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RESEARCH ARTICLE

Growth and morpho-physiological assessments of Indonesian red chili cultivars on early vegetative stage under water stress conditions: A comparison of waterlogging and drought

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ABSTRACT

Red chili pepper *Capsicum annuum* L. var. *annuum* plants are one of the fruity vegetable types that are often cultivated in riparian tropical wetlands but are constrained by water stress such as waterlogging during rainy season and drought in dry season. The aim of this research was to evaluate the growth and morpho-physiological responses of red chili pepper cultivars subjected to waterlogging and drought stress conditions. The experiment was carried out in a strip-plot design with two factors. The first factor was three water stress treatments, namely control (field capacity), waterlogging, and drought. The second factor was six cultivars of Indonesian red chili pepper. The findings indicated that both waterlogging and drought stress had a detrimental impact on the reduction of the growth parameters of red chili pepper such as root, shoot and total dry weight. Chili pepper defended its root weights in response to drought stress (0.653 g plant^{-1}) whereas it preserved shoot weight in response to waterlogging (0.913 g plant^{-1}). In the morphological characters, chili pepper exhibited an increase in specific leaf area expansion in response to both waterlogging (150.82 cm^2) and drought (188.82 cm^2) compared to control (140.91 cm^2), but decreased specific leaf weight during stresses and recovered after 7 d in waterlogging. Leaf chlorophyll content (SPAD) and leaf relative water content (LRWC), as physiological characteristics, also experienced a decline during exposure to both waterlogging and drought during 8 d; yet, SPAD and LRWC able to recover completely at 7 d after waterlogging and drought treatment were terminated.

Key words: Drought stress, leaf relative water content, specific leaf area, waterlogging, wetlands.

INTRODUCTION

Tropical wetlands, including non-tidal riparian wetlands, are a type of suboptimal land, accounting for about 21% of terrestrial land in Indonesia. During the rainy season, the non-tidal riparian wetlands can be flooded for up to 9 mo. Due to this circumstance, most local farmers cultivate crops only once a year at the end of the rainy season after the floodwaters have receded (Lakitan et al., 2018). Affordable technologies for cultivating vegetable crops during the flood period (rainy season) have been developed, including the floating cultivation system after rice harvest in non-tidal riparian wetlands, although further research and testing are still needed (Siaga et al., 2018; 2019a). However, optimal cultivation of vegetable crops in the field (under low tide conditions) requires a fairly long planting period of about 4-5 mo during the transition period (dry to rainy season), which is at risk of experiencing water stress conditions.

The transitional period in non-tidal riparian wetlands has water constraints, including drought in the dry season and gradual water excess in the rainy season, starting from shallow water table, waterlogging and submergence (flood season). Unpredictable floods and droughts due to global climate change are severely affecting crop production (Goto et al., 2021). Affordable technology also needs to be developed for vegetable crops during the transition period. However, the response of vegetable crops in terms of agronomic and morpho-physiological characteristics under abiotic stresses, including waterlogging and drought conditions, needs to be studied.

This research was particularly important in the screening process, which is an essential first step in determining crop yield in relation to genetic traits and environmental factors. Waterlogging and drought stress were contrasting abiotic stresses. Waterlogging stress generally causes adverse effects on plant morpho-agronomic and physiological traits (Ichsan et al., 2021), including a decrease in the rate of plant leaf expansion (Meihana et al., 2023) and root expansion (Siaga et al., 2023), changes in leaf color/reduced leaf chlorophyll content (Zainul et al., 2022), adventitious root formation (Pandey et al., 2021), and decreased plant dry weight (Siaga et al., 2019b). On the other hand, plants also respond to drought stress by slowing growth and photosynthetic activity (Widuri et al., 2018; 2020) and increasing proline accumulation (Avramova et al., 2016).

Red chili (*Capsicum annuum* L.) is well known as one of the fruit vegetables widely consumed by the Indonesian people and is classified as a type of horticultural product with high economic value. Although red chili plants are often cultivated under optimal soils, the plants also have the potential to be cultivated under sub-optimal growth conditions such as riparian tropical wetlands during the transition period (dry to rainy season). Lakitan et al. (2018) reported that in non-tidal riparian wetlands, red chili pepper was cultivated as an additional crop to rice as the main crop. Some farmers started to cultivate chili pepper together with rice cultivation at the edge of rice fields, but there were also farmers who started to cultivate chili pepper in rice fields during the transitional period after rice harvest.

Basically, the main constraints of vegetable production including red chili pepper during the transition period are waterlogging and drought stress. Therefore, the intensification method that can be implemented to deal with these constraints is through the use of cultivars that are resistant to both stresses. The objective of this research was to evaluate the growth and morpho-physiological responses of Indonesian red chili pepper (*Capsicum annum* L.) cultivars exposed to water stresses such as waterlogging and drought stress, and also to obtain varieties resistant to both stresses.

MATERIALS AND METHODS

Plant materials and seedling preparation

Six Indonesian red pepper (*Capsicum annuum* L. var. *annuum*) cultivars used in this study were Laris, Srikandi, Ferosa, Andalas, Kawat and Romario. Before sowing, seeds were soaked in water for about 6 h to select good quality seeds. After germinating for 3 d under a damp cloth, the seeds were sown in seedling trays. Eight-week-old chili seedlings were then transplanted into black bags (size 1 L) filled with growing media consisting of a mixture of mountain soil and compost. Plants were screened for uniformity to minimize size variability for growth and morpho-physiological studies.

Research set up

The experiment was designed as a two-factor split-plot design. The first factor consisted of control, waterlogging, and drought treatments. As a control, the growth medium was watered daily until it reached field capacity. Waterlogging stress was simulated by growing media fully submerged in water (neutral pH), while drought was simulated by 8 d without watering. The second factor was six cultivars of Indonesian red chili pepper. Accordingly, there were 18 combinations of treatments with three replicates in each treatment. Red chili peppers were grown in black polyethylene bags (size 1 L) filled with growing media. For the waterlogging treatment, the chili plants were placed in the container boxes (36 cm length × 24 cm width × 9 cm height) filled with water at a depth of 8 cm.

Plant treatments were initiated at 14 d after transplanting (DAT), terminated after 8 d of exposure, and then allowed to recover for 7 d. For the drought treatment, the chili plants were not deprived of water for a period of

8 d, after which they were allowed to recover for a period of 7 d. On the last day of the recovery period (29 d), chili plants from all treatments were harvested and observed.

Measured parameters and growth analysis

The growth parameters measured in this study were root dry weight (RDW), shoot dry weight (SDW) and total dry weight (TDW). Root weight ratio (RWR), shoot weight ratio (SWR) and shoot to root ratio (SRR) were also observed. The morphological parameters were observed on number of leaves (NoL), total leaf area (TLA), specific leaf area (SLA) and specific leaf weight (SLW). The NoL was counted manually, while TLA was measured using an automated area meter (Hayashi Denko, Tokyo, Japan). The SLA was determined as the ratio of leaf area to leaf dry weight of individual leaves (cm^2 g^{-1}), while SLW corresponded to 1/SLA and was expressed as mg cm^{-2}. The physiological parameters measured in this study were SPAD and leaf relative water content (LRWC). SPAD was measured using a chlorophyll meter (SPAD-502Plus, Konica Minolta, Osaka, Japan). The LRWC was calculated as LRWC (%) = [Fresh weight (FW) - Dry weight (DW)]/[Turgid weight (TW) - DW × 100]. The SLA, SLW, LRWC and SPAD parameters were measured continuously at the end of both the stress and recovery periods.

Statistical analysis

The ANOVA was performed based on a strip-plot design using the Statistical Analysis System (SAS) University Edition (SAS Institute, Cary, North Carolina, USA) for testing the significant effect of the treatments on the red chili pepper. For the significant treatments, the differences among mean values were then evaluated by using the least significant differences (LSD) test at $p \leq 0.05$.

RESULTS AND DISCUSSION

Growth and morpho-physiological characters of red chili pepper exposed to waterlogging and drought

Significant differences ($p \leq 0.05$) were identified in water stress treatments and chili pepper cultivars with respect to all the growth parameters measured (Table 1). These results indicated that red chili pepper plants showed different responses to the conditions of field capacity, waterlogging, and drought. In addition, the chili pepper cultivars used in this study had a high degree of agronomic yield diversity, thereby allowing the cultivars to be used in the process of screening for waterlogging and drought tolerance.

The significant differences ($p \leq 0.05$) were also observed in all water stress treatments with respect to all morphological characters of chili pepper, such as number of leaves (NoL), total leaf area (TLA), specific leaf area (SLA), and specific leaf weight (SLW). However, among all the parameters observed in the chili varieties, TLA, SLA and SLW showed significant differences only at the end of the recovery stress periods. The interaction between water stress treatments and chili cultivars showed a significant effect on all the agronomic parameters, except for the shoot dry weight (SDW) parameter. On the other hand, the interaction between morpho-physiological parameters only affected TLA parameter (Table 1).

Growth parameters of all chili pepper cultivars studied were retarded after waterlogging and drought exposure as indicated by lower root dry weight (RDW), SDW and total dry weight (TDW) in both water stress treatments compared to untreated control plants even after recovery up to 7 d. Furthermore, drought stress treatments for 8 d followed by a recovery period of 7 d resulted in a significant decrease in shoot weight ratio (SWR) and shoot to root ratio (SRR), but an increase in root weight ratio (RWR). Interestingly, the patterns exhibited contrasting results under waterlogging stress (Table 2).

The results of the growth parameters in this study showed the same pattern with the morphological response of chili pepper by experiencing lower NoL and TLA at the end of recovery periods. At the end of water stress treatments, nonsignificant differences in SLA and SLW were detected among control and waterlogging. The effects on SLA and SLW became significant only under drought. The SLA decreased under waterlogging stress at the end of recovery period, it was not affected by drought. In contrast, SLW (organic matter used to produce 1 cm^2 leaf) was found to be higher under waterlogging (7.6 mg cm^{-2}) than under drought and control treatments (4.3 and 5.2 mg cm^{-2}, respectively) (Table 2).

Table 1. Statistical calculation of the growth, morphological and physiological characters of red chili peppers exposed to waterlogging and drought stress. **Significantly different at $p \leq 0.01$; ^{ns}: not significantly different; EoS: end of stress; EoR: end of recovery; RDW, SDW and TDW are root, shoot and total dry weight, respectively; RWR: root weight ratio, SWR: shoot weight ratio; SRR: shoot root ratio; NoL: number of leaves; TLA: total leaf area; SLA: specific leaf area; SLW: specific leaf weight; LRWC: leaf relative water content.

Source of variance	df	Growth parameters					
		RDW	SDW	TDW	RWR	SWR	SRR
Water stress	2	**	**	**	**	**	**
Varieties	5	**	**	**	**	**	**
Interaction	10	**	ns	**	**	**	**
		Morphological parameters					
		NoL	TLA	SLA		SLW	
				EoS	EoR	EoS	EoR
Water stress	2	**	**	**	**	**	**
Varieties	5	ns	**	ns	**	ns	**
Interaction	10	ns	**	ns	ns	ns	ns
		Physiological parameters					
		LRWC			SPAD		
		EoS	EoR		EoS	EoR	
Water stress	2	ns	ns		**	ns	
Varieties	5	ns	ns		**	ns	
Interaction	10	ns	ns		ns	ns	

Table 2. Growth and morpho-physiological characteristics of red chili after exposure to waterlogging and drought stress. Means followed with the same letters within columns are not significantly different based on the LSD at $p \leq 0.05$. ^{ns}: not significantly different.

Parameters	Control	Waterlogging	Drought	LSD 0.05
		Growth parameters		
Root dry weight, g	1.121 ± 0.38^a	0.224 ± 0.11^c	0.653 ± 0.23^b	0.11
Shoot dry weight, g	2.055 ± 0.91^a	0.913 ± 0.51^b	1.089 ± 0.45^b	0.27
Total dry weight, g	3.175 ± 1.12^a	1.137 ± 0.59^c	1.742 ± 0.61^b	0.34
Root weight ratio, g g^{-1}	0.360 ± 0.07^a	0.240 ± 0.13^b	0.389 ± 0.08^a	0.05
Shoot weight ratio, g g^{-1}	0.641 ± 0.07^b	0.760 ± 0.13^a	0.259 ± 0.10^c	0.05
Shoot root ratio, g g^{-1}	1.870 ± 0.51^b	4.298 ± 2.65^a	0.753 ± 0.49^c	0.58
		Morphological parameters		
Number of leaves (sheet)	35.50 ± 14.71^a	11.61 ± 4.94^c	25.06 ± 13.34^b	7.43
Total leaves area, cm^2	132.33 ± 52.81^a	74.14 ± 49.01^b	78.43 ± 50.37^b	24.57
Specific leaf area, cm^2 g^{-1}				
End of stress	140.91 ± 25.21^b	150.82 ± 24.90^b	188.82 ± 53.76^a	23.59
End of recovery	199.51 ± 37.36^b	133.92 ± 19.74^c	237.10 ± 50.42^a	23.89
Specific leaf weight, mg cm^{-2}				
End of stress	7.289 ± 1.17^a	6.798 ± 1.08^a	5.699 ± 1.54^b	0.79
End of recovery	5.178 ± 0.95^b	7.625 ± 1.15^a	4.388 ± 0.89^c	0.61
		Physiological parameters		
Leaf relative water content, %				
End of stress	84.45 ± 4.26	83.05 ± 3.54	74.92 ± 23.45	ns
End of recovery	93.19 ± 7.10	83.10 ±17.66	91.06 ± 16.91	ns
SPAD				
End of stress	50.57 ± 3.97^a	44.24 ± 7.34^b	49.81± 10.53^a	3.98
End of recovery	47.11 ± 4.25	27.23 ± 4.01	44.48 ± 4.98	ns

Waterlogging and drought also eventually decreased physiological parameters, including leaf relative LRWC) and SPAD value in chili peppers (Table 2). However, nonsignificant differences in LRWC and SPAD were observed among water stress treatments at the end of stress and after recovery periods. An exception was observed only for the SPAD value measured 7 d after stress (Table 2). Moreover, LRWC was able to recover after 7 d of recovery in 'Srikandi', 'Laris', 'Kawat' and 'Romario' (Table 2). The TDW and RDW parameters were higher in all cultivars under drought as compared to waterlogging, while SDW parameter was lower in all cultivars studied except 'Ferosa' and 'Andalas' (Table 3).

Table 3. Total dry weight (TDW), root dry weight (RDW) and shoot dry weight (SDW) of six cultivars of red chili peppers after 8 d of waterlogging and drought stress + 7 d of recovery. Means followed with the same letters within columns are not significantly different based on the LSD at $p \leq 0.05$. TDW, RDW, and SDW are total, root, and shoot dry weight, respectively. **Significantly different at $p \leq 0.01$; *significantly different at $p \leq 0.05$; ^{ns}: not significantly different.

Treatments	Cultivars					
	Srikandi	Laris	Ferosa	Andalas	Kawat	Romario
	TDW (g)					
Control	5.46 ± 0.89^{a}	2.80 ± 0.13^{a}	3.20 ± 0.74^{a}	2.91 ± 0.53^{a}	2.26 ± 0.13^{a}	2.42 ± 0.86^{a}
Waterlogging	1.66 ± 0.13^{b}	1.76 ± 0.08^{b}	1.05 ± 0.60^{b}	0.29 ± 0.08^{b}	1.33 ± 0.29^{c}	0.73 ± 0.30^{b}
Drought	2.18 ± 0.25^{b}	2.12 ± 0.54^{b}	1.98 ± 0.55^{b}	1.07 ± 0.81^{b}	1.84 ± 0.12^{b}	1.27 ± 0.44^{ab}
$LSD_{0.05}$	1.07^{**}	0.64^{**}	1.27^{**}	1.12^{**}	0.39^{**}	1.17^{**}
	RDW (g)					
Control	1.73 ± 0.22^{a}	1.24 ± 0.11^{a}	0.95 ± 0.20^{a}	1.16 ± 0.34^{a}	0.80 ± 0.02^{a}	0.85 ± 0.36^{a}
Waterlogging	0.27 ± 0.03^{c}	0.42 ± 0.03^{b}	0.22 ± 0.08^{b}	0.13 ± 0.02^{b}	0.14 ± 0.05^{c}	0.17 ± 0.08^{b}
Drought	0.83 ± 0.11^{b}	0.91 ± 0.27^{a}	0.70 ± 0.16^{a}	0.36 ± 0.14^{b}	0.56 ± 0.04^{b}	0.55 ± 0.16^{ab}
$LSD_{0.05}$	0.27^{**}	0.34^{**}	0.31^{**}	0.42^{**}	0.08^{**}	0.46^{**}
	SDW (g)					
Control	3.73 ± 0.68^{a}	1.56 ± 0.02^{a}	2.26 ± 0.55^{a}	1.75 ± 0.30^{a}	1.46 ± 0.15^{a}	1.57 ± 0.64^{a}
Waterlogging	1.39 ± 0.16^{b}	1.34 ± 0.08^{a}	0.83 ± 0.53^{b}	0.16 ± 0.06^{b}	1.19 ± 0.25^{a}	0.56 ± 0.25^{b}
Drought	1.35 ± 0.18^{b}	1.21 ± 0.26^{a}	1.28 ± 0.50^{ab}	0.71 ± 0.42^{b}	1.28 ± 0.16^{a}	0.72 ± 0.14^{ab}
$LSD_{0.05}$	0.82^{**}	0.32^{**}	1.10^{**}	0.60^{**}	0.36^{**}	0.81^{**}

Under control, the increase in RDW is proportionally associated with an increase in SDW. This association was observed in chili plants that were not subjected to waterlogging and drought. In this study, there was a decrease in the correlation coefficient between the increase in RDW and SDW when the chili plants were exposed to both waterlogging and drought. The correlation coefficients between RDW and SDW under control, waterlogging and drought were 0.77, 0.67 and 0.53, respectively (Figure 1). This finding indicated that under both water stresses, an increase in root weight has less effect on shoot growth than unstressed plant.

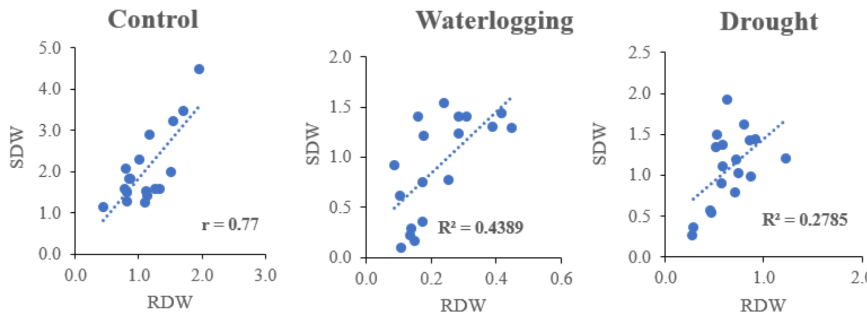

Figure 1. Relationship between root dry weight (RDW) and shoot dry weight (SDW) of red chili pepper under control, waterlogging and drought stress.

Root growth (based on the RWR value) was proportionally similar between drought-treated and control chili plants, indicating that root growth did not receive a higher priority than above-ground organs, as shoot weight ratio (SWR) and shoot root ratio (SRR) were also similar between drought-treated and control plants. The opposite is true under waterlogging conditions. All cultivars studied under waterlogging stress showed an increase in shoot growth, which was higher than the control, but it was in contrast to the root growth parameter, especially in 'Laris' and 'Kawat' (based on RWR value) (Figure 2). According to TLA, 'Laris' and 'Kawat' were comparatively less affected by waterlogging and drought treatments, while the decrease in NoL occurred only under drought stress conditions (Figure 3).

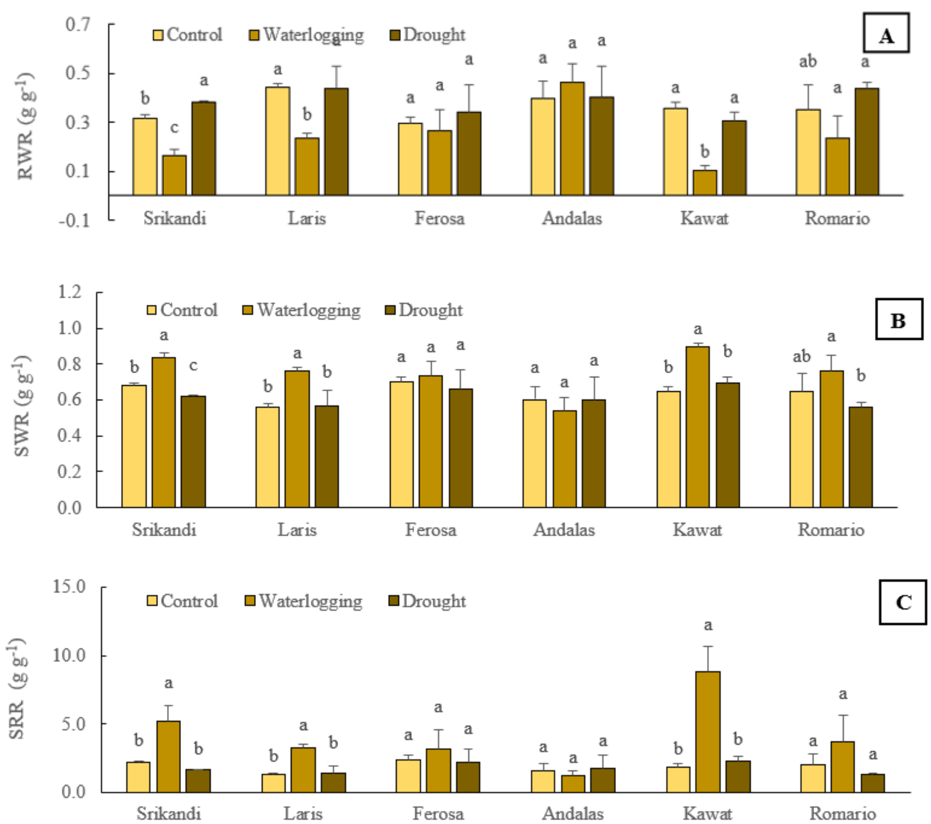

Figure 2. Root weight ratio (RWR) (A), shoot weight ratio (SWR) (B) and shoot-root ratio (SRR) (C) of six cultivars of red chili peppers after 8 d of waterlogging and drought stress + 7 d of recovery.

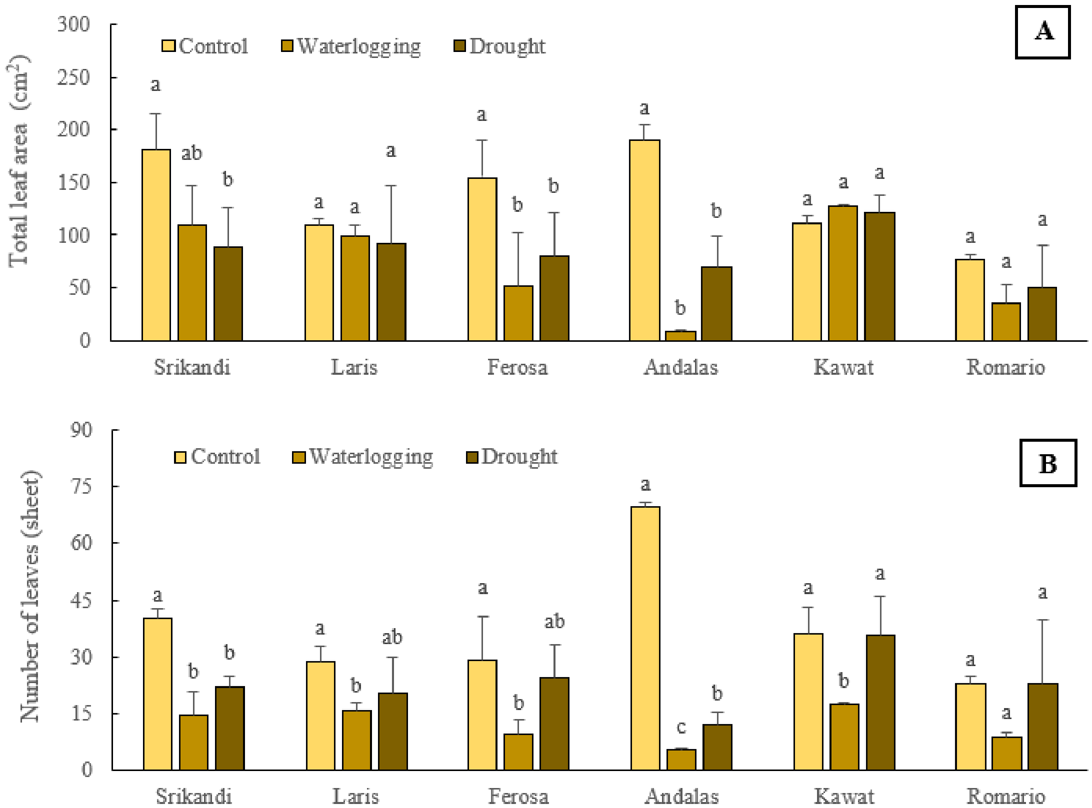

Figure 3. Total leaf area (A) and number of leaves (B) of six cultivars of red chili peppers after 8 d of waterlogging and drought stress + 7 d of recovery.

All chili pepper cultivars displayed the same identical responses during waterlogging and drought and recovery period in SLA and SLW values. SLA values were significantly lower under both water stresses, but significantly higher after recovery period of drought stress for all chili pepper cultivars. Different trends were experienced in SLW, which was significantly higher as compared to the control at the end of both stress conditions. Subsequently, a decline was observed after recovery in drought stress, although it remained, significantly higher under waterlogging stress (Table 4).

Observation of the physiological parameters represented by SPAD and LRWC, revealed that SPAD value showed significant difference among water stress treatments only in 'Andalas' and 'Romario' after water stress exposure, while the decrease of SPAD value was only experienced by them only under waterlogging stress. Conversely, LRWC value demonstrated the significant changes in 'Laris' and 'Kawat' after exposure under water stress conditions and recovery periods. This finding indicated that there was a physiological mechanism to deal with water stress conditions in these two red chilies cultivars (Table 5).

Table 4. Specific leaf area (SLA) and specific leaf weight (SLW) of six cultivars of red chili peppers varieties exposed to waterlogging and drought stress. Means followed with the same letters within columns are not significantly different based on the LSD at $p \leq 0.05$; ns: not significantly different. SLA: Specific leaf area; SLW: specific leaf weight.

Treatments	Cultivars					
	Srikandi	Laris	Ferosa	Andalas	Kawat	Romario
	SLA ($cm^2 g^{-1}$)					
End of stress						
Control	249.6 ± 21.9^a	274.7 ± 12.6^a	227.6 ± 12.0^a	288.3 ± 131.5	239.7 ± 17.3^a	217.2 ± 8.1
Waterlogging	138.1 ± 17.9^b	169.0 ± 22.5^b	157.8 ± 11.5^b	155.2 ± 34.7	127.0 ± 14.7^b	157.9 ± 33.3
Drought	139.2 ± 5.3^b	180.3 ± 44.1^b	183.4 ± 34.1^b	244.7 ± 73.4	190.7 ± 55.4^{ab}	194.6 ± 66.0
$LSD_{0.05}$	33.25	59.04	43.84	ns	69.12	ns
End of recovery						
Control	181.0 ± 21.8^b	228.3 ± 15.9^a	177.0 ± 34.9^{ab}	240.3 ± 37.7	184.8 ± 17.9^a	177.0 ± 50.3^b
Waterlogging	117.5 ± 25.8^c	125.9 ± 7.0^b	122.4 ± 4.9^b	159.1 ± 15.6	146.0 ± 8.5^b	132.6 ± 19.3^b
Drought	245.8 ± 25.3^a	229.5 ± 16.8^a	203.9 ± 39.7^a	287.1 ± 107.1	210.4 ± 20.4^a	246.1 ± 20.2^a
$LSD_{0.05}$	48.74	27.93	61.34	ns	32.90	ns
	SLW ($mg cm^{-2}$)					
End of stress						
Control	4.03 ± 0.35^b	3.64 ± 0.16^b	4.40 ± 0.24^b	4.26 ± 2.60	4.19 ± 0.32^b	4.61 ± 0.17
Waterlogging	7.33 ± 0.99^a	5.99 ± 0.85^a	6.36 ± 0.49^a	6.64 ± 1.33	7.95 ± 0.96^a	6.51 ± 1.24
Drought	7.19 ± 0.28^a	5.82 ± 1.66^a	5.58 ± 1.03^{ab}	4.41 ± 1.60	5.60 ± 1.87^{ab}	5.60 ± 2.05
$LSD_{0.05}$	1.25	2.15	1.34	ns	2.45	ns
End of recovery						
Control	5.57 ± 0.64^b	4.39 ± 0.31^b	5.79 ± 1.06^b	4.24 ± 0.73	5.44 ± 0.51^b	5.79 ± 1.35^{ab}
Waterlogging	8.76 ± 1.72^a	7.96 ± 0.43^a	8.18 ± 0.33^a	6.33 ± 0.64	6.86 ± 0.40^a	7.66 ± 1.21^a
Drought	4.10 ± 0.40^b	4.37 ± 0.33^b	5.05 ± 1.08^b	3.95 ± 1.86	4.79 ± 0.49^b	4.08 ± 0.33^b
$LSD_{0.05}$	2.17	0.72	1.79	ns	0.93	1.90

Table 5. Leaf chlorophyll content (SPAD) and relative water content (LRWC) value of six cultivars of red chili peppers exposed to waterlogging and drought stress. Means followed with the same letters within columns are not significantly different based on the LSD at $p \leq 0.05$. RWC: Relative water content. **Significantly different at $p \leq 0.01$; *significantly different at $p \leq 0.05$; ns: not significantly different.

Treatments	Cultivars					
	Srikandi	Laris	Ferosa	Andalas	Kawat	Romario
	SPAD					
End of stress						
Control	47.5 ± 3.70	47.5 ± 4.70	51.3 ± 1.07	49.7 ± 4.18^a	49.8 ± 4.83	49.2 ± 1.29^a
Waterlogging	51.0 ± 3.20	45.9 ± 2.35	42.2 ± 8.63	35.1 ± 2.60^b	52.2 ± 1.31	39.1 ± 0.40^b
Drought	54.9 ± 6.80	49.8 ± 8.63	53.4 ± 9.15	35.4 ± 10.31^{ab}	59.3 ± 8.52	46.1 ± 5.80^{ab}
$LSD_{0.05}$	ns	ns	ns	13.18*	ns	9.28*
End of recovery						
Control	49.3 ± 1.20	45.7 ± 1.35	46.1 ± 2.50	46.5 ± 7.30	51.0 ± 6.08	44.1 ± 3.40
Waterlogging	46.2 ± 2.70	47.5 ± 1.01	48.7 ± 3.05	43.7 ± 3.86	51.7 ± 3.44	45.6 ± 4.42
Drought	46.1 ± 4.70	44.4 ± 4.33	42.9 ± 4.57	43.3 ± 8.66	46.7 ± 1.65	43.5 ± 7.15
$LSD_{0.05}$	ns	ns	ns	ns	ns	ns
	LRWC (%)					
End of stress						
Control	91.4 ± 1.03	94.4 ± 2.46^a	95.1 ± 1.03	92.3 ± 3.95	96.4 ± 1.11^a	95.5 ± 1.83
Waterlogging	81.2 ± 3.27	80.2 ± 0.40^{ab}	87.8 ± 2.61	83.5 ± 1.79	80.5 ± 3.39^a	85.1 ± 2.62
Drought	71.4 ± 23.69	69.9 ± 17.20^b	88.6 ± 15.21	89.2 ± 8.06	61.5 ± 15.05^b	84.0 ±17.80
$LSD_{0.05}$	ns	20.05**	ns	ns	17.84**	ns
End of recovery						
Control	94.4 ± 0.79^a	93.5 ±1.40^a	85.2 ± 17.44	95.2 ± 0.61	95.5 ± 1.05^a	95.2 ± 0.70^a
Waterlogging	79.6 ± 6.68^b	78.4 ± 8.56^b	85.3 ± 2.79	80.5 ± 2.60	83.1 ± 2.43^b	73.9 ± 17.64^b
Drought	96.1 ± 0.96^a	96.1 ± 1.20^a	96.7 ± 0.09	73.1 ± 41.55	93.5 ± 4.08^a	90.8 ± 8.47^{ab}
$LSD_{0.05}$	7.84*	10.10**	ns	ns	5.60**	20.90**

Screening based on ratio among water stress to unstressed

Data of growth, morphology and physiology were usually used as parameters for screening or selection to explore tolerant and susceptible cultivars. In this study, the comparison among cultivars were observed through the ratio value between water stress treatment and control as unstressed conditions, namely waterlogging/control (W/C) and drought/control (D/C). According to this study, dry weight parameters were used as the first parameters for screening. A comparison of the RDW, SDW, and TDW among chili pepper cultivars showed that 'Laris' and 'Kawat' had significantly higher values than the others under W/C and D/C. In addition, 'Ferosa' also obtained the highest value similar to 'Laris' and 'Kawat' in D/C value. Furthermore, the lowest values of RDW, SDW, and TDW were retrieved by 'Andalas' (Table 6).

Table 6. Water stress ratio of total dry weight (TDW), root dry weight (RDW) and shoot dry weight (SDW) of six cultivars of red chili peppers after 8 d of exposure to waterlogging and drought stress + 7 d of recovery. Means followed with the same letters within columns are not significantly different based on the LSD at $p \leq 0.05$. **Significantly different at $p \leq 0.01$.

Cultivars	Waterlogging/Control			Drought/Control		
	TDW	RDW	SDW	TDW	RDW	SDW
Srikandi	0.31 ± 0.07^{b}	0.16 ± 0.02^{bc}	0.38 ± 0.10^{b}	0.40 ± 0.06^{bc}	0.48 ± 0.07^{ab}	0.12 ± 0.03^{b}
Laris	0.63 ± 0.01^{a}	0.34 ± 0.02^{a}	0.86 ± 0.04^{a}	0.75 ± 0.16^{a}	0.73 ± 0.16^{a}	0.32 ± 0.16^{ab}
Ferosa	0.31 ± 0.11^{b}	0.23 ± 0.03^{b}	0.35 ± 0.15^{b}	0.61 ± 0.05^{ab}	0.73 ± 0.01^{a}	0.27 ± 0.14^{ab}
Andalas	0.10 ± 0.04^{c}	0.12 ± 0.05^{c}	0.10 ± 0.05^{c}	0.34 ± 0.20^{c}	0.31 ± 0.06^{b}	0.18 ± 0.20^{b}
Kawat	0.58 ± 0.10^{a}	0.18 ± 0.06^{bc}	0.81 ± 0.09^{a}	0.82 ± 0.08^{a}	0.70 ± 0.06^{a}	0.45 ± 0.07^{a}
Romario	0.30 ± 0.02^{b}	0.23 ± 0.07^{b}	0.36 ± 0.12^{b}	0.53 ± 0.09^{bc}	0.34 ± 0.28^{a}	0.17 ± 0.05^{b}
$LSD_{0.05}$	0.12^{**}	0.08^{**}	0.18^{**}	0.21^{**}	0.25^{**}	0.22^{**}

As presented in Table 7, the same result was found in W/C and D/C ratios on the morphological parameters, such as NoL and TLA. However, 'Laris' showed the lowest value for SLA, while displaying the highest value for SLW under W/C. Conversely, 'Kawat' presented the opposite results. On the other hand, 'Andalas' showed the lowest values of W/C and D/C in the parameters of NoL and TLA, but obtained higher values for the parameters SLA and SLW under both stresses. Furthermore, it was observed that LRWC and SPAD were not significantly impacted under both stresses across all cultivars at the end of the recovery period. This implied that LRWC and SPAD were not considered as screening parameters in this study (Table 8).

Plants have evolved mechanisms to compensate for unfavorable conditions. Significant changes occur in chili plants exposed to water stress conditions, including waterlogging and drought. Various agronomic and morpho-physiological mechanisms are involved in plant adaptation under water stress. The survival mechanism of plants is demonstrated by the adjustment of biomass accumulation in agronomic parameters. This study revealed that chili pepper increased root weight in response to drought stress. Conversely, it formed more shoots under waterlogging.

Significantly higher SRR and SWR yet lower RWR were obtained in waterlogging-treated plant (Table 2). Since both above- and underground organs were negatively affected by drought, the effects were probably associated with more severe growth restriction in roots than in above ground organs. Waterlogging induced a rapid depletion of available oxygen and restricted aerobic metabolism in roots (Rudolph-Mohr et al., 2017; Siaga et al., 2018). After replacing soil pores with water, the low oxygen concentration in the rooting medium results in insufficient oxygen supply to roots, while oxygen diffusion is much slower in water than in air (Lenzewski et al., 2018).

Table 7. Water stress ratio of number of leaves (NoL), total leaf area (TLA), specific leaf area (SLA) and specific leaf weight (SLW) of six cultivars of red chili peppers after 8 d of exposure to waterlogging and drought stress + 7 d of recovery. Means followed with the same letters within columns are not significantly different based on the LSD at $p \leq 0.05$. **Significantly different in $p \leq 0.01$; *significantly different at $p \leq 0.05$; ^{ns}: not significantly different.

Cultivars	NoL	TLA	SLA	SLW
	Waterlogging/Control			
Srikandi	0.36 ± 0.14^{b}	0.60 ± 0.17^{b}	0.64 ± 0.06^{c}	1.56 ± 0.14^{ab}
Laris	0.56 ± 0.07^{a}	0.90 ± 0.08^{a}	0.55 ± 0.07^{c}	1.82 ± 0.21^{a}
Ferosa	0.37 ± 0.01^{b}	0.40 ± 0.21^{b}	0.70 ± 0.10^{ab}	1.44 ± 0.24^{b}
Andalas	0.11 ± 0.06^{c}	0.04 ± 0.01^{c}	0.67 ± 0.06^{abc}	1.50 ± 0.12^{ab}
Kawat	0.38 ± 0.08^{b}	1.15 ± 0.09^{a}	0.79 ± 0.05^{a}	1.26 ± 0.05^{b}
Romario	0.39 ± 0.02^{b}	0.45 ± 0.21^{b}	0.73 ± 0.13^{ab}	1.39 ± 0.25^{b}
$LSD_{0.05}$	0.14^{**}	0.26^{**}	0.15^{**}	0.32^{**}
	Drought/Control			
Srikandi	0.55 ± 0.10	0.48 ± 0.12^{bc}	1.36 ± 0.02^{a}	0.74 ± 0.01^{b}
Laris	0.69 ± 0.26	0.83 ± 0.47^{ab}	1.00 ± 0.01^{b}	1.00 ± 0.01^{a}
Ferosa	0.93 ± 0.53	0.29 ± 0.18^{bc}	1.15 ± 0.13^{ab}	0.87 ± 0.09^{ab}
Andalas	0.24 ± 0.08	0.18 ± 0.14^{c}	1.16 ± 0.29^{ab}	0.90 ± 0.26^{ab}
Kawat	0.98 ± 0.10	1.09 ± 0.10^{a}	1.14 ± 0.10^{ab}	0.88 ± 0.06^{ab}
Romario	0.95 ± 0.64	0.63 ± 0.50^{abc}	1.37 ± 0.26^{a}	0.75 ± 0.14^{b}
$LSD_{0.05}$	ns	0.53^{*}	0.30^{**}	0.22^{**}

Table 8. Water stress ratio of leaf relative water content (LRWC) and leaf chlorophyll content (SPAD) of six cultivars of red chili peppers after 8 d of waterlogging and drought stress + 7 d recovery time. Means followed with the same letters within columns are not significantly different based on the LSD at $p \leq 0.05$. **Significantly different at $p \leq 0.01$; ^{ns}: not significantly different.

Cultivars	Waterlogging/Control		Drought/Control	
	LRWC	SPAD	LRWC	SPAD
Srikandi	0.84 ± 0.07^{ab}	1.03 ± 0.05^{a}	1.02 ± 0.02^{ab}	0.93 ± 0.07
Laris	0.84 ± 0.10^{ab}	1.00 ± 0.02^{a}	1.03 ± 0.03^{ab}	0.97 ± 0.07
Ferosa	1.03 ± 0.20^{a}	0.92 ± 0.20^{ab}	1.17 ± 0.27^{a}	0.93 ± 0.14
Andalas	0.85 ± 0.03^{ab}	0.76 ± 0.09^{b}	0.77 ± 0.43^{b}	0.93 ± 0.10
Kawat	0.87 ± 0.02^{ab}	1.03 ± 0.12^{a}	0.98 ± 0.03^{ab}	0.92 ± 0.09
Romario	0.78 ± 0.19^{b}	0.87 ± 0.06^{ab}	0.95 ± 0.09^{ab}	0.99 ± 0.22
$LSD_{0.05}$	0.22^{**}	0.19^{**}	0.38^{**}	ns

Increased ethylene and CO_2 concentrations in roots trapped in the rhizosphere, due to the slow diffusion of these molecules in water, inhibited root elongation (Munir et al., 2019). However, root elongation as a mechanism to search for more water is more likely to be developed by plants under drought conditions than shoot elongation. Under drought stress, biomass is stored in the roots and the direction of growth shifts from aboveground to underground. This indicates plants allocate more biomass to roots to induce deeper root architecture (Ahmad et al., 2016; Avila et al., 2020). A decrease in the SRR ratio is associated with an increase in the proportion of assimilate that is redirected to root elongation (Sharp and Davies, 1989). It is also linked to the adaptation of cellular osmotic potential (Pilon et al., 2019). Meanwhile, plants increased stomatal regulation to maintain internal water availability, which led to a decrease in stomatal index and leaf size to limit water loss (Lestari et al., 2023).

All red chili pepper cultivars decreased the number of leaves and leaf area expansion in response to waterlogging and drought (Figure 3). The decrease in the number of leaves and leaf area expansion during stress has been identified as a protective response of plants to maintain water loss by maintaining the stability and extensibility of cell membranes (Anjum et al., 2011). This is consistent with the results of higher specific leaf weight observed in this study (Table 4). On the other hand, high values of SLA represent a lower metabolic cost to maintain 1 cm^2 of leaf area and, consequently, higher productivity. Our results showed that SLA was higher in drought stress than in waterlogging, and there was nonsignificant difference between control and drought treatments. However, it occurred after 8 d of recovery (Table 4). The duration and level of stress determine the ability of a plant to recover. Recovery occurs when plants are able to improve stomatal aperture and stomatal pore size (Zhu et al., 2019). Goto et al. (2021) also reported that stress conditions led to a decrease in stomatal conductance and leaf water potential in chili pepper.

Related studies have also revealed a decrease in photosynthetic activity and LRWC under water stress conditions (Toscano et al., 2016; Yang et al., 2023). The LRWC is an appropriate estimate of plant water status in terms of cellular hydration under the possible effects of both leaf water potential and osmotic adjustment. In this study, SPAD and LRWC, as physiological parameters, were affected only after stress exposure and returned to a similar state compared to the control after the recovery period.

Sahitya et al. (2019) reported that the drought-tolerant chili pepper was able to conserve water to limit the following negative effects. Plants also have adaptation mechanisms by accumulating biochemical metabolites at higher levels than normal conditions, mainly proline and total phenolic compounds (Pacheco et al., 2021; Wassie et al., 2023). Under waterlogging, biochemical characteristics such as ethylene and proline increase rapidly as an early flood signal (Sasidharan and Voesenek, 2015). Gas exchange, stomatal conductance, and CO_2 assimilation are disrupted under hypoxic or anoxic conditions. Reactive oxygen species (ROS) production is also increased, causing oxidative damage in plant cells (Pandey et al., 2021). However, despite their destructive activity, ROS molecules acted as second messengers at low concentrations. The ROS served as signaling molecules in response to various stresses, whereas at high concentrations, ROS caused exacerbating damage to cellular components (Sharma et al., 2012). 'Laris' and 'Kawat' in this study evolved this mechanism as an adaptive strategy to survive not only under drought stress, but also under waterlogging stress (Table 5).

Based on the results of this study, morphological and physiological parameters were used as supporting parameters for the screening process to identify the tolerant and susceptible cultivars of red chili pepper under water stress conditions including waterlogging and drought. According to W/C and D/C (Tables 6 and 7), 'Laris' and 'Kawat' were categorized as resistant and tolerant, respectively, under waterlogging and drought stress conditions. This was identified by the highest value of W/C ratio and D/C ratio on the parameters of total dry weight, root dry weight, shoot dry weight, number of leaves and total leaf area. Meanwhile, 'Ferosa' showed resistance under drought stress but was found to be susceptible to waterlogging. Furthermore, 'Srikandi', 'Andalas' and 'Romario' were categorized as susceptible in both water-stressed conditions. In this study, the tolerant and susceptible cultivars were evaluated by examining the phenotypic characters as an initial screening process.

Lestari et al. (2023) reported that genetic factors had a greater influence on morpho-physiological traits under different environmental conditions. Genetic approaches are also needed to support early indication within screening research, such as the use of molecular markers as a tool to estimate the genetic diversity of plant species in the genomic era (Rini and Nuraisyah, 2021). However, screening for natural genetic variation in drought and waterlogging tolerance-related traits, including a combination of agronomic and physiological traits (Mohammadi and Golkari, 2022), root system architecture, water and N fixation efficiency, and yield performance indices, has proven valuable in identifying the best resources for genetic studies (Valliyodan et al., 2017).

CONCLUSIONS

The growth and morpho-physiological responses of chili pepper to the stresses of drought and waterlogging were different in each cultivar. Waterlogging and drought are two types of abiotic stress with opposite characteristics. Root organs are one of the important plant organs that respond very differently to these two stresses. Root weight was higher under drought stress than under waterlogging stress, while leaf specific weight increased under both stresses. Leaf chlorophyll content (SPAD) and leaf relative water content (LRWC) also decreased when exposed to both waterlogging and drought. The recovery time given after the application of both stresses was able to improve SPAD and LRWC of chili plants, even they could not recover completely, but did not have a significant effect on the recovery of plant dry weight conditions compared to control conditions. In this study, 'Laris' and 'Kawat' are categorized as resistant cultivars in waterlogging and drought which potentially could be cultivated in tropical wetlands during the transitional period (dry to rainy), while 'Ferosa' is a drought-resistant cultivar but susceptible to waterlogging.

Author contribution

Conceptualization: E.S., J-I.S., B.L., D.S.R. Methodology: E.S., L.I.W., J-I.S. Software: E.S. Validation: J-I.S. B.L. Formal analysis: E.S., L.I.W. Resources: J-I.S., S.Y. Data curation: E.S., J-I.S., D.S.R. Writing-original draft: E.S. Writing-review & editing: E.S., D.S.R., L.I.W, S.Y. Visualization: E.S. Supervision: J-I.S., B.L., S.Y. Project administration: E.S., D.S.R. Funding acquisition: E.S., J-I.S., D.S.R. All co-authors reviewed the final version and approved the manuscript before submission.

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