J Bangladesh Agril Univ 18(S1): 788–794, 2020 https://doi.org/10.5455/JBAU.17313

ISSN 1810-3030 (Print) 2408-8684 (Online)

Journal of Bangladesh Agricultural University

Journal home page: http://baures.bau.edu.bd/jbau

Special issue: International Conference on Sustainable Agriculture (ICSA) 2019

Water-soluble Carbohydrates in Rice Shoots as Affected by Submergence Stress at Vegetative Stage

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ARTICLE INFO

Article history
Received: 09 Dec 2019
Accepted: 21 Oct 2020
Published: 30 Nov 2020

Keywords
Shoot reserves, Non-structural carbohydrates, Leaf greenness, Submergence stress, and Recovery

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ABSTRACT

Submergence stress is one of the most important constraints for the productivity of rice in Bangladesh. A pot experiment was conducted at the net house of the Department of Crop Botany, Bangladesh Agricultural University during Aman season from July 2018 to December 2018 to study the changes in water-soluble carbohydrates in rice plant during the submergence stress and the recovery. The experiment consisted of two factors—(i) rice cultivars (Binadhan-11 and Binadhan-12 as submergence tolerant and BRRI dhan49 as susceptible) and (ii) submergence stress (both control and submerged for 14 days at vegetative stage). Submergence stress was imposed by dipping the pot grown plants into a water tank about 90 cm depth of water for 14 days. After 14 days, plants were removed from the tank and grown in net house. Samplings were done at 0, 5, 10, 14 and 40 days after submergence to measure the contribution of shoot reserves, leaf greenness and shoot dry mass for their survival. Tolerant rice cultivars Binadhan-11 and Binadhan-12 had higher initial soluble carbohydrates than the susceptible one, BRRI dhan49. Under submerged condition the tolerant cultivars showed slow depletion of water-soluble carbohydrate compared to susceptible one. Higher carbohydrate contents in tolerant cultivars might act as buffer stock during submergence for their better survival and growth.

Introduction

Rice is a staple food for over 3.5 billion of the world's population and also it contributes in ensuring the food security for many countries including Africa and Asia (Oladosu *et al.,* 2020; Chukwu *et al.,* 2019). It can be widely grown in varied environmental conditions that ranged from sea coasts to high altitudes (Oladosu *et al.,* 2020). It is also the major food crop of about 160 million people in Bangladesh. Over 11.52 million hectare of land in Bangladesh is dedicated to rice production and producing about 36.4 million tons of rice (BBS, 2019). However, the geographical location and environmental conditions of Bangladesh are also much favorable for rice cultivation unless sometimes it may be affected by some abiotic stresses. For instance, transplant Aman rice covers 5.62 million hectares (49.82% of total rice area) of land with a production of 14.05 million tons (BBS, 2019). Meanwhile, farmers are facing various environmental stresses like flooding, drought, salinity etc. which may lead to the complete reduction in rice production in some cases (Karim *et al.,* 2018). Among the abiotic stresses, submergence is one of the important factors in the flash flood prone rice growing environment (Mackill *et al.,* 1993). The major rice growing areas are greatly suffered by flooding which may be due to the excess water from river discharge, excessive rainwater and tidal movements (Oladosu *et al.,* 2020). Surprisingly, one-third of total rice cultivated areas are deep-water and rainfed lowland ecosystems, which account for about 50 million hectares (Bailey-Serres and Voesenek, 2008) and these areas are prone to heavy flooding, which may be resulted due to poor drainage systems of the excessive rainwater during the rainy season (Oladosu *et al.,* 2020). Likewisely, in Bangladesh flood is also mainly caused by heavy rainfall as well as the overflow of nearby river and canals and sometime in tidal movement as in coastal region. Alarmingly, more than half of rice crop growing land is submergence prone during kharif season in Bangladesh (Iftekharudullah *et al.,* 2015; Bailey-Serres *et al.,* 2010). Most importantly, plants are subjected to the

Cite This Article
Hossain, M.M., Hossain, M.A., Hassan, M.J., Karim, M.M., Pramanik, M.H.R. 2020. Water-soluble Carbohydrates in Rice Shoots as Affected by Submergence Stress at Vegetative Stage. *Journal of Bangladesh Agricultural University*, 18(S1): 788–794. https://doi.org/10.5455/JBAU.17313

stresses of low light, limited gas diffusion, effusion of soil nutrients, mechanical damage, and increased susceptibility to pests and diseases during submergence (Nishiuchi *et al.,* 2012; Ram *et al.,* 2002).

Moreover, upon deep water flooding, plants used to increase its intermodal distance and thereby increased stem length to escape from the submergence. In addition, after the flood recedes, affected plants are subjected to lodging and eventually that may leads to death due to the exhaustion of reserved nutrients within few days. On the other hand, during flash flood, plant growth is restricted but able to resume after the occurrence of the flood (Winkel *et al.,* 2013). Singh *et al.,* 2017 defined flooding tolerance, in this case, as the plant's ability to survive 10 to 14 days of complete submergence and able to continue their growth process after the escape from flood with little damage to plant morphology.

Although, rice plant has some adaptive traits for tolerance of submergence and formation of the aerenchyma is common in these cases that actually ensure the internal aeration between shoot and roots (Pedersen *et al.,* 2020; Yamauchi *et al.,* 2019; Armstrong, 1980; Colmer, 2003; Colmer and Pedersen, 2008a). In addition, aerenchyma provides an internal path for low-resistance gas-phase diffusion of oxygen into and along roots (Yamauchi *et al.,* 2018). Moreover, a micro layer of air trapped between submerged leaves and the surrounding water, also contributed to the internal aeration and thereby increased the submergence tolerance in rice (Colmer and Pedersen, 2008b). Rice plant under submergence also known to use some other strategy to escape from the stresses. Such as, suppression of shoot elongation to preserve carbohydrates for a long period (10–14 days) under submerged conditions and here, submergence tolerant cultivars can restart their growth during desubmergence by using preserved carbohydrates in shoot (Colmer and Voesenek, 2009; Bailey-Serres and Voesenek, 2008) and another strategy is the fast elongation of internodes to rise above the water level and is used usually by deep water rice cultivars (Xu *et al.,* 2006; Hattori *et al.,* 2009). Actually, during submergence, plant experienced limited photosynthetic assimilation (Panda and Sarkar, 2013) as well as energy crisis under oxygen deficit condition (Gibbs *et al.,* 2000), meanwhile Non-Structural Carbohydrate (NSC) is water soluble sugar and it played a crucial role in surviving under submerged condition. NSCs are utilized during submergence stress to supply energy for growth and maintenance metabolism (Bhaduri *et al.,* 2020). Higher levels of NSCs in the plants prior to submergence and lower rates of their depletion for maintenance processes during submergence are important for survival (Jackson and Ram, 2003, Fukao *et al.*, 2006). Moreover, higher content of residual carbohydrate is also crucial for recovery after de-submergence and utilization (Hattori *et al.,* 2009). Hassan *et al.,* 2018 also reported that DM content decreased with submergence stresses in an experiment on shoot WSCs of rice under submergence stress. Furthermore, the present research was designed to study clearly about the NSC accumulation and utilization by rice plant during submergence stress at vegetative stage and during the recovery after desubmergence.

Materials and Methods

Experimentation

A pot experiment was conducted in plastic pots at the net house of the Department of Crop Botany, Bangladesh Agricultural University, Mymensingh during the period from July 2018 to December 2018. The experiment was laid out as two factorial (rice cultivars and submergence stress) Completely Randomized Design (CRD) with 6 treatments and 3 replications. Three rice cultivars used in the experiment were Binadhan-11 Binadhan-12 (tolerant) and BRRI dhan49 (susceptible). A total of 30 pots (10L) were prepared with soil mixed with well decomposed cow dung (2:1). Each pot contained about 10 kg of soil and cow dung mixture. Fertilizers were applied as basal dressing as follows: Urea, TSP, MoP, Gypsum and Zinc = 0.75, 0.55, 0.25, 0.15, and 0.06 g pot^{-1}.

Submergence stress were imposed by dipping of pot grown rice plants into a water tank with full of water. The water tank was first partially filled with tap water of about 0.5 m height and half of the total pots of 20 days old rice plants were placed in the water of the tank one by one with much care; and then the tank was filled with water to submerge the plants completely. The light intensity of the tank water at 15 cm and 30 cm depth were measured as 65.72 and 47.32 µmol $m^{-2}s^{-1}$, respectively by Light meter (Model: LI–250A, Licor Bio Sciences, USA). Furthermore, the light intensity of outer atmosphere was 240 µmol $m^{-2}s^{-1}$. Dissolved oxygen concentration in tank water was recorded by DO meter (HANNA Instrument, Intl.) and it was 10.50 ppm. The temperature of tank water was 30.8 °C. The height of the water level in the tank were kept constant by adding required water twice in a day during the submergence stress. After 14 days of submergence, the plants were removed from the water tank after draining the water from the tank using a siphoning pipe. The plants were grown with proper care after desubmergence for about a month as recovery. The control plants were maintained with sufficient water and management practices. Intercultural operations such as, irrigation, weeding and spraying of pesticides were done as and when necessary to ensure normal growth.

Sampling and measurements

Three hills of each cultivar were sampled at 0, 5, 10, 14 and 40 days after submergence. The shoots were dried in an oven at 80 °C for 3 days and were weighed to get shoot dry mass (DM) and then stored for the measurement of water-soluble carbohydrates (WSCs) using the anthrone method (Yemm and Willis, 1954). The Leaf greenness of the fully expanded upper most leaves was measured on different sampling dates during submergence and recovery in all cultivars with a chlorophyll meter (SPAD–502; Konica Minolta Sensing Inc., Osaka, Japan). SPAD readings were taken at three positions (near base, near apex and middle) of the leaf immediately after the sampling for shoot DM and WSCs, and were averaged for each leaf. Three leaves were measured and the readings were averaged for a pot.

Estimation of water-soluble carbohydrates (WSCs)

The WSCs in shoots were extracted and measured using anthrone method (Yemm and Willis, 1954) as described by Hossain *et al.* (2011). The dried shoots were milled to be rough powder after chopping for a while. First extraction was done with some weighed powder with 80% ethanol at 60°C for 30 min and the 2 successive 15–min extractions were done with distilled water. The extracts were combined and evaporated to dryness at 65°C. The dried carbohydrates were then resolved in 5 mL distilled water and a fraction of the extract solution (about 1 ml) was taken in a micro-centrifuge tube *(*1.5 mL) with charcoal powder. Powder and extract solution were mixed with a vortex (touch mixer) and then the solution was centrifuged at 5000 rpm for 5 min to make the solution clear. Then the solutions were diluted 10 times with distilled water and the diluted solution (0.1 ml) was mixed with ice-cold anthrone reagent (5 mL). After heating for 10 min in a boiling-water bath and subsequently cooling with ice water, the absorbance reading was taken with a spectrophotometer at 620 nm. The content of WSCs in the sample was calculated as mg WSCs per gram of shoots dry mass using regression equation and the amount of WSCs in shoots was estimated based on the dry mass of shoots (Ehdaie *et al.*, 2006).

Statistical analysis

All data were analyzed statistically using MS Office Excel application. Data were analyzed by calculating means and standard errors of means (SEM).

Results

Changes in Shoot Dry Mass (DM)

Shoot DM content for three different rice cultivars is presented in Figure 1 and showed that shoot DM content in rice changed with the submergence duration and shoot DM was higher in control than the stressed plant irrespective of the cultivars. Moreover, it has been revealed that tolerant cultivar had higher DM both in stress condition and after the receding from the submergence. Tolerant cultivar, e.g. Binadhan-11 and Binadhan-12 had the higher shoot DM at 14 days after submergence (0.69 g plant^{-1} and 0.61 g plant^{-1}, respectively in stress condition) than the susceptible cultivar BRRI dhan49 (0.44 g plant^{-1}). Similar trend also found at different days after submergence. Furthermore, after the removal of the stress, the shoot DM content was higher in tolerant cultivars (1.432 g plant^{-1} and 1.24 g plant^{-1} for Binadhan-11 and Binadhan-12, respectively) at 40 days after submergence than the susceptible cultivar BRRI dhan49 (0.84 g plant^{-1}) at stressed condition. Higher shoot DM may be the one of the responsible characters for tolerant cultivars to be tolerant under submergence stress.

Changes in leaf greenness

Significant variations were found in leaf greenness as evaluated by SPAD values among the cultivars as presented in Figure 2. At 40 days after de-submergence, the cultivars showed higher SPAD values in stress condition than the control may be due to the higher physiological activity for the removal of stress. After the escape from the submerged condition, the tolerant cultivars (Binadhan-11, Binadhan-12) showed higher leaf greenness for a long time than the susceptible cultivar (BRRI dhan49). In stressed condition, leaf greenness was also higher in tolerant cultivars (24.5 and 25.0 for Binadhan-11 and Binadhan-12, respectively) than the susceptible cultivar BRRI dhan49 (21.9) at 14 days after submergence and similar trend were also found in other sampling dates.

Changes in WSCs in shoot

Water-soluble carbohydrates (WSCs) are the main reserves in shoots and the changes in WSCs both in control and stress conditions are presented in Figure 3. Variations were found in WSCs in shoots at different periods during submergence stress. At 14 days after the imposition of stress the WSCs were higher in tolerant cultivars (0.96 mg g^{-1} and 0.53 mg g^{-1} dry mass for Binadhan-11 and Binadhan-12, respectively) than the susceptible cultivar BRRI dhan49 (0.51 mg g^{-1} dry mass) and similar trends were found during the period of submergence stress. Moreover, during recovery at 40 days after submergence, the WSCs were also higher in the tolerant cultivars, e.g. Binadhan-11 and Binadhan-12 (4.62 mg g^{-1} and 3.73 mg g^{-1} dry mass respectively) than the susceptible cultivar BRRI dhan49 (1.16 mg g^{-1} dry mass) in stressed plants. In general, tolerant cultivar possessed higher WSCs content at submerged condition than the susceptible cultivars and this criterion might be responsible for stress tolerance.

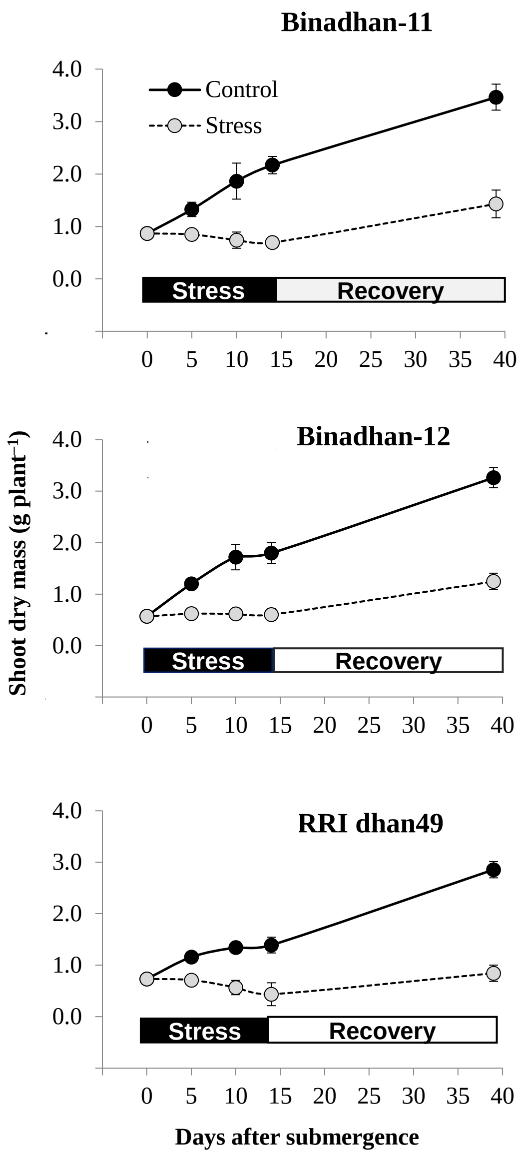

Figure 1. Shoot dry mass in three rice cultivars as affected by submergence stress. Vertical bars represent standard errors of means (n = 3).

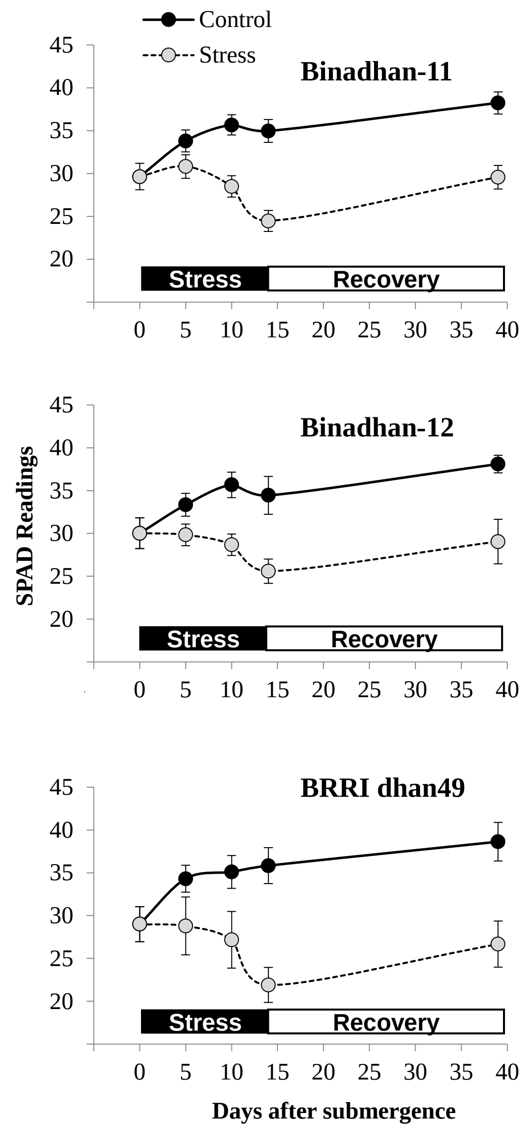

Figure 2. Leaf greenness (SPAD values) in three rice cultivars as affected by submergence stress. Vertical bars represent standard errors of means (n = 3).

Discussion

The energy and carbon crisis in flooded plants poses the largest threat to survival. Sometime starvation is ameliorated through increased gas exchange via arenchyma and adventitious root development (Liu *et al.,* 2020). However, flooding responses such as reduced protein synthesis and down regulation of secondary metabolism most likely are coordinated via elaborate sugar sensing mechanism (Yamauchi *et al.,* 2019). Submergence tolerance in rice is governed by a number of factors out of which high carbohydrate status prior to the submergence is much more important. From the present experiment, it was found that high carbohydrate content of the cultivars both in control and stress conditions are related to tolerant cultivars whereas the lower carbohydrate content in shoot categorized under susceptible cultivar (Figure 3). Higher levels of initial carbohydrate act as buffer stock during submergence and the slow continuous supply of carbohydrate helped for the survival and growth of rice. Metabolic energy required by the plant during submergence is supplied from the stored carbohydrate in tissue. Irrespective of cultivars it was found that there was reduction of carbohydrate content of shoot in stressed condition.

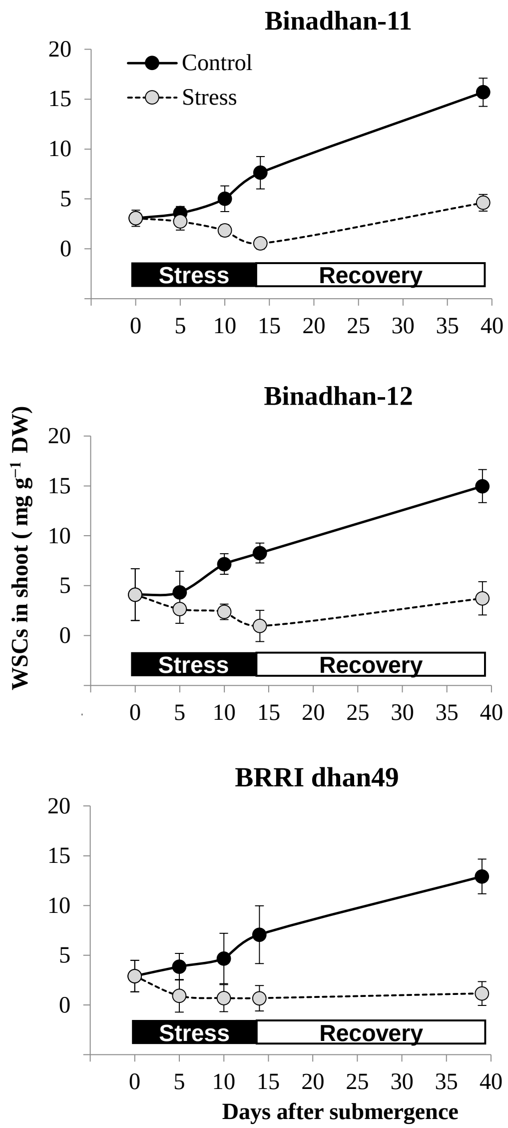

Figure 3. WSCs in shoot (mg g^{-1} DW) in three rice cultivars as affected by submergence stress. Vertical bars represent standard errors of means (n = 3).

It has been well documented that under submerged condition there was decrease in stomatal conductance, intercellular CO_2 concentration as well as denaturing of the photosynthetic machineries was occurred (Colmer *et al.,* 2014; Sarkar *et al.*, 2006; Karim *et al.,* 2019).

Under submerged condition the rate of depletion of carbohydrate is very slow in the tolerant genotypes in comparison with susceptible genotypes. Drastic reduction of carbohydrate leads to higher rate of anaerobic fermentation and production of ethanol at toxic level which caused damage to the genotypes (Setter *et al.*, 1989). Again, due to more amylase activity in the leaf and stem of tolerant genotypes survival percentage was more. The survival percentage is highly correlated with the carbohydrate present in the stem and leaf (Das *et al.,* 2005) to which the present findings strongly agreed.

Non-structural carbohydrate contents before and after submergence are important for providing energy needed for maintenance metabolism during submergence and for regeneration and recovery of seedlings after submergence. Non-structural carbohydrate contents before submergence were highest in the shoots of both tolerant and susceptible cultivar. Survival after submergence is substantially dependent on the level of NSC remaining in shoots after submergence; where the variation in survival depends on NSC content remain in shoot (Hassan *et al.,* 2018; Karim *et al.,* 2019).

Conclusion

Carbohydrate content of all three rice cultivars decreased with the increase of submergence duration. Maximum reduction in carbohydrate content due to submergence stress was noted in susceptible cultivar BRRI dhan49 under 14 days of submergence. However, tolerant rice cultivars had high initial water soluble carbohydrate and lower percent reduction in soluble carbohydrate during submergence and thereby it may be said that, higher water soluble carbohydrate could be beneficial for survival during submergence.

Acknowledgement

This research was supported by a Research Grant (2016/115/MoST) from Ministry of Science and Technology, Government of the People’s Republic of Bangladesh.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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