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Hydrogen peroxide priming alleviates chilling stress in rice (*Oryza sativa* L.) by enhancing oxidant scavenging capacity

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ABSTRACT

Chilling is a substantial stressor for plants. In fact, some biochemical reactions involved in growth and development of plant are sensitive to temperature. In particular, chilling stress represents a severe issue for plant growth and productivity and strategies to alleviate the stress is an important goal for agriculturists. While, hydrogen peroxide (H_2O_2) acts as a signalling molecule and its role in preventing several abiotic stresses like heat, salinity, drought etc. is well understood. Thus, the present study tested the effects of H_2O_2 priming in mitigation of chilling stress at germination and seedling stage of rice. The rice seeds were treated with H_2O_2 (5, 10 and 15 mM H_2O_2) solution for 24 h and exposed to chilling stress either for 6 h d^{-1} or 12 h d^{-1} for 7 days. Results revealed that chilling stress seriously impeded germination indices (germination percentage, germination rate index, coefficient of velocity of germination and mean germination time), morphological parameters (shoot length, root length and fresh weight), total chlorophyll content and antioxidant enzymes (catalase and ascorbate peroxidase) activity. On the other hand, priming with H_2O_2 (5 mM, 10 mM and 15 mM) displayed protective effects on germination indices and growth parameters and conferred a significant tolerance against chilling stress. Priming with H_2O_2 also significantly protected chlorophyll from chilling-induced degradation. Our results provide a strong foundation that priming with H_2O_2 confers a positive physiological effect by enhancing antioxidant enzymes capability (increased catalase and ascorbate peroxidase activity) of chilling stressed rice plant. Among the concentrations, 10 mM H_2O_2 performed relatively better in chilling stress alleviation. Therefore, this technique can be used for improved rice seedling production in northern part of Bangladesh under low temperature condition.

Keywords: Antioxidant enzymes, chilling stress, cold injury, germination indices, rice seedling, Bangladesh

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1 Introduction

Almost half of the humankind of the earth consumes rice (*Oryza sativa* L.) as a staple food (Fairhurst and Dobermann, 2002). Mostly, Asian people solely eats greater than 90% of this rice (Mohanty et al., 2013). Bangladesh is the fourth-largest rice grower in the world where about 34.7 million metric tons of rice is produced annually and around 75% of the arable land is utilized for its production (BBS, 2017; Ahmed et al., 2017). Feeding the ever-increasing population using the inadequate resources is one of the major challenges that present agriculturalists and plant scientists of Bangladesh are facing. Recently the country has attained food self-sufficiency but to sustain the status is the foremost task because due to the climatic change rice cultivation is being hampered by different abiotic stresses such as drought, salinity, flooding and extreme or low temperature (Osmani et al., 2016; Amin et al., 2015).

Among these abiotic stresses, cold stress is a minor stress in Bangladesh, but recently because of severe cold wave during winter season it becomes problematic for some crops including rice (Rashid and Yasmeen, 2018). Due to global climatic change the intensity of cold stress increasing day by day. Importantly, this year lowest ever temperature in history at 2.6 °C was recorded in northern districts (Bangladesh Meteorological Department 2018). Before transplanting the Boro rice seedlings in main field, rice seeds are sown in seed bed in the month of December. Because of the extreme low temperature the growth of rice seedlings is being hampered during December-January in northern region of Bangladesh (BRRI, 2017; Rashid and Yasmeen, 2018). As well as the quality of rice seedling hampered which ultimately causes lower crop yield. Sometimes, farmers do not get adequate seedlings for transplanting because of the seedling death due to cold injury (BRRI, 2016; Rashid and Yasmeen, 2018). Thus, rice production being hampered mainly in northern part of Bangladesh due to cold stress. Particularly, the low temperature leads to poor germination, discoloration and swallowed seedling, eventually makes unhealthy seedlings during the seedling stage (Yea et al., 2008; Lukatkin et al., 2012). In this stage, the cold injury usually appears on the leaves as a symptom of wilting, discoloration and inhibition of growth at the 3rd to 4th leaf stage (Hyun et al., 2016). At the early growth stage in rice, the low temperature stress affects the newly emerging leaves to be lack of chlorophyll (Tewari and Tripathy, 1998). Ultimately, low temperature potentially reduces the rate of growth and the establishment of plants and decreases the photosynthetic area, upon which continued growth is dependent (Yadav, 2010; Hussain et al., 2018).

Plants are subjected to oxidative stress when exposed to abiotic stresses including chilling (Hussain et al., 2016, 2018). Chilling stress imposed excess reactive oxygen species (ROS) production and accumulation in plant's tissue which ultimately leads to oxidative damage at cellular and sub-cellular level, impaired the membranes of cell, ionic balance disruptions, and deactivation of enzymes and proteins (Hussain et al., 2018; Tarchoune et al., 2010). Moreover, the over-accumulated ROS interrupts different cellular macromolecules including DNA, lipids etc. which are linked with various physiological and biochemical disorders in plants (Das and Roychoudhury, 2014). Plants usually have a very competent and advanced antioxidant defence mechanism to regulate the over-accumulation of ROS (Arif et al., 2016) which comprised of different enzymatic (e.g., catalase, CAT; ascorbate peroxidase, APX) and non-enzymatic (e.g., ascorbic acid, carotenoids and glutathione) antioxidants (Gill and Tuteja, 2010; Chen et al., 2015). The efficient ROS scavenging capacity has been allied with tolerance of plants to different environmental stresses including chilling (Gill and Tuteja, 2010). In order to accelerate the efficiency of oxidant scavenging systems under stressful condition scientists are finding different approaches and seed priming can be an effective one.

Priming is possibly a vital means to provoked tolerance in plants against environmental stresses (Hossain et al., 2015). Among different priming agents, the priming with hydrogen peroxide (H_2O_2) may metabolically prepare plant to fight against the chilling stress because H_2O_2 is a signal molecule that overexpress stress related genes (Hossain et al., 2015). It has been previously shown that pre-treatment of *Zoysia matrella* plants with low concentrations of H_2O_2 induced chilling tolerance (Wang et al., 2010). H_2O_2 treatments improved osmotic stress resistance of two cucumber varieties by activating antioxidant system (Liu et al., 2009). Terzi et al. (2014) also observed that exogenous applications of H_2O_2 at low concentration alleviated membrane damages and significantly decreased lipid peroxidation of maize plants under osmotic-stressed conditions. Low doses of H_2O_2 can increase mass and length of roots (Korystov and Narimanov, 1997). Exogenous H_2O_2 also mediates the growth of primary root, lateral roots, and root hairs (Jiang et al., 2012) and significantly promote the formation and growth of adventitious roots of cucumber (Li et al., 2007). H_2O_2 as a stress signalling molecule could trigger the activation of antioxidant capacity in plants to alleviate the oxidative damage and leading to improve physiological attributes of the plant under stress (He and Gao, 2009; Goud and Kachole, 2011). From the above discussion it is clear that, H_2O_2 priming can modulates antioxidant activities under chilling stress. So this technique could be used to mitigate the chilling effect in rice seedlings in the northern region of Bangladesh.

Therefore, the present experiments were con-

ducted to investigate the ability of exogenous H_2O_2 priming to promote growth and stimulate stress associated defensive mechanisms of rice under chilling stress.

2 Materials and Methods

2.1 Experimental setup

Rice (cv. BRRI dhan29, a high yielding rice cultivar) seeds were surface sterilized with 2.5% sodium hypochlorite for 8 minutes and subsequently washed several times with sterilized distilled water. In the next step, the disinfected seeds were soaked in H_2O_2 (5, 10 and 15 mM H_2O_2) solution for 24 h. After that, about one hundred H_2O_2-treated or untreated seeds were placed on bloating paper per petri dish and 10 ml of distilled water was used daily to ensure water supply. These petri dishes were placed in a growth chamber at 70% relative humidity in 12 h : 12 h dark - light condition for germination. Two temperature conditions (*viz.* 6 h 4 °C/ 24 h and 12 h 4 °C/ 24 h) were maintained to impose the chilling stress. The control seeds were grown at 25±2 °C temperature conditions. Therefore, the treatment combinations were: No chilling stress (CS) (T1, control), 6 h d^{-1} CS (T2), 12 h d^{-1} CS (T3), 6 h d^{-1} CS + 5 mM H_2O_2 (T4), 6 h d^{-1} CS + 10 mM H_2O_2 (T5), 6 h d^{-1} CS + 15 mM H_2O_2 (T6), 12 h d^{-1} CS + 5 mM H_2O_2 (T7), 12 h d^{-1} CS + 10 mM H_2O_2 (T8), 12 h d^{-1} CS + 15 mM H_2O_2 (T9).

2.2 Measurement of germination indices

Seeds were considered as germinated when the radical reached 2 mm in length. From 2nd day after incubation (DAI), numbers of germinated seeds were recorded up to 4th DAI and by using these germination counts, several germination indices were calculated, including germination percentage (GP), germination rate index (GRI) and mean germination time (MGT) (Kader, 2005), as well as coefficient of velocity of germination (CVG) Kader and Jutzi (2004).

$$GP\ (\%) = \frac{S_g}{S_T} \tag{1}$$

$$CVG\ (\%\ d^{-1}) = \frac{\sum N_i}{\sum N_i T_i} \times 100 \tag{2}$$

$$GRI\ (\%\ d^{-1}) = \frac{\sum N_i}{I} \tag{3}$$

$$MGT\ (d) = \frac{\sum N_i T_i}{\sum N_i} \tag{4}$$

Where, GP is germination (%), S_g and S_T are number of seeds germinated and set for germination, respectively. N_i is the number of seeds germinated on day i and T_i is the number of days from sowing. The CVG gives an indication of the rapidity of germination: it is increased by increasing the number of germinated seeds and reducing the time required for germination. GRI is reflected the percentage of germination on each day of the germination period, where higher GRI values are indicated higher and faster germination, which in turn is indicated lower MGT.

2.3 Growth performance measurement

At 7th DAI, different growth parameters were evaluated. The growth parameters were assessed by measuring shoot length (SL), root length (RL), fresh weight (FW). Shoot length was measured from shoot base to the leaf tip and root length was measured from root base to the root tip. Twenty seedlings from each treatment were weighted for the determination of FW. Finally, the FW was expressed as mg $plant^{-1}$.

2.4 Determination of chlorophyll content

Total chlorophyll content (TCC) extraction was done by taking 0.05 g of fresh shoot with 10 mL of 80% acetone for 7 days in dark condition. The absorbance of acetone supernatant was recorded at 645 and 663 nm wave lengths in a UV-VIS spectrophotometer (Shimadzu, UV-1201, Tokyo, Japan) to determine the TCC according to the method developed by Lichtenthaler (1987) and the results were expressed as mg g^{-1} FW.

2.5 Antioxidant enzymes activity assay

The shoots of 7-day-old germinated rice seeds were used for antioxidant enzymes *viz.* catalase (CAT, EC: 1.11.1.6) and ascorbate peroxidase (APX, EC: 1.11.1.11) activity determination. The CAT activity was determined by following the method of Aebi (1974). The activity of CAT was calculated from the decrease in absorbance at 240 nm per minute when the extinction coefficient of H_2O_2 was 39.4 M^{-1} cm^{-1} and the result was expressed as 'mmol min^{-1} g^{-1} FW'. APX activity was determined by following the method of Nakano and Asada (1981). The activity of APX were calculated from the change in absorbance at 290 nm per minute when the extinction coefficient was 2.8 mM^{-1} cm^{-1}. All the absorbance was taken in a UV-VIS spectrophotometer (Shimadzu, UV-1201, Tokyo, Japan). The activity of APX was expressed as 'μmol min^{-1} g^{-1} FW'.

2.6 Statistical analysis

One-way analysis of variance was performed by feeding the data to Minitab 17.0 statistical software. Different letters denote the statistically significant differences between treatments at P<0.05, according to

Fisher's least significant difference test. Data provided as means ± standard errors of three replications for each treatment.

3 Results

3.1 Effect on seed germination

Several seed germination parameters, including germination percentage (GP), germination rate index (GRI), coefficient of velocity of germination (CVG) and mean germination time (MGT) were determined to estimate the detrimental effects of chilling (6 h, short period and 12 h, long period) on germination and the potential ameliorative effects of H_2O_2 on chilling stressed rice seedlings (Fig. 1). Under chilling stress conditions, rice seeds showed lower GP after 76 h compared to control. Compared to control, GRI and CVG were dropped by 20.04 and 22.48%, respectively in response to 6 h and 33.64 and 27.64% in response to 12 h chilling stress, while MGT was increased by 29.11% in 6 h stress and 38.03% in 12 h chilling stress. However, these parameters mostly affected in 12 h chilling stress. On the other hand, exogenous application of H_2O_2 increased GP, GRI, and CVG and decreased MGT of chilling stress (both 6 h and 12 h) in rice seedling. Among the concentration of H_2O_2, the 10 mM H_2O_2 showed highest efficiency in chilling stress mitigation and increased GP, GRI, and CVG by 145.14, 72.3 and 48.45% while decreased MGT by 48.45% in response to 6 h chilling stress relative to chilling stress only seedlings.

3.2 Effect on seedlings growth

To figure out the effect of H_2O_2 on chilling stress alleviation, we also examined several growth parameters such as SL, RL and FW of rice seedling (Fig. 2). The SL, RL and FW were significantly reduced by 48.57, 52.93 and 41.51% in response to 6 h chilling stress and 62.74, 70.99 and 60.74% in response to 12 h chilling stress compared to that of stress free control plants. On the other hand, all the concentration of H_2O_2 displayed protective behaviour against short term and long term chilling stress. Among different concentration of H_2O_2, 10 mM H_2O_2 showed highest tolerance against chilling stress and increased SL, RL and FW by 50.22, 43.09 and 50.34% in 6 h chilling stress and 94.78, 116.93 and 96.32% in 12 h chilling stress compared to that of chilling stressed only plants.

3.3 Effect on leaf pigments

Chilling stressed rice seedling leaves exhibited a marked decrease in total chlorophyll content (TCC) by 33.67 and 68.13% in response to 6 h and 12 h chilling stress compared to stress free control plants (Fig. 3a). On the other hand all three different concentration of H_2O_2 priming displayed a protective function on TCC. Where, 10 mM H_2O_2 showed highest protection in TCC and increased TCC by 15.63 and 62.60% in 6 h and 12 h chilling stress compared to chilling stress only plants.

3.4 Effect on ROS scavenging capacity

To evaluate positive impact of H_2O_2 priming on chilling stress we examined CAT and APX activity of the treatment of rice seedling (Fig. 3b,c). Chilling stress displayed a significant increase in CAT activity by 23.42 and 41.44% in response to 6 h and 12 h chilling and APX activity by 24.17 and 45.49% in response to 6 h and 12 h chilling stress compared to stress free control plants. On the other hand all three different concentration of H_2O_2 displayed a protective function on CAT and APX activity. Among these concentrations 10 mM H_2O_2 displayed highest increase in both short and long duration chilling condition. In addition, 10 mM H_2O_2 increased CAT activity by 154.11 and 175.38% and APX activity by 111.87 and 156.52% in chilling stressed plants compared to chilling stress only plants.

4 Discussion

Germination of seed is considered as the most significant step for determining the success or debacle of crop establishment. Field crops are extremely sensitive to chilling particularly during germination and early phases of seedling development. Each seed requires optimum temperature for germination which confer seeds to generate healthy seedling. But due to extreme temperature, the normal germination indices and growth can be affected (Hussain et al., 2018). In the present study, chilling stress caused a considerable reduction of GP, GRI, and CVG, while the time required to acquire a faster germination (MGT) was increased in rice seeds, especially under prolong chilling condition (Fig. 1). Previously, several studies have documented the delayed and non-uniform germination of rice under chilling stress (da Cruz and Milach, 2004; Ye et al., 2009), wheat (Aflaki et al., 2017) and *Vicia faba* L. (Anaya et al., 2018) under salt stress. Chilling stress is known to thermodynamically limit the kinetics of various physiological as well as metabolic functions in plants (Ruelland et al., 2009) which finally evokes a detrimental effect on germination indices of rice seeds. On the other hand, H_2O_2 priming exerted a beneficial effect on these parameters and compensated chilling induced negative effects (Fig. 1). Protective role of H_2O_2 on germination indices was also reported in rice and maize under chilling stress (Naim, 2015; Li et al., 2017) and cucumber seed under $NaHCO_3$ stress (Sun et al., 2010). Among H_2O_2

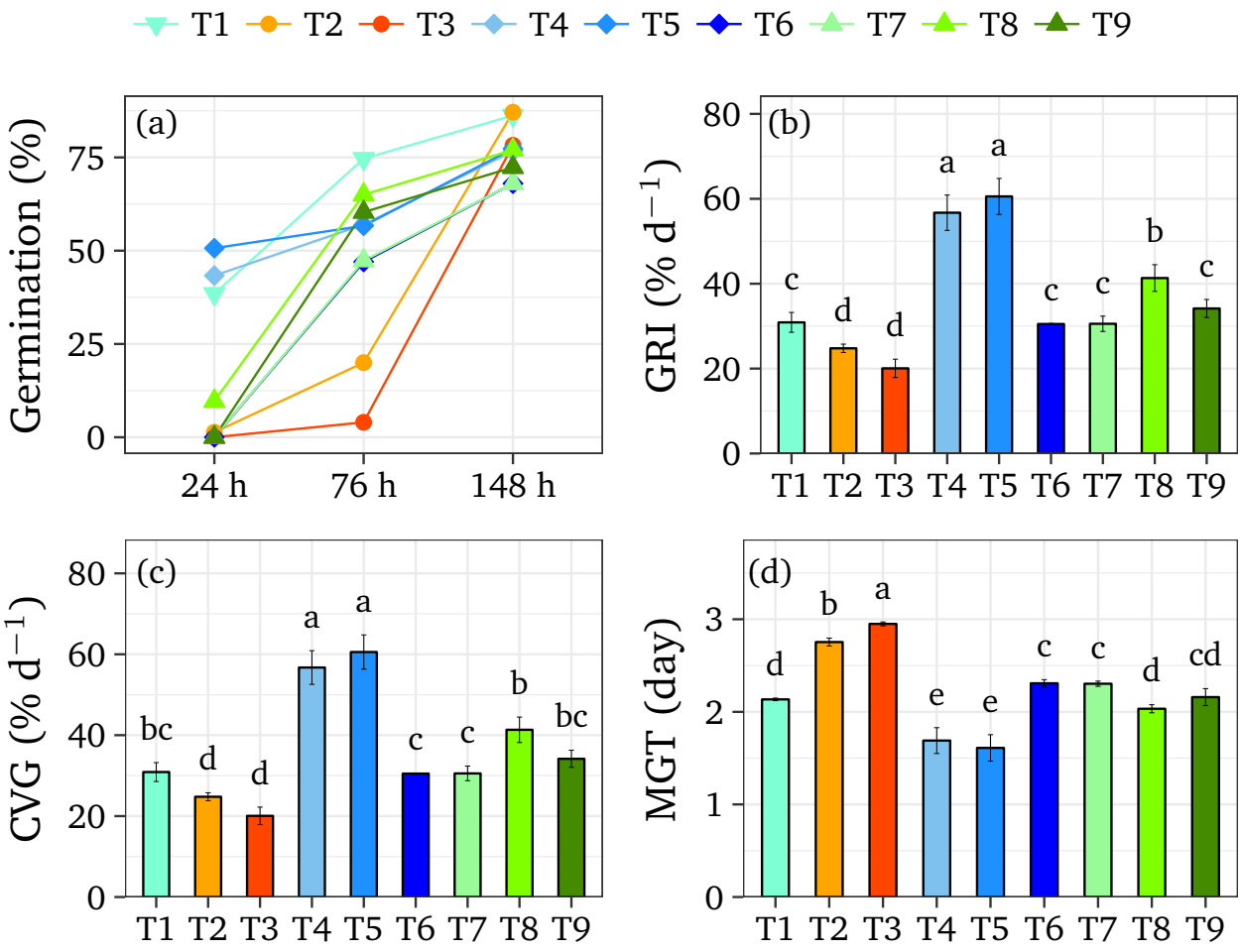

Figure 1. Effects of hydrogen peroxide (H_2O_2) priming on (a) germination (%), GP (b) germination rate index, GRI (c) coefficient of velocity of germination, CVG and (d) mean germination time, MGT of rice seeds under chilling stress. Data represented in figure is the mean of three replicates for each treatment (n = 3). Letter on top of bar denotes the statistically significant difference at P<0.05 (Fisher's least significant difference test). No chilling stress (CS) (T1), 6 h d^{-1} CS (T2), 12 h d^{-1} CS (T3), 6 h d^{-1} CS + 5 mM H_2O_2 (T4), 6 h d^{-1} CS + 10 mM H_2O_2 (T5), 6 h d^{-1} CS + 15 mM H_2O_2 (T6), 12 h d^{-1} CS + 5 mM H_2O_2 (T7), 12 h d^{-1} CS + 10 mM H_2O_2 (T8), 12 h d^{-1} CS + 15 mM H_2O_2 (T9).

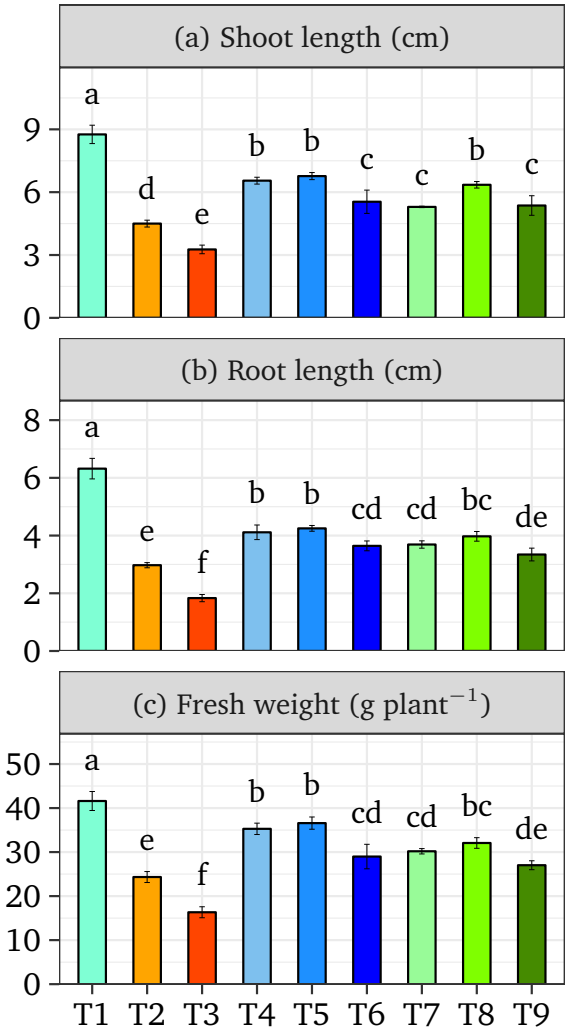

Figure 2. Effects of H_2O_2 priming on (a) shoot length, SL (b) root length, RL and (c) fresh weight, FW of rice seedlings grown under chilling stress. No chilling stress (CS) (T1), 6 h d^{-1} CS (T2), 12 h d^{-1} CS (T3), 6 h d^{-1} CS + 5 mM H_2O_2 (T4), 6 h d^{-1} CS + 10 mM H_2O_2 (T5), 6 h d^{-1} CS + 15 mM H_2O_2 (T6), 12 h d^{-1} CS + 5 mM H_2O_2 (T7), 12 h d^{-1} CS + 10 mM H_2O_2 (T8), 12 h d^{-1} CS + 15 mM H_2O_2 (T9).

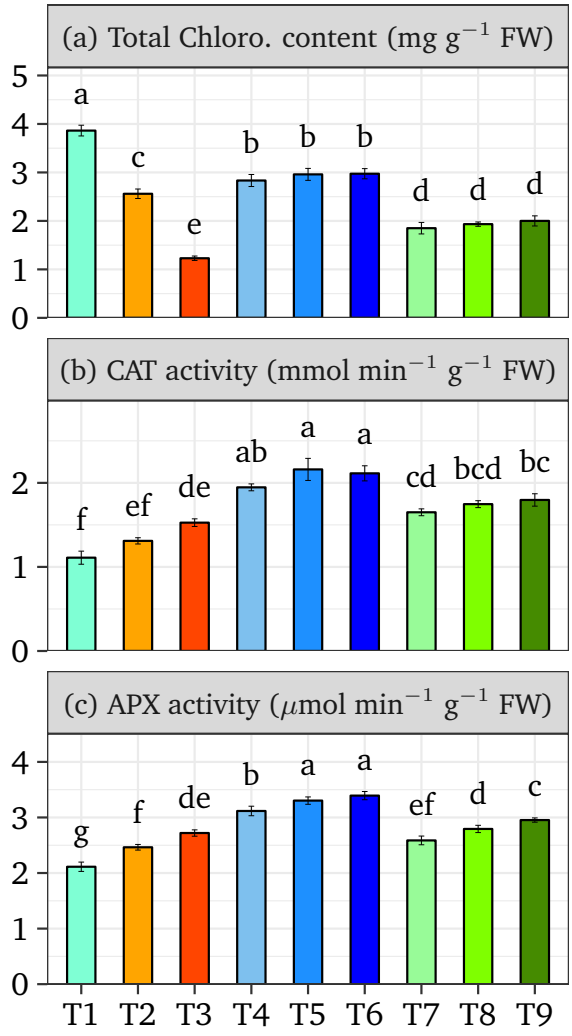

Figure 3. Effects of H_2O_2 priming on (a) total chlorophyll content, TCC (b) catalase activity, CAT and (c) ascorbate peroxidase activity, APX of rice seedlings grown under chilling stress condition. No chilling stress (CS) (T1), 6 h d^{-1} CS (T2), 12 h d^{-1} CS (T3), 6 h d^{-1} CS + 5 mM H_2O_2 (T4), 6 h d^{-1} CS + 10 mM H_2O_2 (T5), 6 h d^{-1} CS + 15 mM H_2O_2 (T6), 12 h d^{-1} CS + 5 mM H_2O_2 (T7), 12 h d^{-1} CS + 10 mM H_2O_2 (T8), 12 h d^{-1} CS + 15 mM H_2O_2 (T9).

concentrations, 10 mM and 15 mM showed the highest protection against short term chilling stress and conferred the best performance on germination indices while showed relatively lower protection under long term chilling stress (Fig. 1). Thus H_2O_2 priming treatment is useful for rice seeds germination acceleration and seedling quality improvement under chilling stress.

Like germination index, chilling stress also hamper plant growth and biomass of plants in seedling stage. In our current experiment root length, shoot length, and fresh weight of plants were decreased markedly in response to chilling stress as also observed some other crop plants (Xing et al., 2011; Hussain et al., 2016; Thakur et al., 2010). Chilling stress limits root growth and development by decreasing root length, biomass, and morphology which ultimately decrease volume of the root system for up taking the nutrients and water (Cutforth et al., 1986; Stewart et al., 1990). This reduced nutrient and water uptake impact on overall morphology of plants which is indicated by decreased shoot length and fresh weight (Fig. 2). However, priming with H_2O_2 reduced the chilling induced negative effects on these parameters by improving root length, shoot length and fresh weight of plants (Fig. 2). Similar result was reported in *Zoysia matrella* under chilling stress (Wang et al., 2010), wheat (Li et al., 2010), rice (Roy et al., 2016) and *Allium cepa* (El-Mageed, 2016) plants under different abiotic stresses. H_2O_2 might activated different signalling mechanism which ultimately modulated growth promoting gene expression and antioxidant defence system that improved growth and biomass of plants (Prasad, 1994; Hossain et al., 2015).

Rate of photosynthesis is an important determinant of growth and development of plants which solely depends on capturing light energy by chlorophyll. Thus chlorophyll content is regarded as an index to reveal the abiotic stress resistance of plants (Smillie and Hetherington, 1983; Gengmao et al., 2014; Asaeda and Rashid, 2017; Parveen et al., 2017). In the present study, TCC in rice leaves was declined markedly in relation to the increasing time duration of chilling stress (Fig. 3a) as also observed in bermuda grass under chilling stress (Fan et al., 2015). This declination of TCC might hampered photosynthesis of plants that ultimately reduced plant growth and biomass (Fig. 2 & Fig. 3a). Chilling stress might increase the level of ROS which injured membrane of chloroplast and reduced chlorophyll of rice plants. On the other hand priming with H_2O_2 elevated TCC in chilling stressed plants (Fig. 3a). Similar enhancement of TCC after H_2O_2 treatment was observed in drought stressed cucumber seedling (Sun et al., 2016). Priming with H_2O_2 elevated TCC perhaps by protecting chloroplast membrane from chilling induced injury or up regulating chlorophyll synthetic enzyme.

Plants are sessile in nature. Thus, it cannot move the location when it encounter with unfavourable environment. But through the course of evolution, plant develops some defence mechanism to counteract the unfavourable environment induced stress through regulating enzymatic and non-enzymatic antioxidant. In our experiment, chilling stress increased CAT and APX activity significantly (Fig. 3b,c) as also observed in tomato under cold stress (Iseri et al., 2013), maize (Tahjib-Ul-Arif et al., 2018) and *Allium cepa* plants under salt stress (El-Mageed, 2016). But this level of increase of the APX and CAT is not sufficient for protecting plant from chilling induced stress. Thus deterioration of growth and biomass occurred in current experiment (Fig. 2). On the other hand priming with H_2O_2 further increased CAT and APX activity and protected rice plants from short term chilling stress more effectively than long term chilling that is visualized by improved growth and biomass (Fig. 2 & Fig. 3b,c) as also observed in different plants such as tomato (Iseri et al., 2013) and *Allium cepa* plants (El-Mageed, 2016). Improved enzymatic antioxidant might help to reduce ROS which subsequently protected membranes and cell machineries which ultimately conferred tolerance rice plants (Das and Roychoudhury, 2014).

Finally it could be concluded that, the H_2O_2 priming enhanced growth and photosynthetic pigments in rice seedlings and ensure better protection against chilling-induced oxidative stress by enhancing antioxidant enzymes. Among different concentrations, 10 mM H_2O_2 performed better in terms of germination indices, growth and pigment protection. Therefore, the 10 mM H_2O_2 priming can be used to produce quality seedlings under chilling stress condition.

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Conflict of Interest

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

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