https://doi.org/10.17221/472/2019-PSE

Exogenous salicylic acid and hydrogen peroxide attenuate drought stress in rice

Abdullah Al Mamun Sohag[1], *Md. Tahjib-Ul-Arif*[1]*, *Marián Brestič*[2,3], *Sonya Afrin*[4], *Md. Arif Sakil*[1], *Md. Tahmeed Hossain*[1], *Mohammad Anowar Hossain*[1], *Md. Afzal Hossain*[1]

[1]*Department of Biochemistry and Molecular Biology, Faculty of Agriculture, Bangladesh Agricultural University, Mymensingh, Bangladesh*
[2]*Department of Plant Physiology, Faculty of Agrobiology and Food Resources, Slovak University of Agriculture in Nitra, Nitra, Slovak Republic*
[3]*Department of Botany and Plant Physiology, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences Prague, Prague, Czech Republic*
[4]*Department of Soil Science, Bangladesh Agricultural University, Mymensingh, Bangladesh*

**Corresponding author: tahjib@bau.edu.bd*

Abdullah Al Mamun Sohag and Md. Tahjib-Ul-Arif contributed equally to this work.

Citation: Sohag A.A.M., Tahjib-Ul-Arif M., Brestič M., Afrin S., Sakil M.A., Hossain M.T., Hossain M.A., Hossain M.A. (2020): Exogenous salicylic acid and hydrogen peroxide attenuates drought stress in rice. Plant Soil Environ., 66: 7–13.

Abstract: Hydrogen peroxide (H_2O_2) and salicylic acid (SA) exhibit protective effects against a wide array of stresses. In this study, we investigated the relative efficacy of exogenous H_2O_2 and SA in conferring drought tolerance in rice (*Oryza sativa* L.). The experiment was repeated two times, firstly in a hydroponic system and secondly in soil. The results revealed that drought hampered germination indices, seedling growth, photosynthetic pigments, and water content, whereas increased proline content. It also triggered higher H_2O_2 production and consequently elevated lipid peroxidation, which is a particular indication of oxidative damage. However, exogenous H_2O_2 or SA treatment effectively alleviated oxidative damage in rice seedlings both in hydroponic and soil systems *via* upregulating antioxidant enzymes. Nevertheless, regulation of proline level and augmentation of plant-water status were crucial to confer drought tolerance. Exogenous H_2O_2 or SA also protected photosynthetic pigments from oxidative damage that might help to maintain normal photosynthesis under drought. Besides, 5 mmol/L H_2O_2 and 0.5 or 1 mmol/L SA showed similar effectiveness on mitigating drought stress. Finally, our findings suggest that exogenous H_2O_2 or SA could evenly be effectual in the amending growth of rice seedlings under drought conditions.

Keywords: abiotic stress tolerance; phytohormone; signaling molecule; water stress

Rice (*Oryza sativa* L.) is the staple food for nearly half of the world's population and is cultivated in approximately 160 million hectares of land globally, mostly in Asia, where about 46.6% of the world population resides (Prasad et al. 2017). As the world population is increasing alarmingly fast, it is an earnest need to increase the rice production several folds to feed the population. In contrast, rice is a drought-sensitive crop, and every year encounters a vast amount of yield loss globally. Moreover, climate change has been altering the rainfall pattern; thereby, at present, drought has become a very serious concern for rice farming (Fahad et al. 2017, 2019).

Drought impedes plant productivity by altering the physiological processes. It causes the generation of the excessive amount of reactive oxygen species (ROS), which alters the metabolic and oxidative homeostasis of plant cells (Hussain et al. 2018). Later, excessive

Supported by the Bangladesh Agricultural University Research System, Project No. 2016/15/AU-GC.

https://doi.org/10.17221/472/2019-PSE

ROS promotes membrane lipid peroxidation (Noctor et al. 2018). Also, in leaves, excessive ROS accretion can lead to senescence of leaves due to the breakdown of photosynthetic pigments (Hussain et al. 2018, Noctor et al. 2018). Thus, the interaction between ROS and antioxidant defense systems substantially governs the plant's drought tolerance competences (Hussain et al. 2018). Plants possess antioxidants, both enzymatic (catalase (CAT); ascorbate peroxidase (APX); and guaiacol peroxidase (GPOX)) and non-enzymatic, to scavenge ROS (Noctor et al. 2018). Thus, upgrading antioxidants is an efficient tactic to counter the drought-induced oxidative stress.

Salicylic acid (SA) plays a vital role in many physiological routes of plants, and several studies stated the use of SA in stress mitigation (Maruri-López et al. 2019). Likewise, H_2O_2 acts as a signaling molecule at mild levels which operates versatile functions in plants. It also regulates plant metabolism by cooperating with other hormones and signaling molecules and confers stress tolerance (Smirnoff and Arnaud 2019). The latest studies showed that the exogenous H_2O_2 augmented abiotic stress tolerance of different plants (Banerjee and Roychoudhury 2019, Latef et al. 2019).

Taking these facts into account, we examined the effects of exogenous SA or H_2O_2 on drought stress mitigation in rice both hydroponic and soil systems in order to compare their efficacy in drought mitigation at the germination and seedling stage. Furthermore, to the best of our knowledge, it is the first report that evaluated the relative efficiency of SA and H_2O_2 both under hydroponic and soil systems.

MATERIAL AND METHODS

Treatments and growth parameters measurement. The germination and growing of rice (cv. BRRI dhan29) seedlings in hydroponic were done as previously stated by Tahjib-Ul-Arif et al. (2019). In the germination stage study, seeds were soaked in H_2O_2 (5 and 10 mmol/L) or SA (0.5 and 1 mmol/L) solution in the dark for 24 h followed by incubation in Petri dishes containing 20 mL water or 15% PEG-6000 for 7 days. In seedling stage trial, 7-day-old seedlings were exposed to 15% PEG-6000 containing nutrient solution (Cooper 1996), and H_2O_2 (5 and 10 mmol/L) or SA (0.5 and 1 mmol/L) were applied in foliage (10 mL/spray/pot) at 1-day interval. The 10 L nutrient solution contained, KH_2PO_4 (2.63 g), KNO_3 (5.83 g), $Ca(NO_3)_2{\cdot}4\ H_2O$ (10.03 g), $FeSO_4{\cdot}7\ H_2O$ (2.00 g), $MgSO_4{\cdot}7\ H_2O$ (0.79 g), $MnSO_4$ (0.061 g), H_3BO_3 (0.017 g), $CuSO_4 {\cdot}5\ H_2O$ (0.004 g), Na_2MoO_4 (0.003 g), and $ZnSO_4{\cdot}7\ H_2O$ (0.0044 g). In soil-based study, 50 germinated seeds were sown in each pot having 750 g soil (silty loam; pH, 6.12; electrical conductivity, 0.25 dS/m; cation exchange capacity, 20.4 cmol/kg; exchangeable Na^+, 0.38 cmol/kg; exchangeable K^+, 0.15 cmol/kg; total nitrogen, 0.12% and organic carbon, 1.19%), and grown in well-watered condition for 10 days, and later the irrigation was stopped, and H_2O_2 or SA (10 mL/spray/pot) at 1-day interval were applied. After 7 days, germination indices, morphological parameters, and relative water content (RWC) were measured as reported by Tahjib-Ul-Arif et al. (2019).

Determination of proline (Pro), H_2O_2, MDA, and SPAD chlorophyll. Pro, H_2O_2, and MDA (malondialdehyde) contents were determined following the method of Tahjib-Ul-Arif et al. (2018). Chlorophyll (*Chl*) content in terms of SPAD (soil plant analysis development) values was recorded using a portable SPAD 502 Plus meter (Konica-Minolta, Tokyo, Japan). In each measurement, the SPAD reading was repeated 5 times from the leaf tip to base, and the average was used for analysis.

Antioxidant enzyme activity assay. Fresh leaves (0.05 g) were homogenized in 50 mmol ice-cold potassium phosphate buffer (pH 8.0). After centrifuging the homogenate at 11 500 × g for 10 min at 4 °C, the supernatant was separated and used for the determination of the activity of CAT (EC 1.11.1.6), APX (EC 1.11.1.11) and GPOX (EC: 1.11.1.7) according to Tahjib-Ul-Arif et al. (2018).

Statistical analysis. The data were subjected to a one-way or two-way analysis of variance using Minitab 17 (Pennsylvania, USA), followed by Tukey's test ($P < 0.05$).

RESULTS

Exogenous H_2O_2 or SA improved germination indices. Drought stress notably decreased final germination percentage (FGP); coefficient of the velocity of germination (CVG); germination rate index (GRI); plumule length (PL); radicle length (RaL), and plumule fresh weight (PFW), whereas increased mean germination time (MGT) compared with control. On the contrary, exogenous H_2O_2 (5 and 10 mmol/L) or SA (0.5 and 1 mmol/L) increased FGP, CVG, GRI, PL, RaL, and PFW, whereas decreased MGT compared with only drought-stressed plants (Table 1).

Exogenous H_2O_2 or SA enhanced growth and photosynthetic pigment. Drought stress (hydroponic and soil condition) resulted in a pointed de-

https://doi.org/10.17221/472/2019-PSE

Table 1. The effects of exogenous hydrogen peroxide (H_2O_2) or salicylic acid (SA) on germination and growth at germination stage under drought

Treatment	Germination indices				Growth parameters		
	FGP (%)	CVG (%/day)	GRI (%/day)	MGT (day)	PL (cm/plant)	RaL (cm/plant)	PFW (mg/plant)
Control	83.11 ± 1.3^{a}	32.20 ± 0.8^{a}	75.56 ± 2.4^{a}	3.16 ± 0.09^{b}	12.98 ± 0.6^{a}	8.76 ± 0.6^{a}	34.52 ± 0.9^{a}
Drought (D)	71.11 ± 3.46^{b}	27.25 ± 1.0^{b}	53.31 ± 3.1^{b}	3.76 ± 0.09^{a}	5.52 ± 0.2^{c}	7.56 ± 0.1^{a}	4.38 ± 0.2^{c}
D + 5 mmol/L H_2O_2	82.22 ± 1.6^{ab}	30.24 ± 0.5^{ab}	67.96 ± 2.6^{a}	3.36 ± 0.06^{ab}	7.21 ± 0.0^{bc}	8.45 ± 0.1^{a}	10.04 ± 0.5^{b}
D + 10 mmol/L H_2O_2	84.0 ± 1.6^{a}	32.26 ± 0.5^{a}	77.36 ± 1.3^{a}	3.14 ± 0.06^{b}	7.35 ± 0.1^{b}	9.13 ± 0.1^{a}	9.42 ± 0.2^{b}
D + 0.5 mmol/L SA	85.11 ± 2.0^{a}	31.52 ± 0.8^{a}	74.05 ± 2.9^{a}	3.08 ±0.04^{b}	7.87 ± 0.2^{b}	8.87 ± 0.1^{a}	9.76 ± 0.3^{b}
D + 1 mmol/L SA	89.44 ± 1.0^{a}	31.53 ± 0.3^{a}	73.65 ± 1.0^{a}	3.21 ±0.03^{b}	7.35 ± 0.3^{b}	8.35 ± 0.5^{a}	10.13 ± 0.1^{b}

Values are presented as mean ± standard error (n = 3). Data having the same letter(s) in the column do not differ significantly (Tukey's test P < 0.05). FGP – final germination percentage; CVG – coefficient of the velocity of germination; GRI – germination rate index; MGT – mean germination time; PL – plumule length; RaL – radicle length; PFW – plumule fresh weight

crease in the growth and biomass in terms of shoot length (SL), root length (RL), and shoot fresh weight (SFW) (Table 2, Figure 1). However, exogenous H_2O_2 (5 and 10 mmol/L) or SA (0.5 and 1 mmol/L), both in hydroponic and soil conditions, notably alleviated the drought-induced inhibition of growth compared with drought-stressed plants. Among the doses, 5 mmol/L H_2O_2, or 0.5 and 1 mmol/L SA showed the highest productivity in enhancing the growth of rice plants in soil-based drought conditions. In soil conditions, drought markedly reduced the SPAD *Chl*. Conversely, H_2O_2 (5 mmol/L) or SA (0.5 and 1 mmol/L) treatment markedly increased the SPAD *Chl* of rice plants compared with only drought-exposed seedlings.

Exogenous H_2O_2 or SA declined endogenous H_2O_2 and MDA contents. The endogenous H_2O_2 and MDA contents were significantly increased in rice leaves when exposed to drought both in hydroponic and soil conditions (Figure 2A, B). Oppositely, both in hydroponic and soil conditions, when drought-stressed plants were treated with H_2O_2 (5 and 10 mmol/L) and SA (0.5 and 1 mmol/L) showed a marked reduction in endogenous H_2O_2 and MDA content as compared with the only drought-exposed plants.

Exogenous H_2O_2 or SA improved RWC and regulated Pro content. RWC of rice leaves radically fell due to drought exposure (hydroponic and soil condition), which in turn increased the Pro content markedly (Figure 2C, D). However, H_2O_2 (5 and 10 mmol/L) or SA (0.5 and 1 mmol/L) treatment decreased the Pro content and increased the leaf RWC in drought-stressed plants compared with only drought-stressed plants.

Table 2. The effects of exogenous hydrogen peroxide (H_2O_2) or salicylic acid (SA) on the growth of rice seedlings grown under drought

Treatment	Hydroponics experiment			Soil experiment		
	SL (cm)	RL (cm)	SFW (mg/plant)	SL (cm)	SFW (mg/plant)	SPAD
Control	18.10 ± 0.8^{a}	9.06 ± 0.2^{ab}	67.33 ± 0.5^{a}	26.75 ± 0.3^{a}	145.66 ± 0.3^{a}	20.63 ± 0.5^{a}
Drought (D)	9.93 ± 0.6^{c}	10.80 ± 0.1^{a}	34.00 ± 1.2^{d}	17.76 ± 0.3^{c}	56.86 ± 1.6^{d}	12.00 ± 0.9^{d}
D + 5 mmol/L H_2O_2	15.96 ± 0.8^{ab}	7.20 ± 0.4^{b}	56.33 ± 1.0^{b}	21.33 ± 0.5^{b}	83.80 ± 1.0^{b}	17.06 ± 0.1^{b}
D + 10 mmol/L H_2O_2	13.10 ± 0.8^{bc}	7.33 ± 0.4^{b}	56.66 ± 1.8^{b}	21.06 ± 0.2^{b}	74.06 ± 0.3^{c}	13.63 ± 0.4^{cd}
D + 0.5 mmol/L SA	11.96 ± 0.6^{bc}	7.70 ± 0.2^{b}	46.33 ± 1.2^{c}	21.80 ± 0.7^{b}	87.20 ± 1.0^{b}	15.00 ± 0.04^{bc}
D + 1 mmol/L SA	12.83 ± 0.8^{bc}	7.96 ± 0.6^{b}	49.33 ± 1.1^{c}	21.46 ± 0.4^{b}	84.40 ± 1.4^{b}	15.86 ± 0.2^{bc}

Values are presented as mean ± standard error (n = 3). Data having the same letter(s) in the column do not differ significantly (Tukey's test P < 0.05). SL – shoot length; RL – root length; SFW – shoot fresh weight; SPAD – soil plant analysis development

https://doi.org/10.17221/472/2019-PSE

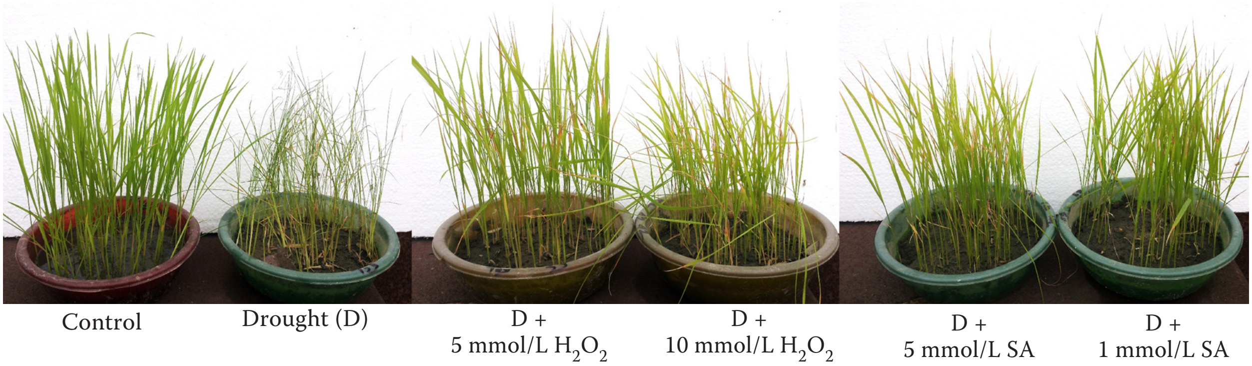

Figure 1. Phenotypic appearance of rice seedlings grown without watering for 7 days with exogenous hydrogen peroxide (H_2O_2) or salicylic acid (SA)

Exogenous H_2O_2 or SA enhanced antioxidant enzyme activities. Drought in hydroponics increased CAT and APX activity, and in soil increased CAT and GPOX activity (Figure 3). Moreover, the activity of CAT and GPOX increased radically when treated with exogenous 5 and 10 mmol/L H_2O_2 or 0.5 and 1 mmol/L SA both in hydroponic and soil drought conditions. The APX activity increased due to the application of H_2O_2 or SA in soil, and 5 mmol/L H_2O_2 in hydroponic drought condition.

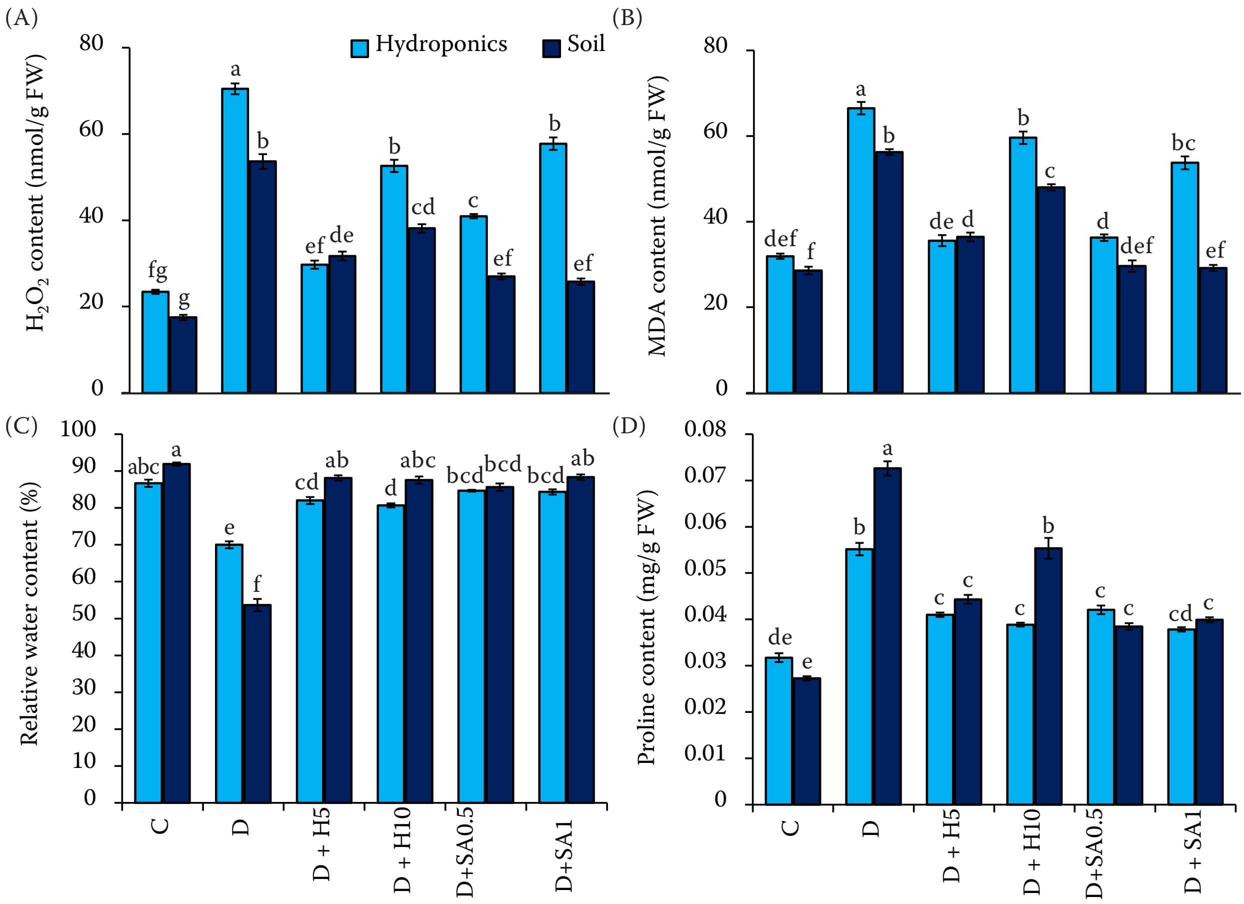

Figure 2. Effect of exogenous hydrogen peroxide (H_2O_2) or salicylic acid (SA) on (A) endogenous H_2O_2 content; (B) malondialdehyde (MDA) content; (C) relative water content, and (D) proline content in rice seedlings. Data are presented as mean ± standard error (n = 3) and different letters indicate significant difference (Tukey's test, $P < 0.05$). C – control; D – drought; D + H5 – drought + 5 mmol/L H_2O_2; D + H10 – D + 10 mmol/L H_2O_2; D + SA0.5 – D + 0.5 mmol/L SA; D + SA1 – D + 1 mmol/L SA; FW – fresh weight

https://doi.org/10.17221/472/2019-PSE

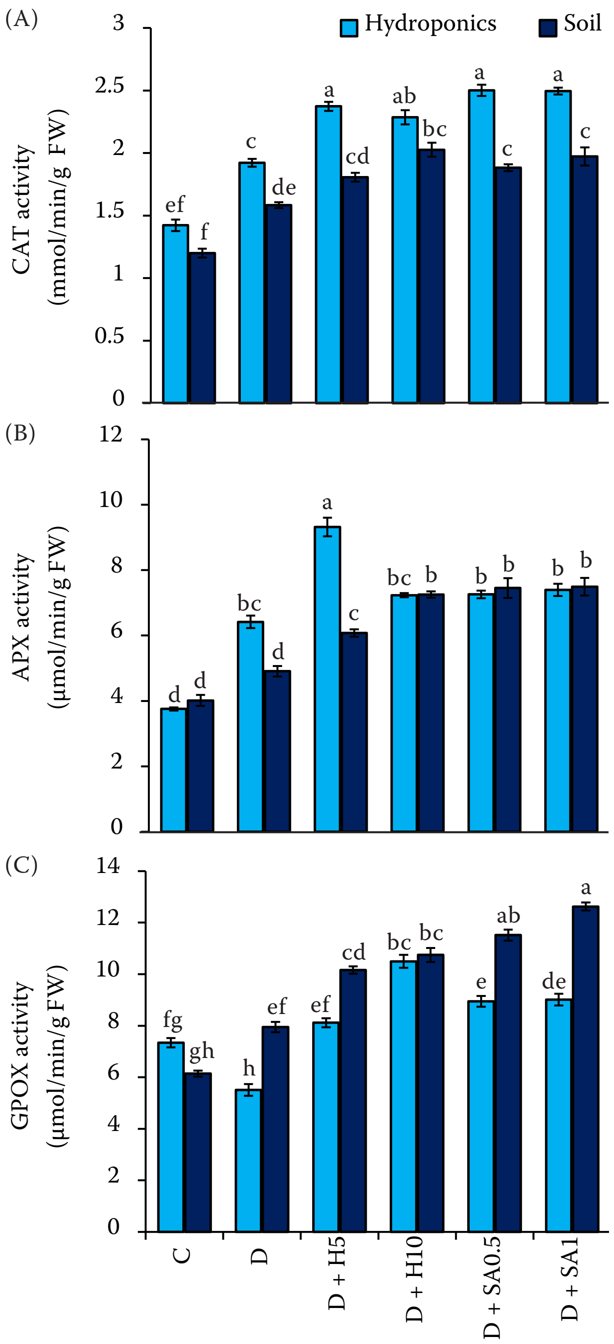

Figure 3. Effect of exogenous hydrogen peroxide (H_2O_2) or salicylic acid (SA) on (A) catalase (CAT); (B) ascorbate peroxidase (APX), and (C) guaiacol peroxidase (GPOX) activities in rice seedlings. Other details are same as Figure 2

DISCUSSION

Effective approaches are needed for improving the drought tolerance of rice during the early growth stage to ensure sustainable yield. It is well reported that H_2O_2 and SA upregulate many physiological processes, and here we investigated their relative effects on drought mitigation in rice.

Seed germination is highly subtle to water availability, and limited water caused reduced germination indices (Toscano et al. 2017), which is in line with our results. Specifically, FGP, CVG, GRI, MGT, and the growth decreased under drought (Table 1), as also observed in kenaf (Tang et al. 2019). Drought decreases gibberellins, which, in turn, reduce α-amylase activity (Liu et al. 2018), which might be triggered by the drought-induced impairment of germination indices (Table 1). On the contrary, the exogenous application of H_2O_2 or SA reduced the drought-induced inhibition of germination indices (Table 1), as also mentioned in Crownvetch under drought (Ma et al. 2007).

At the seedling stage, the growth and biomass retardation were found both in hydroponic and soil drought condition, which might happen due to the reduced photosynthetic pigment and increased ROS production (Table 2, Figures 1 and 2). Similar results were also reported in alfalfa (Tani et al. 2019). On the contrary, H_2O_2 or SA treatment notably alleviated drought-induced inhibition of growth and photosynthetic pigment of rice plants (Table 2), similar effects observed in cucumber (Sun et al. 2016) and wheat (Kang et al. 2013). Moreover, in the current trial, RWC decreased markedly alone with the increasing Pro content in response to drought to compensate for the drought-induced water loss in rice plants (Figure 2C, D). A similar result was reported in drought-stressed mung bean (Nahar et al. 2015). Alternatively, both H_2O_2 or SA application increased the RWC, and application of SA and low dose of H_2O_2 decreased Pro content, but high dose of H_2O_2 showed no effect on Pro content (Figure 2C, D), as also observed in *Cymbopogn flexuosus* and cucumber under drought (Idrees et al. 2010, Sun et al. 2016). This finding suggests that the application of SA or H_2O_2 might activate plant defensive system and helped plant to adjust the water status under drought, but, the high dose of H_2O_2 was less effective to alleviate drought stress as reflected by the lower SFW and SPAD values in 10 mmol/L H_2O_2-treated drought-stressed plants (Table 1).

Drought amplified endogenous H_2O_2 and MDA contents in the current study, which corroborates with the findings of Alam et al. (2013) and Farooq et al. (2010). ROS can attack membrane lipids and alters the membrane permeability, and protection from such effect is a key stress tolerance system (Choudhury et al. 2017).

https://doi.org/10.17221/472/2019-PSE

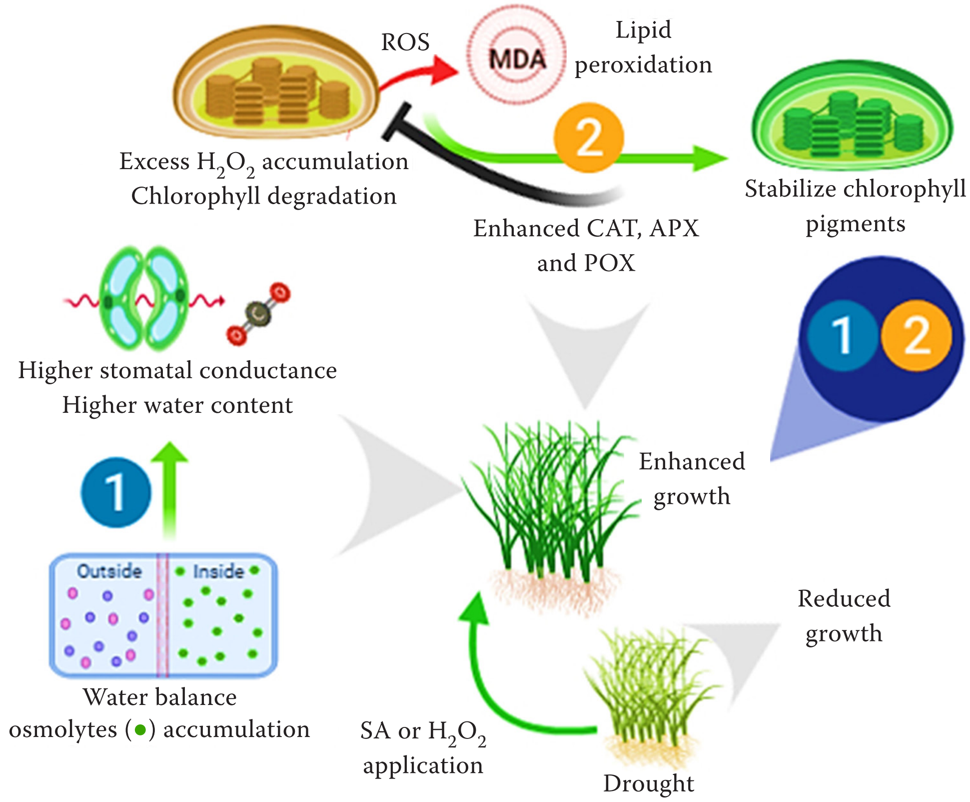

Figure 4. Mechanisms of exogenous salicylic acid (SA)- and hydrogen peroxide (H_2O_2)-mediated drought tolerance in rice. ROS – reactive oxygen species; CAT – catalase; APX – ascorbate peroxidase; POX – peroxidase

H_2O_2 or SA treatment has been displayed to decrease the endogenous H_2O_2, which in turn decreased MDA content (Figure 2A, B). This is in accordance with the previous studies that reported a decreased H_2O_2 and MDA in mustard (Alam et al. 2013) and rice (Farooq et al. 2010) under osmotic stress. To investigate the ROS scavenging mechanism, we further analyzed the enzymatic antioxidants. In our experiment, CAT, APX, and GPOX showed a slight increment under drought, but this increment is not sufficient to neutralize the excessive H_2O_2. A similar result was also observed in drought-stressed (Zhang and Kirkham 1994) and salt-stressed (Latef et al. 2019) wheat. However, H_2O_2 or SA treatment augmented the CAT, APX and GPOX activity further under drought, which consequently lowered the level of H_2O_2 in drought-stressed plants (Figures 2A and 3). Similar results were also found in soybean (Guler and Pehlivan 2016), mustard under drought (Alam et al. 2013), and in salt-stressed wheat (Latef et al. 2019).

In conclusion, the present study demonstrated that the exogenous application of 5 mmol/L H_2O_2 or 0.5 and 1 mmol/L SA equally improved water stress tolerance of rice seedlings. The beneficial effects of H_2O_2 or SA treatments might be attributed to H_2O_2- or SA-mediated alleviation of drought-induced over-accumulation of ROS, possibly by enhancing the activities of antioxidant enzymes (Figure 4). In addition, exogenous H_2O_2 or SA application was found to be effective in osmotic adjustment (Figure 4). Overall, the application of H_2O_2 or SA could be recommended to farmers as an effective measure for the better establishment of early seedlings of rice under drought environments.

REFERENCES

Alam M.M., Hasanuzzaman M., Nahar K., Fujita M. (2013): Exogenous salicylic acid ameliorates short-term drought stress in mustard (*Brassica juncea* L.) seedlings by up-regulating the antioxidant defense and glyoxalase system. Australian Journal of Crop Science, 7: 1053–1063.

Banerjee A., Roychoudhury A. (2019): Abiotic stress tolerance in plants by priming and pretreatment with hydrogen peroxide. In: Hasanuzzaman M., Fotopoulos V. (eds.): Priming and Pretreatment of Seeds and Seedlings. Singapore, Springer, 417–426.

Choudhury F.K., Rivero R.M., Blumwald E., Mittler R. (2017): Reactive oxygen species, abiotic stress and stress combination. The Plant Journal, 90: 856–867.

https://doi.org/10.17221/472/2019-PSE

Cooper A. (1996): ABC of Nft: Nutrient Film Technique: The World's First Method of Crop Production Without a Solid Rooting Medium (181P). Chicago, International Specialized Book Services.

Fahad S.C., Bajwa A.A., Nazir U., Anjum S.A., Farooq A., Zohaib A., Sadia S., Nasim W., Adkins S., Saud S., Ihsan M.Z., Ihsan M.Z., Alharby H., Wu C., Wang D.P., Huang J.L. (2017): Crop production under drought and heat stress: Plant responses and management options. Frontiers in Plant Science, 8: 1147.

Fahad S.C., Adnan M., Noor M., Arif M., Alam M., Khan I.A., Ullah H., Wahid F., Mian I.A., Jamal Y., Basir A. (2019): Major constraints for global rice production. In: Hasanuzzaman M., Fujita M., Nahar K., Biswas J. (eds.): Advances in Rice Research for Abiotic Stress Tolerance. Cambridge, Woodhead Publishing, 1–22.

Farooq M., Wahid A., Lee D.-J., Cheema S.A., Aziz T. (2010): Drought stress: Comparative time course action of the foliar applied glycinebetaine, salicylic acid, nitrous oxide, brassinosteroids and spermine in improving drought resistance of rice. Journal of Agronomy and Crop Science, 196: 336–345.

Guler N.S., Pehlivan N. (2016): Exogenous low-dose hydrogen peroxide enhances drought tolerance of soybean (*Glycine max* L.) through inducing antioxidant system. Acta Biologica Hungarica, 67: 169–183.

Hussain H.A., Hussain S., Khaliq A., Ashraf U., Anjum S.A., Men S., Wang L. (2018): Chilling and drought stresses in crop plants: Implications, cross talk, and potential management opportunities. Frontiers in Plant Science, 9: 393.

Idrees M., Khan M.M.A., Aftab T., Naeem M., Hashmi N. (2010): Salicylic acid-induced physiological and biochemical changes in lemongrass varieties under water stress. Journal of Plant Interactions, 5: 293–303.

Kang G.Z., Li G.Z., Liu G.Q., Xu W., Peng X.Q., Wang C.Y., Zhu Y.J., Guo T.C. (2013): Exogenous salicylic acid enhances wheat drought tolerance by influence on the expression of genes related to ascorbate-glutathione cycle. Biologia Plantarum, 57: 718–724.

Latef A., Hamed A.A., Kordrostami M., Zakir A., Zaki H., Saleh O.M. (2019): Eustress with H_2O_2 facilitates plant growth by improving tolerance to salt stress in two wheat cultivars. Plants (Basel), 8: 303.

Liu L., Xia W., Li H., Zeng H., Wei B., Han S., Yin C. (2018): Salinity inhibits rice seed germination by reducing α-amylase activity via decreased bioactive gibberellin content. Frontiers in Plant Science, 9: 275.

Ma H., Chong K., Deng X.W. (2007): Rice research: Past, present and future. Journal of Integrative Plant Biology, 49: 729–730.

Maruri-López I., Aviles-Baltazar N.Y., Buchala A., Serrano M. (2019): Intra and extracellular journey of the phytohormone salicylic acid. Frontiers in Plant Science, 10.

Nahar K., Hasanuzzaman M., Alam M.M., Fujita M. (2015): Glutathione-induced drought stress tolerance in mung bean: Coordinated roles of the antioxidant defence and methylglyoxal detoxification systems. AoB Plants, 7.

Noctor G., Reichheld J.P., Foyer C.H. (2018): ROS-related redox regulation and signaling in plants. Seminars in Cell and Developmental Biology, 80: 3–12.

Prasad R., Shivay Y.S., Kumar D. (2017): Current status, challenges, and opportunities in rice production. In: Chauhan B., Jabran K., Mahajan G. (eds.): Rice Production Worldwide. Cham, Springer, 1–32.

Smirnoff N., Arnaud D. (2019): Hydrogen peroxide metabolism and functions in plants. New Phytologist, 221: 1197–1214.

Sun Y., Wang H., Liu S., Peng X. (2016): Exogenous application of hydrogen peroxide alleviates drought stress in cucumber seedlings. South African Journal of Botany, 106: 23–28.

Tahjib-Ul-Arif Md., Afrin S., Polash M.A.S., Akter T., Ray S.R., Hossain Md.T., Hossain M.A. (2019): Role of exogenous signaling molecules in alleviating salt-induced oxidative stress in rice (*Oryza sativa* L.): A comparative study. Acta Physiologiae Plantarum, 41: 69.

Tahjib-Ul-Arif Md., Roy P.R., Sohag A.A.M., Afrin S., Rady M.M., Hossain M.A. (2018): Exogenous calcium supplementation improves salinity tolerance in *BRRI dhan28*; a salt-susceptible high-yielding *Oryza sativa* cultivar. Journal of Crop Science and Biotechnology, 21: 383–394.

Tang D.F., Wei F., Qin S.X., Khan A., Kashif M.H., Zhou R.Y. (2019): Polyethylene glycol induced drought stress strongly influences seed germination, root morphology and cytoplasm of different kenaf genotypes. Industrial Crops and Products, 137: 180–186.

Tani E., Chronopoulou E.G., Labrou N.E., Sarri E., Goufa M., Vaharidi X., Tornesaki A., Psychogiou M., Bebeli P.J., Abraham E.M. (2019): Growth, physiological, biochemical, and transcriptional responses to drought stress in seedlings of *Medicago sativa* L., *Medicago arborea* L. and their hybrid (Alborea). Agronomy, 9: 38.

Toscano S., Romano D., Tribulato A., Patanè C. (2017): Effects of drought stress on seed germination of ornamental sunflowers. Acta Physiologiae Plantarum, 39: 184.

Zhang J.X., Kirkham M.B. (1994): Drought-stress-induced changes in activities of superoxide dismutase, catalase, and peroxidase in wheat species. Plant and Cell Physiology, 35: 785–791.

Received: August 28, 2019
Accepted: December 2, 2019
Published online: January 8, 2020