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Morpho-physiological responses of chili peppers (*Capsicum annuum*) to short-term exposure of water-saturated rhizosphere

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Abstract

Chili pepper is frequently grown by local farmers at riparian wetland during dry season in Indonesia. However, during the last decade, unpredictable distribution and intensity of rainfall have increasingly threatened chili pepper production at the wetlands due to untimely water-saturated rhizosphere (WSR) occurrences. WSR is a condition when all pores within root zone were filled with water. This condition can be simulated by adding water into growing substrate until a thin layer of water was visible above substrate surface. Two Indonesian varieties (Laris and Romario) and one Japanese variety (Takanotsume) were used in this study. Aim of this study was to evaluate morpho-physiological effects of short-term (4 days) WSR exposure in chili pepper. Results of this study revealed that roots suffered more than aerial organs as indicated by the increase of shoot/root ratio from 4.56 at pre-exposure to 7.03 at end of the exposure. Total leaf area significantly reduced since larger older leaves were replaced by newly developed smaller leaves. Relative water content (RWC) in all organs was decreased, but did not reach a detrimental level. Leaf RWC was decreased from 83.6% at pre-exposure to 77.8% after the exposure; however, leaf RWC was able to rebound to 81.5% after 7 days of recovery. Photosynthetic and transpiration rates sharply decreased, associated with decrease in stomatal conductance during WSR exposure. Chlorophyll fluorescence also sharply declined. Gas exchange parameters did not significantly recover after 7 days of recovery in all varieties. Meanwhile, SPAD values were not affected by WSR exposure.

Keywords: abiotic stress; chlorophyll fluorescence; leaf size; leaf water content; net photosynthesis; oxygen deficiency; root damage; SPAD value; stomatal closure; transpiration.

Abbreviations: Fv/Fm_ratio of measured fluorescence to maximum fluorescence; NoL_number of leaves; RWC_relative water content; S/R ratio_dry weight ratio of shoot to root; TDW_total dry weight; TLA_total leaf area; WSR_ water-saturated rhizosphere.

Introduction

About 21 percent of terrestrial areas in Indonesia are wetlands, including non-tidal riparian wetland. Most area in Indonesia categorized as tropical rain forest climate with high annual rainfall. Flooding, waterlogging, and high soil water table are prominent threats to agriculture at the wetland ecosystem. Annual distribution of rainfall has been much harder to predict during the last few decades and more frequent harvest failures have been reported due to unexpected water-related factors, including water-saturated within rhizosphere of cultivated crops. It is almost impossible to drain excess water at a flat landscape in typical wetlands in Indonesia.

Water-saturated rhizosphere (WSR) is a condition when soil/substrate pores surround plant roots are completely filled with water. Under unsaturated condition, the rhizosphere had higher water content than bulk soil due to effect of mucilage at the root–soil interface. (Carminati et al., 2010; 2011). However, there was no difference in water content between the rhizosphere and the bulk soil under WSR condition. The problem associated with WSR was oxygen deficiency. This hypoxic condition reduced respiration and resulted in a severe energy crisis for crop metabolism (Yamauchi et al., 2018); as consequences, it inhibited growth and reduced yield in most of terrestrial crops (Herzog et al., 2016).

At present, cropping intensity at riparian wetlands in Indonesia is very low. Most local farmers only grow one rice crop annually at end of rainy season, after flood water has subsided (Lakitan et al., 2018a; 2019a). Increasing cropping intensity at riparian wetlands is very challenging. While affordable technologies have been developed for crop cultivation during flooding period (rainy season), including floating culture system (Lakitan et al., 2019b; 2019c; Siaga et al., 2018; 2019; Ramadhani et al., 2018); crop cultivation after rice harvesting at riparian wetlands still need much more efforts to be further explored and developed. Some researchers have conducted studies for overcoming those agronomic constraints, including gradual soil drying due to prolonged dry season (Widuri et al., 2017; 2018) or for anticipating probable early rainy season which causing shallow water table (Susilawati and Lakitan, 2019; Lakitan et al., 2018b; Meihana et al., 2017) or flooding (Lakitan et al., 2019c; 2018c).

The aim of this study was to enrich our understanding on physiological responses of chili pepper to water-saturated rhizosphere and relating this acquired knowledge to our previous findings in agronomic researches. Chili pepper was used since this crop was frequently grown after rice harvesting at riparian wetlands in Indonesia due to its economic value. Combination of agronomic and physiological knowledge could be used in developing appropriate practices for minimizing risks associated with occurrence of the WSR in chili pepper cultivated at riparian wetlands.

Results

Growth dynamic during and after exposure to water-saturated rhizosphere

Growth of all varieties studied was affected by WSR. Their growth decreased slowly on first and second day after WSR exposure, but afterward, growth sharply decreased on third and fourth day after WSR exposure. Visual response of chili pepper was shown as wilted and curled leaves. During recovery time, chili pepper resumed their growth by aborting the larger older leaves and developing smaller new leaves.

After being allowed to recover for 7 days, dry weights of the WSR-exposed plants were halted to less than half of those in untreated control plants in all varieties studied. Moreover, this cutbacks were more pronounced in roots than shoot, as indicated by increases in S/R ratio. Amongst the three varieties, S/R ratio of Laris was found to be significantly higher than that of Takanotsume, indicating that the Takanotsume exhibit relatively higher portion of its dry weight allocated to root compared to Laris did (Table 1). However, based on total dry weight, there was no significant difference in shoot and root dry weight accumulation after the short-term exposure amongst the three chili pepper varieties.

Relative water content (RWC) of leaf and stem significantly declined due to WSR exposure but that of roots did not. Interestingly, chili pepper was able to recuperate its leaf RWC only after 7 days. Difference in RWC among varieties studied was only observed in stem RWC between Romario and Takanotsume (Table 1).

There were differences in total dry weight amongst varieties studied after WSR exposure, also after 7 days of recovery. Laris exhibited less severely affected by WSR exposure, compared to Romario and Takanotsume varieties. After 7 days of recovery, Laris and Romario performed better than Takanotsume based on dry weight accumulation. However, there were negligible differences in whole-plant RWC amongst varieties studied after 4 days of exposure to WSR and after 7 days of recovery from the WSR treatment (Fig 1).

In normal and healthy plants, increase in number of leaves (NoL) is proportionally associated with increase in total leaf area (TLA). This association was observed in chili pepper plants unexposed to WSR. In this study, increase in NoL did not significantly follow by increase in TLA if the chili plants were exposed to WSR for 4 days. This phenomenon justified that the WSR-exposed plants produced smaller new leaves. The new leaves were developed for replacing the fallen older leaves with larger surface are. Correlation coefficients between NoL and TLA were 0.86 in WSR-exposed and 0.06 in control unexposed plants, respectively. This finding indicated that under stressful WSR condition, leaf formation in chili pepper was not affected but expansion of leaf blade was significantly retarded (Fig 2).

Non-linear positive correlation between total leaf area (TLA) and total dry weight (TDW) was observed in control chili peppers, unexposed to WSR. In this case, during early development, small young leaf increased its weight or visually became thicker small leaf; then, rapid blade expansion phase to near maximum size; and finally, followed by accumulation of dry weight after final size had been established (Fig 2).

Effects of water-saturated rhizosphere on photo-related parameters

All of NoL, TLA, SPAD, and chlorophyll fluorescence (Fv/Fm) significantly decreased after exposure to 4-day WSR and after being allowed to recover for 7 days, except for Fv/Fm after recovery. During 4-day WSR exposure and 7-day recovery period, NoL slightly increased in Laris, was relatively stagnant in Romario, and slightly decreased in Takanotsume. Meanwhile, TLA consistently decreased in all three varieties. These trends indicated that for each fallen larger old leaf, the chili pepper produced more than one new but smaller leaves in Laris, produced smaller leaves at about similar number with fallen leaves in Romario variety, and produced smaller or similar size leaves at less than number of fallen larger old leaves in Takanotsume (Fig 3).

Takanotsume naturally exhibited lower SPAD value and the value further decreased if this variety was exposed to WSR. In contrast, SPAD values increased in Laris and Romario if the plants exposed to WSR. SPAD value has been commonly used for non-destructive estimation of leaf chlorophyll content. Meanwhile, chlorophyll fluorescence has been known to be associated with photosynthetic activity in the PS II. In this study, chlorophyll fluorescence significantly decreased in all chili pepper varieties after 4 days exposure to WSR and slightly increased during recovery period. However, Laris bounced back its chlorophyll fluorescence value to near pre-WSR level (Fig 3).

Photosynthesis rate significantly dropped in all chili pepper varieties within short period of WSR exposure. Declining pattern of photosynthesis was similar to that of stomatal conductance and transpiration rate. This implied that both photosynthesis and transpiration rates were dominantly regulated by stomatal conductance. In all gas exchange parameters measured, Laris performed significantly better than the other two varieties (Fig 4).

At pre-exposure to WSR stomatal conductance varied between 0.15 to 0.35 µmol H_2O m^{-2} s^{-1} and photosynthetic rates varied from 12.25 to 22.25 µmol CO_2 m^{-2} s^{-1}. After 4 days of WSR exposure, stomatal conductance sharply dropped to less than 0.10 µmol H_2O m^{-2} s^{-1} and photosynthetic rates may be completely halted or sharply dropped to less than 10 µmol CO_2 m^{-2} s^{-1}. During a week of

Table 1. Dry weight and relative water content in chili peppers exposed to water-saturated rhizosphere.

Treatments	Dry Weight (g)			S/R Ratio	Relative Water Content (%)			
	Shoot	Root	Total		Leaves	Stem	Root	Total
Time of measurement (T)								
Before WSR	0.822 c[z]	0.183 c	1.006 c	4.561 b	83.61 a	84.89 a	93.87 a	87.85 a
After WSR	1.653 b	0.262 b	1.840 b	7.028 a	77.77 b	81.78 b	91.16 b	83.43 b
Recovery	2.360 a	0.387 a	2.747 a	6.785 a	81.52 ab	82.01 b	87.74 c	83.28 b
Water-saturated Rhizosphere (WSR)								
Control	2.220 a	0.402 a	2.622 a	5.362 b	84.37 a	85.08 a	91.81 a	86.94 a
WSR	1.004 b	0.153 b	1.107 b	6.888 a	77.57 b	80.70 b	90.04 a	82.77 b
Varieties (V)								
Laris	1.792 a	0.284 a	2.048 a	6.757 a	78.90 a	82.80 ab	91.23 a	84.21 b
Romario	1.586 a	0.278 a	1.839 a	6.101 ab	81.36 a	81.57 b	91.09 a	84.50 ab
Takanotsume	1.457 a	0.271 a	1.705 a	5.516 b	82.65 a	84.31 a	90.46 a	85.85 a

[z]Means followed by the same letters within columns of each treatment and measured trait are not significantly different based on the LSD at $P \leq 0.05$.

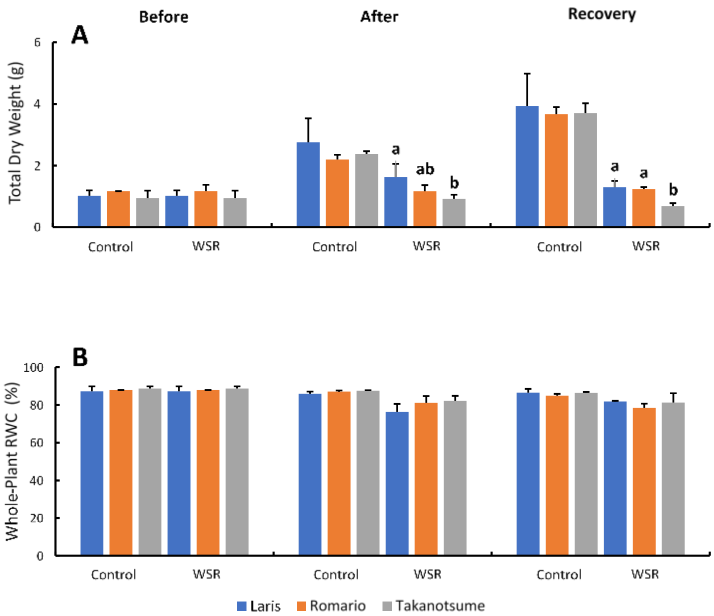

Fig 1. Impact of water-saturated rhizosphere on total dry weight and whole-plant relative water content amongst chili pepper varieties. Different letters above bars indicated significant differences among varieties for WSR-exposed plants. No letter indicated the differences among varieties were not significant based on the LSD at $P \leq 0.05$.

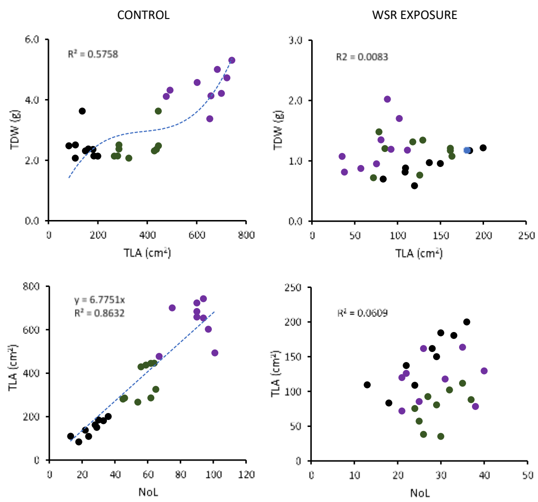

Fig 2. Correlations between number of leaves (NoL), total leaf area (TLA), and total dry weight (TDW) in control and WSR-exposed chili peppers.

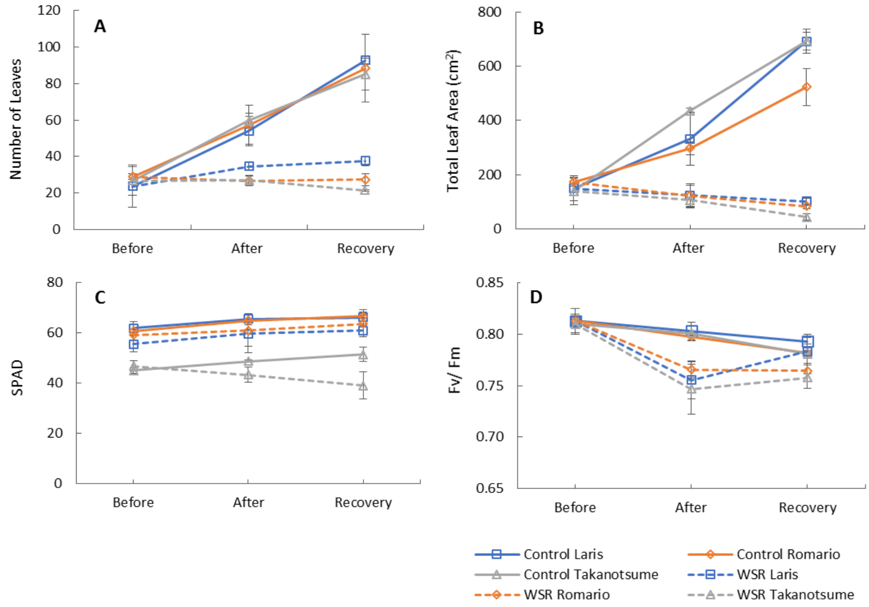

Fig 3. Number of leaves, total leaf area, SPAD value, and chlorophyll fluorescence (Fv/Fm) in three chili pepper varieties during exposure and recovery from water saturated rhizosphere treatment.

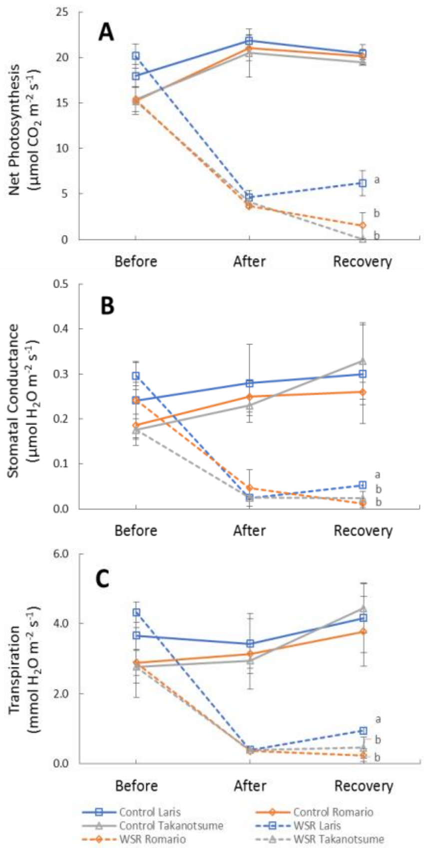

Fig 4. Photosynthesis rate (A), stomatal conductance (B), and transpiration rate (C) in three chili pepper varieties exposed to water-saturated rhizosphere (broken line) and unexposed control plants (solid line). Different letters at end of each line indicated significant differences among varieties. No letter indicated the differences among varieties were not significant based on the LSD at $P \leq 0.05$.

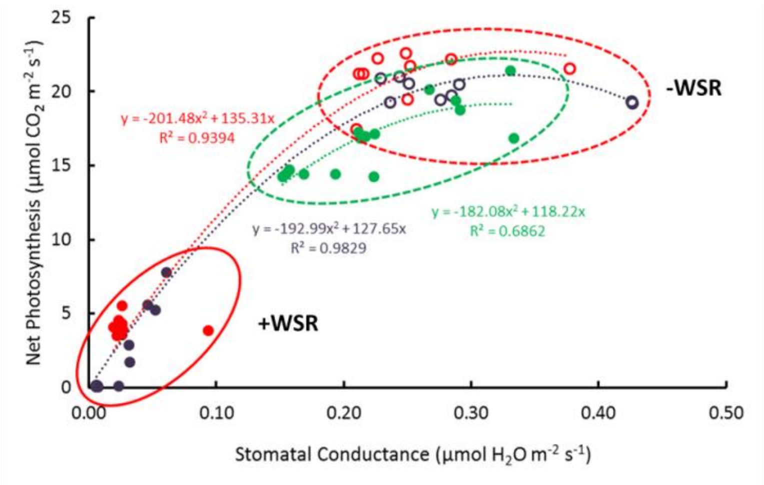

Fig 5. Relationship between stomatal closure and declining photosynthesis rate in chili pepper exposed to water-saturated rhizosphere at pre-exposure (green cluster), during exposure (solid line red cluster), and at post-exposure (broken line red cluster).

recovery, photosynthesis and stomatal conductance have not been significantly recovered; in the same period, those in control plants have noticeably increased (Fig 5).

Discussion

Effects on morphology and water status

The WSR triggered rapid depletion of available oxygen and restricted aerobic metabolism in roots (Rudolph-Mohr et al., 2017; Hossain and Uddin, 2011). Oxygen supply to roots is restricted as soon as air in soil pores was replaced by water. Oxygen diffusion is much slower in water than in the air (Lenzewski et al., 2018). Chili pepper is suspected does not have a specific anatomical feature and metabolisms to overcome oxygen deficit; therefore, its roots are vulnerable to this oxygen-deficient condition.

Munir et al. (2018) reported that inhibition of root extension was associated with increase of ethylene in roots and high CO_2 concentration entrapped within rhizosphere due to slow diffusion of these molecules in water; however, the most damaging effect, even causing death of root tips, was due to O_2 deficiency. Short-term or partial exposure to WSR did not set off permanent effect to roots in some plants, as Lakitan et al. (2018b) reported that roots were able to regrow after water-saturated condition gradually diminished.

In this study, inhibition of root growth in chili pepper exposed to WSR was indicated by significant increase of the shoot/root ratio. However, the ratio eventually decreased (as indicator of root regrowth) after 7 days of recovery, but did not reach the pre-exposure level (Table 1). The chili pepper varieties used in this study clearly required longer time (more than 7 days) to fully recover from short-term exposure to WSR.

Damaged roots decrease water uptake capacity of respective plants. Moreover, the lower root water uptake capacity reduces water supply to aerial organs. Low water supply to leaf might also be paired with continuous water loss via transpiration. These two factors decreased water content in aerial organs, especially leaf, as observed in this study (Table 1).

Leaf expansion rate was directly associated with leaf water content in chili pepper (Widuri et al., 2017). High water content increased internal hydraulic pressure which played direct role in cell enlargement and, in turn, also increased tissue volume and organ size (Turc et al., 2016). In this study, chili pepper plants produced smaller new leaves during WSR exposure and this trend was extended to the first seven days of recovery period. Consequently, it decreased TLA. Non-linier positive correlation between TLA and TDW indicated that specific leaf weight was not constant during leaf development (Fig 2).

Impacts on leaf gas exchanges

Smaller leaf might be perceived as an unfortunate consequence or an active survival strategy in plants exposed to abiotic stress, such as due to WSR. Smaller individual leaf or lower total leaf area per plant leads to less light capturing surfaces for photosynthesis. Light energy captured in photosynthesis is mainly regulated by total of leaf surface area, canopy architecture, and its chlorophyll density. Meanwhile, less total leaf surface area leads to lower transpiration rate; therefore, reducing water loss.

Higher photosynthetic rate and lower transpiration rate are preferred for an efficient crop production. However, CO_2 uptake for photosynthesis and water loss due to transpiration occurs through stomata; therefore, both photosynthesis and transpiration are directly affected by changes of stomatal conductance.

For compensating smaller leaf area, some plant has ability to increase their leaf chlorophyll density. Leaf chlorophyll content has been commonly estimated base on SPAD value. This indirect and non-destructive approach has been proven to be accurate (Jiang et al., 2017; Ling et al., 2011; Coste et al., 2010; Mielke et al., 2010) and reliable (Agarwal and Gupta, 2018; Costa et al., 2018; Lin et al., 2018). In this study, SPAD value increased in Laris and Romario after being exposed to WSR and further increased during recovery period; but in contrast, SPAD value in Takanotsume decreased (Fig 3).

Chlorophyll inflorescence (Fv/Fm) value in all chili pepper varieties decreased during WSR exposure. However, at 7 days after recovery, the Fv/Fm in Laris variety rebounded to a comparable level to that of unexposed control plants (Fig 3). Many studies have indicated that Fv/Fm value correlated with photosynthetic rate (Murchie and Lawson, 2013; Dias and Brüggemann, 2010). The Fv/Fm in healthy plants is around 0.81 to 0.83, indicating maximum quantum efficiency of photosynthesis in most of cultivated plants (Robredo et al., 2010). In this study, Fv/Fm decreased to around 0.75 after 4 days exposure to WSR (Fig 3). The decline in Fv/Fm value indicated that WSR-exposed plant was experiencing abiotic stresses. Measurements using gas exchange system, confirming that net photosynthetic rate sharply declined after 4-day WSR exposure in all chili pepper varieties studied. This finding was in line with decline of chlorophyll florescence. However, during recovery period, only Laris showed slight recovery. The other two varieties (Romario and Takanotsume) had not indicated any sign of recovery (Fig 4). Decrease of net photosynthetic rate, beside due to decrease in quantum efficiency, also associated with stomatal closure (decrease in stomatal conductance) which limited CO_2 influx to substomatal cavity. Decrease in net photosynthetic rate has been observed in most of plants under any abiotic stresses (Cavalcante et al., 2018;Fadoul et al., 2018; Gururani et al., 2015). Decrease in stomatal conductance was not only decrease photosynthetic rate but also decrease transpiration rate (Fig 4). Impact of these two decreases was contradictory. While decrease in photosynthetic rate limits carbon fixation for plant growth; in contrary, decrease in transpiration rate helps conserving water content in plant organs, especially leaves. Ability of plant to reduce water loss during abiotic stress helps the plant to recover during post-stress period. Correlation between photosynthetic rate, transpiration rate, and stomatal conductance were recognized in this study (Fig 5). The challenge in the relationship among these parameters was to ensure adequate CO_2 uptake for carbon fixation in chloroplasts and at the same time to maintain optimal leaf temperature via evaporative cooling and to manage water loss for ensuring a suitable level of whole plant water status. Both guard cells of stomata and chloroplast in mesophyll cells responded to external and internal signals and there was a strong linkage between stomatal dynamics and mesophyll photosynthesis (Miner et al., 2017). If water content of guard cells decreases, the guard cells loss their turgidity and stomatal closure occurs, causing decrease in stomatal conductance. At some point, its starts to limit CO_2 uptake and H_2O outflow, causing both photosynthetic and transpiration rates to decrease. Restricted transpiration process increases leaf temperature; in turn, higher leaf temperature interferes plant metabolisms. Meanwhile, further increase of water loss via transpiration reduces water content in leaf and whole plant. These are what generally occur in plant under abiotic stresses. Exposure chili pepper to WSR clearly exhibits these physiological symptoms.

Materials and Methods

Plant materials and seedling preparation

Two varieties of Indonesian and one variety of Japanese chili peppers were used in this study. Laris and Romario are commercial chili pepper varieties in Indonesia, as Takanotsume variety is in Japan. Prior to sowing, all seeds were hydro-primed for six hours in tap water and then uniformly spread in between layers of wet clothes for three days for inducing seeds to germinate. Germinated seeds were selected and sown in seedling trays filled with soil-compost mix. Homogenous seedlings at age of 8 weeks were transplanted into containers filled with similar soil-compost mix as used in seedling preparation. Dimension of the container was 90 cm length x 60 cm width x 20 cm depth. WSR treatment was simulated by adding water into growing substrate up until a thin layer of water was established above substrate surface. Seedlings were grown in cool spring of T^o_{max} < 20ºC at the Tropical Crop Science Laboratory, Kagoshima University in March but gradually warm up during later growth stage until August 2018.

Experimental design and procedures

Strip Plot Design was employed in this experiment. Two horizontal strips were assigned for seedlings unexposed and exposed to WSR for 4 days. Three vertical strips were assigned for the three selected chilli pepper varieties. Each treatment combination (WSR x Variety) was replicated three times. The WSR exposure was started at 7 days after transplanting and terminated after 4 days of exposure; then, excess water in all WST treatments was freely drained as the chili pepper plants were allowed to recover. Measurements were taken prior to, during, and after 7 days of recovery from WSR exposure.

Parameters measured and instruments used

Measurements focused on morphological and physiological characters of chili peppers treated with WSR exposure. Untreated chili peppers were used as control plants. Parameters measured were clustered into: (1) dry weights of roots, shoot and total biomass; (2) relative water contents in roots, stem, leaf, and averaged whole-plant; (3) leaf characteristics including number of leaves (NoL) per plant, total leaf area (TLA) per plant, leaf SPAD value, and leaf chlorophyll fluorescence (Fv/Fm); and (4) photosynthetic parameters including net photosynthesis rate, stomatal conductance, and transpiration rate.

NoL and TLA were measured using automation area meter (Hayashi Denko AAM-9), SPAD measured using chlorophyll meter (Konica Minolta SPAD-502Plus), chlorophyll fluorescence using flourometer (AquaPen-C AP-C 100), and photosynthetic parameters using portable photosynthesis system (Licor Li-6400).

Statistical analysis

The analysis of variance (ANOVA) was done using the Statistical Analysis System (SAS) University Edition based on the strip-plot design. For significant treatments on any measured parameters, differences among mean values were tested using the Least Significant Differences (LSD) test at $p \leq 0.05$.

Conclusion

Short-term (4 days) water-saturated rhizosphere significantly affected some morphological and physiological traits in chili pepper. Roots suffered more than aerial organs as indicated by increase in the shoot/root ratio. Total leaf area was significantly reduced as fallen larger older leaves during and after WSR exposure was replaced by newly developed smaller leaves. Lower total leaf area directly decreased light capturing surface for photosynthesis but conserving leaf water content by limiting transpiration. However, relative water content in all organs still decreased; even though, they were not reach detrimental level to the plants. Both net photosynthetic and transpiration rates sharply decreased associated with decrease in stomatal conductance during WSR exposure and did not significantly recovered after seven days of the WSR exposure was terminated. In line with net photosynthetic rate, chlorophyll fluorescence also sharply declined. Meanwhile, SPAD values were not affected by WSR exposure, except for Takanotsume. Among three chili peppers studied, Laris performed better than the other two varieties under WSR condition.

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References

Agarwal A, Gupta SD (2018) Assessment of spinach seedling health status and chlorophyll content by multivariate data analysis and multiple linear regression of leaf image features. Comput Electron Agr. 152: 281-289.

Carminati A, Moradi AB, Vetterlein D, Vontobel P, Lehmann E, Weller U, Vogel H-J, Oswald SE (2010) Dynamics of soil water content in the rhizosphere. Plant and Soil. 332(1-2): 163-176.

Carminati A, Schneider CL, Moradi AB, Zarebanadkouki M, Vetterlein D, Vogel HJ, Hildebrandt A, Weller U, Schüler L, Oswald SE (2011) How the rhizosphere may favor water availability to roots. Vadose Zone J. 10(3): 988-998

Cavalcante PGS, dos Santos CM, Filho HCLW, Avelino JRL, Endres L (2018) Morpho-physiological adaptation of *Jatropha curcas* L. to salinity stress. Aust J Crop Sci. 12(4): 563-571.

Costa FS, de Lima AS, Magalhães ID, Chaves LHG, Guerra HOC (2018) Fruit production and SPAD index of pepper (*Capsicum annuum* L.) under nitrogen fertilizer doses. Aust J Crop Sci. 12(1): 11-15.

Coste S, Baraloto C, Leroy C, Marcon É, Renaud A, Richardson AD, Roggy JC, Schimann H, Uddling J, Hérault B (2010) Assessing foliar chlorophyll contents with the SPAD-502 chlorophyll meter: a calibration test with thirteen tree species of tropical rainforest in French Guiana. Ann Forest Sci. 67(6): 607-607.

Dias MC, Brüggemann W (2010) Limitations of photosynthesis in *Phaseolus vulgaris* under drought stress: gas exchange, chlorophyll fluorescence and Calvin cycle enzymes. Photosynthetica. 48(1): 96-102.

Fadoul HE, El Siddig MA, Abdalla AWH, El Hussein AA (2018) Physiological and proteomic analysis of two contrasting Sorghum bicolor genotypes in response to drought stress. Aust J Crop Sci. 12(9): 1543-1551.

Gururani MA, Venkatesh J, Tran LSP (2015) Regulation of photosynthesis during abiotic stress-induced photoinhibition. Mol Plant. 8(9): 1304-1320.

Herzog M, Striker GG, Colmer TD, Pedersen O (2016). Mechanisms of waterlogging tolerance in wheat–a review of root and shoot physiology. Plant Cell Environ. 39(5): 1068-1086.

Hossain MA, Uddin SN (2011) Mechanisms of waterlogging tolerance in wheat: Morphological and metabolic adaptations under hypoxia or anoxia. Aust J Crop Sci. 5(9): 1094-1101.

Jiang C, Johkan M, Hohjo M, Tsukagoshi S, Maruo T (2017) A correlation analysis on chlorophyll content and SPAD value in tomato leaves. HortResearch. 71: 37-42.

Lakitan B, Hadi B, Herlinda S, Siaga E, Widuri LI, Kartika K, Lindiana L, Yunindyawati Y, Meihana M (2018a) Recognizing farmers' practices and constraints for intensifying rice production at Riparian Wetlands in Indonesia. NJAS-Wageningen J Life Sci. 85:10-20.

Lakitan B, Kadir S, Wijaya A (2018b) Tolerance of common bean (*Phaseolus vulgaris* L.) to different durations of simulated shallow water table condition. Aust J Crop Sci. 12(4): 661-668.

Lakitan B, Iwanaga H, Kartika K, Kriswantoro H, Sakagami JI (2018c) Adaptability to varying water levels and responsiveness to NPK fertilizer in yellow velvetleaf plant (*Limnocharis flava*) Aust J Crop Sci. 12(11): 1757-1764.

Lakitan B, Lindiana L, Widuri LI, Kartika K, Siaga E, Meihana M, Wijaya A (2019a) Inclusive and ecologically-sound food crop cultivation at tropical non-tidal wetlands in Indonesia. Agrivita J Agric Sci. 41(1): 23-31.

Lakitan B, Siaga E, Kartika K, Yunindyawati Y (2019b) Use of *Scleria poaeformis* as biomaterial in etno-agricultural practice at riparian wetlands in Indonesia. Bulg J Agric Sci. 25(4): 320-325.

Lakitan B, Juliani F, Sodikin E (2019c) Ability of *Limnocharis flava* to escape from episodic submersion by rapid elongation of its leaf petiole. Bulg J Agric Sci. 25(5): 314–319.

Lenzewski N, Mueller P, Meier RJ, Liebsch G, Jensen K, Koop-Jakobsen K (2018) Dynamics of oxygen and carbon dioxide in rhizospheres of *Lobelia dortmanna*–a planar optode study of belowground gas exchange between plants and sediment. New Phytol. 218(1): 131-141.

Ling Q, Huang W, Jarvis P (2011) Use of a SPAD-502 meter to measure leaf chlorophyll concentration in *Arabidopsis thaliana*. Photosynth Res. 107(2): 209-214.

Lin PC, Tsai YC, Hsu SK, Ou JH, Liao CT, Tung CW (2018) Identification of natural variants affecting chlorophyll content dynamics during rice seedling development. Plant Breeding. 137(3): 355-363.

Meihana M, Lakitan B, Susilawati S, Harun MU, Widuri LI, Kartika K, Siaga E, Kriswantoro H (2017) Steady shallow water table did not decrease leaf expansion rate, specific leaf weight, and specific leaf water content in tomato plants. Aust J Crop Sci. 11(12): 1635-1641.

Mielke MS, Schaffer B, Li C (2010) Use of a SPAD meter to estimate chlorophyll content in *Eugenia uniflora* L. leaves as affected by contrasting light environments and soil flooding. Photosynthetica. 48(3): 332-338.

Miner GL, Bauerle WL, Baldocchi DD (2017) Estimating the sensitivity of stomatal conductance to photosynthesis: a review. Plant Cell Environ. 40(7): 1214-1238.

Munir R, Konnerup D, Khan HA, Siddique KH, Colmer TD (2018) Sensitivity of chickpea and faba bean to root-zone hypoxia, elevated ethylene and carbon dioxide. Plant Cell Environ. Wiley Online Library, https://doi.org/10.1111/pce.13173

Murchie EH, Lawson T (2013) Chlorophyll fluorescence analysis: a guide to good practice and understanding some new applications. J Exp Bot. 64(13): 3983-3998.

Ramadhani F, Lakitan B, Hasmeda M (2018) Decaying *Utricularia*-biomass versus soil-based substrate for production of high quality pre-transplanted rice seedlings using floating seedbeds. Aust J Crop Sci. 12(12): 1983-1988.

Robredo A, Pérez-López U, Lacuesta M, Mena-Petite A, Muñoz-Rueda A(2010) Influence of water stress on photosynthetic characteristics in barley plants under ambient and elevated CO_2 concentrations. Biologia Plantarum. 54(2): 285-292.

Rudolph-Mohr N, Tötzke C, Kardjilov N, Oswald SE (2017) Mapping water, oxygen, and pH dynamics in the rhizosphere of young maize roots. J Plant Nutr Soil Sc. 180(3): 336-346.

Siaga E, Lakitan B, Sidik H, Bernas SM, Wijaya A, Lisda R, Ramadhani F, Widuri LI, Kartika K, Meihana M (2018) Floating culture system of chili pepper (*Capsicum annum* L.) during high flooding period at riparian wetland in Indonesia. Aust J Crop Sci. 12(5):808-816.

Siaga E, Lakitan B, Sidik H, Bernas SM, Widuri LI, Kartika K (2019) Searching for an appropriate procedure in preparing rice seedling utilizing floating seedbed at tropical riparian wetland in Indonesia. Bulg J Agric Sci 25(4): 326–336.

Susilawati S, Lakitan B (2019) Cultivation of common bean (*Phaseolus vulgaris* L.) subjected to shallow water table at riparian wetland in South Sumatra, Indonesia. Aust J Crop Sci. 13(1): 98-104.

Turc O, Bouteillé M, Fuad-Hassan A, Welcker C, Tardieu F (2016) The growth of vegetative and reproductive structures (leaves and silks) respond similarly to hydraulic cues in maize. New Phytol. 212(2): 377-388.

Widuri LI, Lakitan B, Hasmeda M, Sodikin E, Wijaya A, Meihana M, Siaga E (2017) Relative leaf expansion rate and other leaf-related indicators for detection of drought stress in chili pepper (*Capsicum annuum* L.). Aust J Crop Sci. 11(12): 1617-1625.

Widuri LI, Lakitan B, Sodikin E, Hasmeda M, Meihana M, Kartika K, Siaga E (2018) Shoot and root growth in common bean (*Phaseolus vulgaris* L.) exposed to gradual drought stress. Agrivita J Agric Sci. 40(3): 442-452.

Yamauchi T, Colmer TD, Pedersen O, Nakazono M (2018) Regulation of root traits for internal aeration and tolerance to soil waterlogging-flooding stress. Plant Physiol. 176(2): 1118-1130.