R. E., Meyer, W. S., McNeill, A. & Tyerman, S. D. Waterlogging in Australian agricultural landscapes: a review of plant responses and crop models. *Crop Pasture Sci.* **64**(6), 549–562. https://doi.org/10.1071/CP13080 (2013).
55. Matsunami, T., Jung, G. H., Oki, Y. & Kokubun, M. Effect of waterlogging during vegetative stage on growth and yield in super nodulating soybean cultivar sakukei. *Plant Prod. Sci.* **10**(1), 112–121. https://doi.org/10.1626/pps.10.112 (2007).

Acknowledgements
Authors are thankful to ICAR–National Institute of Abiotic Stress Management, Baramati, Maharashtra for supporting this research through umbrella project: genetic garden (IXX15674). Also appreciate the co-operation of Department of Agronomy, University of Agricultural Sciences, Bengaluru, Karnataka during experimentation. We acknowledge the kind support of "Phenotyping of pulses for enhanced tolerance to drought and heat (OXX01737)" project.

Author contributions
Vinay M. Gangana Gowdra, B.S. Lalitha, Hanamant M. Halli, Jayadeva H.M.: Conceptualization, investigation, methodology, data curation, writing original draft, supervision, and resources. E. Senthamil, Priyanka Negi, Basavaraj P.S., Harisha C.B., Boraiah K.M., Sandeep B. adavi, Suresha P.G., Raghavendra Naragund, Ganesh Mohite and K. Sammi Reddy: Formal analysis, software, visualization, writing original draft, and writing review and editing.

Funding
Authors are thankful to National Institute of Abiotic Stress Management, Baramati and NICRA project (OXX01737) for the support during experimentation.

Declarations

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-91780-9.

Correspondence and requests for materials should be addressed to V.M.G.G. or H.M.H.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.