DOI: 10.1007/s11099-018-0830-8 PHOTOSYNTHETICA 56 (4): 1237-1248, 2018

REVIEW

Hydrogen peroxide in regulation of plant metabolism: Signalling and its effect under abiotic stress

T.A. KHAN*, M. YUSUF**, and Q. FARIDUDDIN***,+

*College of Life Science and Technology, Huazhong Agricultural University, Wuhan-430070, Hubei, China**
*Department of Biology, College of Science, United Arab Emirates University, P.O. Box: 15551, Al Ain, Abu Dhabi, UAE***
*Plant Physiology and Biochemistry Section, Department of Botany, Aligarh Muslim University, Aligarh-202002, India****

Abstract

In plants, hydrogen peroxide (H_2O_2) acts as a signalling molecule that facilitates various biochemical and physiological processes. H_2O_2 is a versatile molecule, involved in several cellular processes both under stress and stress-free conditions. In regulating plant metabolism under stress conditions, exogenous application of H_2O_2 also plays a pivotal role which is manifested in improved growth, photosynthetic capacity, and antioxidant protection. Abiotic stress is an inevitable environmental factor that extensively affects and reduces growth, quality, yield, and productivity of plants**.** Several signalling pathways involved in H_2O_2-mediated stress and defense responses have been extensively studied and there is ample scope of additional research that could further clarify the mechanism and modulating factors which regulate these pathways. An attempt has been made to dissect the role of H_2O_2 under low temperature stress and how it affects plant growth and development, photosynthetic capacity, regulation of antioxidant system, and signalling.

Additional key words: antioxidants; hydrogen peroxide; low temperature; photosynthesis; reactive oxygen species; signalling**.**

Introduction

Hydrogen peroxide (H_2O_2) plays diverse roles in plants and acts as a signalling molecule. In the past two decades, evidence has been accumulating to address involvement of H_2O_2 in stress responses in plants; but how it interacts with phytohormones and the ways how signals are involved in biological processes remain fragmentary and still to be unravelled in detail. H_2O_2 mediates complex biological functions in plants because of its properties of free radical, small size, and high diffusibility (Leshem *et al.* 1998). In last ten years, various researchers tried to study the role of H_2O_2 as a signalling molecule. Because of its low reactivity compared to other types of reactive oxygen species (ROS), it has relatively long-life span and small size of H_2O_2 molecules is very helpful to cross biological membranes, facilitating signalling functions (Noctor *et al.* 2014). ROS may interact selectively with a target molecule that perceives the increase of ROS concentration and translates this information into signals that direct the plant responses to stress. ROS would be ideally more suited to act as such signaling molecules. There are several mechanisms for ROS production, some of which are rapid and controllable, and there are numerous mechanisms for rapid removal of ROS (Apel and Hirt 2004). The antioxidant systems, including detoxifying enzymes, play a pivotal role in regulating the H_2O_2 concentration (Noctor and Foyer 1998). Thus, antioxidant enzymes are emerging as key regulators of the multitude of pathways that respond to H_2O_2. In fact, both the production and scavenging

---

Received 20 July 2017, *accepted* 9 March 2018, *published as online-first* 21 June 2018.

+Corresponding author; email: qazi_farid@yahoo.com

Abbreviations: APX – ascorbate peroxidase; C_i – internal CO_2 concentration; CAT – catalase; DHAR – dehydroascorbate reductase; g_s – stomatal conductance; GPX – glutathione peroxidase; GR – glutathione reductase; MDHAR – monodehydroascorbate reductase; MAPK – mitogen-activated protein kinase; NPK1 – *Nicotiana* protein kinase 1; Φ_{PSII} – photochemical efficiency of PSII; POX – peroxidase; P_N – net photosynthetic rate; q_P – photochemical quenching coefficient; ROS – reactive oxygen species; SOD – superoxide dismutase; SPAD – soil and plant analysis development.

Acknowledgements: The authors gratefully acknowledge financial support provided by the Council of Science and Technology, Uttar Pradesh [Project No. CST/D-615], India.

of H_2O_2 in plant cells seems to be an integrated network that are responsible for triggering biological responses. However, H_2O_2 plays a versatile role in plants at low concentration; it acts as a signalling molecule and is also involved in the mitigation of numerous abiotic and biotic stresses (He *et al.* 2009, Mittler *et al.* 2011, Dietz *et al.* 2016). At higher concentrations, it induces the onset of cell death (Gechev and Hille 2005, Karuppanapandian *et al.* 2011, Bhattacharjee 2012). It plays an important role in plant cell wall reinforcement (cross-linking of cell wall structural proteins, lignification), production of phytoalexin, and resistance augmentation against diverse stresses (Gill and Tuteja 2010, Ahmad 2014). H_2O_2 is a key regulator in a broad range of physiological and biological processes such as germination and seedling growth (Wahid *et al.* 2008), photosynthesis (Noctor and Foyer 1998, Fariduddin *et al.* 2014, Khan *et al.* 2015, Hasan *et al.* 2016), stomatal movement, cell growth, and development (Deng *et al.* 2012), antioxidant systems (Khan *et al.* 2015, 2016, Hasan *et al.* 2016), and senescence (Peng *et al.* 2005). Therefore, it has been reported that the endogenous content of H_2O_2 depends on its production rates and utilization by antioxidant systems (Hung *et al.* 2005, Terzi *et al.* 2014). It has been described that H_2O_2 plays pivotal roles in modulating defense response of plants to diverse environmental stresses, such as salt stress (Li *et al.* 2011, Ashfaque *et al.* 2014), oxidative stress (Morita *et al.* 1999, Iseri *et al.* 2013), nickel stress (Khan *et al.* 2016), copper stress (Guzel and Terzi 2013, Fariduddin *et al.* 2014), heat stress (Wang *et al.* 2014), and chilling stress (Yu *et al.* 2003, Wang *et al.* 2010). In addition to this, exogenous application of H_2O_2 could be an effective approach for enhancing stress tolerance and improving productivity of crop plants under various abiotic stresses.

Role of hydrogen peroxide in plant growth and development

H_2O_2 is involved in many growth and developmental processes of plants, including root gravitropism and root system development (Ma *et al.* 2014, Hernandez-Barrera *et al.* 2015), stomatal movement, cell growth and development (Deng *et al.* 2012), formation of adventitious roots (Dunand *et al.* 2007), cell wall development (Carol and Dolan 2006), stomatal aperture regulation (Ge *et al.* 2015), and programmed cell death (Van Breusegem and Dat 2006, Cheng *et al.* 2015, Vavilala *et al.* 2015). Generally, H_2O_2 was used as a stimulant for inducing germination. Soaking seeds in H_2O_2 improved their germination in many plants, including barley, spinach, camphor, almond, and *Zinnia elegans*, *Panicum virgatum*, *Andropogon gerardii*, and *Sorghastrum nutans* (Chen and Lin 1994, Fontaine *et al.* 1994, Ogawa and Iwabuchi 2001, Sarath *et al.* 2007, Zeinalabedini *et al.* 2009, Barba-Espin *et al.* 2011). It has been shown that presown seed primed with H_2O_2 improved seed quality, resulting in better germination performance and greater vigour, while moderately abolishing aging effects on seeds (Wojtyla *et al.* 2016). Recently, Hasan *et al.* (2016) reported that foliar application of H_2O_2 increased growth parameters in *Vigna unguiculata.* Low concentration of H_2O_2 positively affected the adventitious root growth of marigold and sweet potato seedlings (Deng *et al.* 2012, Liao *et al.* 2012). Several plant hormones have been documented to interact with H_2O_2 during germination and early plant growth (Barba-Espin *et al.* 2010). The encouraging effect of H_2O_2 on seed germination could be due to scavenging of H_2O_2 which resulted in higher production of O_2 required for mitochondrial respiration and metabolic activities in spinach (Katzman *et al.* 2001). Another explanation is that H_2O_2 is helpful in cracking hard seeds, permitting them to interact with water (Chen and Lin 1994). On the other hand, the pericarp and seed coat often contain phenolic compounds and alkaloids, which inhibit seed germination (Tao and Buta 1986, Bhattacharyya *et al.* 1999); these can be oxidized by H_2O_2 (Ogawa and Iwabuchi 2001). It has been suggested that NADPH oxidases are involved in the production of ROS during seed germination (Liu *et al.* 2007) and in breaking its dormancy (Oracz *et al.* 2009). Likewise, hydroxyl radical ($OH^{\cdot}$)-mediated cell wall loosening during seed germination and seedling growth have been reported (Müller *et al.* 2009). Moreover, treatment with H_2O_2 during early stage of plants also generated positive effect on germination that, without H_2O_2 treatment, was delayed by temperature stress (Çavusoglu and Kabar 2010). Treatment of seeds with H_2O_2 overcame the delay in germination induced by salt and temperature stress. The proteomic analysis indicated that H_2O_2 induced the expression of proteins related to plant signalling and development (Barba-Espin *et al.* 2010). Therefore, the redox state could be modulated by H_2O_2 corroborated with the expression of proteins involved in signalling and development during the early stage of seedling growth.

Physiological roles of hydrogen peroxide

Hydrogen peroxide and photosynthesis

Photosynthesis is the main source of carbon assimilation in plants. Increasing either photosynthetic efficiency or total plant photosynthetic capacity (delaying leaf senescence) results in the enhanced production of photoassimilates (van Camp 2005). It has been established that H_2O_2 affects the net photosynthetic rate and the related attributes in plants (Fariduddin *et al.* 2014, Khan *et al.* 2015, Hasan *et al.* 2016). Khandaker *et al.* (2012) also noted that exogenous application of H_2O_2 increased photosynthetic rates and dry matter content of the leaves in wax apple under field conditions. There is a number of reports available where the effects of H_2O_2 on photosynthesis have been examined but diversity exists among these observations (Table 1).

The reason for the H_2O_2-mediated increase in photosynthetic efficiency could be due to the fact that H_2O_2 treatments increased the maximum carboxylation rate of Rubisco (V_{cmax}) and initial Rubisco activity, but had no effects on the total activity of Rubisco. This indicates that H_2O_2 mainly regulates the activation state of Rubisco, possibly through the action of Rubisco enzyme (Jiang *et al.* 2012). H_2O_2 treatments also significantly increased the photochemical efficiency of PSII (Φ_{PSII}). Φ_{PSII} is determined by photochemical quenching coefficient (q_P) and maximum quantum yield of PS II (F_v/F_m). The inductions of Φ_{PSII} by H_2O_2 were mainly attributed to q_P but not related to F_v/F_m (Jiang *et al.* 2012). It was reported that q_P is controlled by the demand for ATP and NADPH in the Calvin cycle (Nogues and Baker 2000). The increased activity of the Calvin cycle induced by H_2O_2, therefore, could have contributed to the higher value of q_P.

Table 1. Effect of H_2O_2 on various photosynthetic traits in different plants.

Mode of H_2O_2 application	Plant species	Response	Reference
Exogenous	*Brassica juncea*	Increased net photosynthesis (P_N), g_s, and C_i	Khan *et al.* 2016
Foliar spray	*Vigna unguiculata*	Improved P_N and quantum yield of PSII	Hasan *et al.* 2016
Foliar spray	*Vigna radiata*	Improved photosynthesis and related attributes (P_N, C_i, and g_s values)	Fariduddin *et al.* 2014
Pretreated seedlings	*Oryza sativa*	Improved quantum yield of PSII	Uchida *et al.* 2002
Exogenous	*Oryza sativa*	Regulated P_N and higher activities of phosphoenolpyruvate carboxylase	Ren *et al.* 2014
Exogenous	*Syzygium samarangense*	Increased P_N	Khandaker *et al.* 2012
Exogenous	*Tagetes erecta*	Increased photochemical quenching coefficient (q_P), leading to transfer of more excited light-energy to PSII reaction centre	Liao *et al.* 2012
Foliar spray	*Cucumis sativus*	Enhanced the photochemical efficiency of PSII (Φ_{PSII}) and q_P	Jiang *et al.* 2012
Pretreatment of seed	*Triticum aestivum*	Increased P_N	He *et al.* 2009
Pretreatment of seeds	*Triticum aestivum*	Photosynthetic pigments and P_N increased	Ashfaque *et al.* 2014
Foliar spray	*Glycine max*	Increased the P_N, E, and g_s	Ishibashi *et al.* 2011
Seed soaking	*Vigna radiata*	Enhanced P_N, E, and g_s	Khan *et al.* 2015
Foliar spray	*Zea mays*	Improved the P_N, E, and g_s, and C_i	Gondim *et al.* 2013
Exogenous	*Vigna radiata*	Induced generation of NO in the guard cells and other cell	Lum *et al.* 2002

Hydrogen peroxide, oxidative stress and antioxidant system

Reactive oxygen species (ROS) are continuously generated during various metabolic processes in mitochondria, chloroplast, peroxisomes, and cytoplasm which disturb normal metabolism through damage of lipids, proteins, and nucleic acids when produced in excess (Hernandez *et al.* 2001, Ahmad *et al.* 2010, Anjum *et al.* 2015). Plants throughout their life are prone to oxidative damage induced by environmental factors due to their sessile nature (Hippeli and Elstner 1996). In addition to this, various abiotic stress factors can also lead to overproduction and accumulation of ROS (H_2O_2, superoxide anion, and hydroxyl radicals; Becana *et al.* 1998, Noctor and Foyer 1998, Gill and Tuteja 2010, Das and Roychoudhury 2014), generating oxidative stress (Das and Roychoudhury 2014, Mostofa *et al.* 2014, Nahar *et al.* 2014). One of the mechanisms actively employed by plants to overcome oxidative stress is activation of antioxidants. Plants have evolved various enzymatic and non-enzymatic antioxidant systems that are involved in protecting plants against oxidative stress (Pastori and Foyer 2002, Foyer and Noctor 2005). Catalase (CAT), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), superoxide dismutase (SOD), glutathione peroxidase (GPX), glutathione reductase (GR) are the key antioxidant enzymes that constitute major defence system against ROS (Payton *et al.* 2001, Fan and Huang 2012, Jahan and Anis 2014). SOD form the first line of defence against ROS, dismutating superoxide to H_2O_2, while APX, GPX, and CAT subsequently detoxify H_2O_2. The detoxification of H_2O_2 through APX involves a series of events occurring during ascorbate-glutathione cycle (AsA-GSH cycle). Among the non-enzymatic antioxidants GSH and ascorbate play a key role in biological system which include regulation of gene performance (Wingate *et al.* 1988, May *et al.* 1998, Krika *et al.* 2012, Kapoor *et al.* 2015), working as a precursor in the synthesis of phytochelatin and an important component of AsA-GSH cycle. Stress-tolerant plants have higher activities of antioxidant enzymes, including CAT, POX, SOD, and GR (Pinhero *et al.* 1997, Zhang *et al.* 1995).

Studies with transgenic plants that overexpress antioxidant enzymes also substantiate the importance of the antioxidant system for stress tolerance (Holmberg and Bülow 1998). Pretreatment with H_2O_2 has been shown to protect maize seedling from chilling injury by induction of peroxidases and mitochondrial catalase (Prasad *et al.* 1994a, Prasad *et al.* 1994b). H_2O_2 is also implicated as a part of a systemic signal that sets up an acclimatory response to high-light stress in *Arabidopsis* (Karpinski *et al.* 1999). Various studies have also emphasised the role of glutathione and ascorbate in plants signalling (Baier *et al.* 2000, Horling *et al.* 2003, Foyer and Noctor 2003). A correlation between H_2O_2 and antioxidant capacity have been reported in several plant species, such as *Brassica juncea* (Verma *et al.* 2013, Khan *et al.* 2016) *Vigna radiata* (Fariduddin *et al.* 2014, Khan *et al.* 2015), soybean (Ishibashi *et al.* 2011), *Vigna unguiculata* (Hasan *et al.* 2016), tomato (Zhou *et al.* 2012, Iseri *et al.* 2013), cucumber (Xia *et al.* 2009), and maize (Gondim *et al.* 2013). Sofo *et al.* (2015) discussed the role of H_2O_2 in plants experiencing water deficit and salinity and how CAT and APX activities are regulated at a gene level under these conditions. Moreover, transgenic plants overexpressing ROS-scavenging enzymes, such as SOD (Alscher *et al.* 2002), APX (Wang *et al.* 1999), GR (Foyer *et al.* 1995), and GPX (Roxas *et al.* 1997, 2000) showed enhanced tolerance to osmotic, temperature, and photoinhibition. The accumulation of proline is also reported to play a significant role in decreasing the photodamage of thylakoid membranes by scavenging the superoxide radicals (Ashraf and Foolad 2007, Banu *et al.* 2009). *α*-tocopherols, lipid-soluble antioxidants are considered as scavengers of ROS and lipid radicals in plants (Hollander-Czytko *et al.* 2005). Tocopherols are reflected as a major antioxidant in biomembranes, where they are involved as both antioxidant and non-antioxidant functions. They are considered general antioxidants for protecting membrane stability, including quenching or scavenging ROS as singlet oxygen. Out of four isomers of tocopherols (α-, β-, γ-, δ-) found in plants, α-tocopherol has the maximum antioxidative activity due to the occurrence of three methyl groups in its molecular structure (Kamal-Eldin and Appelqvist 1996). Carotenoids are pigments that are common in plants and microorganisms. These lipid-soluble antioxidants play important roles in plant metabolism and oxidative-stress tolerance. Carotenoids also provide protection *via* quenching of toxic ROS (Gill and Tuteja 2010, Kubis *et al.* 2014). Glycine betaine (GB) acts as a key osmoprotectant having significant potential to alleviate harmful effect produced by a variety of abiotic stresses in many organisms including algae, fungi, cyanobacteria, animals, and some higher plants (Türkan and Demiral 2009). In response to numerous environmental stresses, mainly drought and salinity, GB is stored in chloroplasts of some plant species and likewise, reported in diverse kind of microbes (Ranganayakulu *et al.* 2013).

Role of hydrogen peroxide in tolerance to abiotic stresses

H_2O_2 is generated due to exposure of various stresses, and many researchers have suggested that H_2O_2 plays a key role in acclimatization and cross-tolerance (Neill *et al.* 2002). Therefore, endogenous H_2O_2 production has been shown to increase as a result of the chilling stress in maize seedlings, where exogenous application of H_2O_2 increased tolerance to chilling stress (Prasad *et al.* 1994a). The application of H_2O_2 at low concentrations improved plant tolerance to heat stress (Gao *et al.* 2010), chilling (Gong *et al.* 2001), salt stress (Azevedo Neto *et al.* 2005, Li *et al.* 2011), aluminium-induced oxidative stress (Xu *et al.* 2010), and heavy metal stress (Lin *et al.* 2004, Hu *et al.* 2009, Fariduddin *et al.* 2014, Khan *et al.* 2016). Hossain *et al.* (2015) suggested that pretreatment of seeds or seedlings with H_2O_2, or combined application of H_2O_2 and abiotic stress, protected the plants under abiotic stresses by renewal of redox-homeostasis and alleviation of oxidative loss to membranes, proteins, and lipids and by modulating stress-signalling pathways. It has been also confirmed that the pretreatment with H_2O_2 in nutrient solution induces acclimation to salt stress in rice and maize seedlings, respectively (Uchida *et al.* 2002, Azevedo Neto *et al.* 2005). There is a number of reports where the effects of H_2O_2 on various abiotic stresses have been examined but diversity exists among these observations (Table 2).

Signalling of hydrogen peroxide

H_2O_2 functions as a signalling molecule including both intracellular as well as intercellular signals in numerous processes. This is of particular interest because intercellular signal molecule needs to be transported across at least one membrane. H_2O_2 can be naturally generated in a variety of normal cell types, either constitutively or in response to various stimuli (Burdon *et al.* 1995). Numerous stress conditions induce production of ROS such as $O_2^{\cdot -}$ and H_2O_2 in plant tissues (Desikan *et al.* 2003). ROS are highly reactive molecules and can oxidize all types of cellular components which leads to increase in lipid peroxidation, denaturation, and breakage of DNA strands, protein modification, and even cell death (Sharma *et al.* 2012, Anjum *et al.* 2015). Therefore, it is important to eliminate ROS to avoid low temperature or other stress-induced injuries in plants. These include heat, low temperature, ultra-violet (UV) light, pathogens, elicitors, and ozone stresses. Elevated contents of H_2O_2 have been observed during chilling stress in winter in wheat leaf where chilling temperature of 4°C triggered a three-fold rise in H_2O_2 concentration within 1 min (Okuda *et al.* 1991). Similarly, H_2O_2 contents also raise up during chilling of non-acclimated maize seedlings (Gondim *et al.* 2010). Moreover, H_2O_2 plays an important role in transduction of defense signals in plants and could induce gene expression and protein synthesis (Apostol *et al.* 1989, Burdon *et al.* 1995) in favour of tolerance mechanism.

Table 2. Effect of H_2O_2 on plants under various abiotic stresses.

Plant species	Type of stress	Response	Reference
Vigna radiata	Copper	Alleviated the toxic effects of copper stress by improving the photosynthetic attributes and activity of antioxidant enzymes which was reflected in better growth of plants	Fariduddin *et al.* 2014
Triticum aestivum	Salt	Improved the salt tolerance of the seedlings	Wahid *et al.* 2007
Citrus aurantium	Salt	Alleviated salinity-induced protein carbonylation and altered the accumulation levels of S-nitrosylated proteins in leaf	Tanou *et al.* 2009
Tagetes erecta	Drought	Protected the ultrastructure of mesophyll cells, improved photosynthetic performance and alleviated the negative effects of drought	Liao *et al.* 2012
Brassica juncea	Nickel	Improved the toxic effects of nickel stress by improving photosynthetic related attributes and induced antioxidant enzymes (APX and GR) and higher GSH production	Khan *et al.* 2016
Zea mays	Water deficit	Induced antioxidant system and nutrient relation in maize plants	Ashraf *et al.* 2015
Brassica juncea	Drought	Encouraged defence response in mustard seedlings by activation of methylglyoxal detoxification pathways	Hossain and Fujita 2013
Zea mays	UV radiation	Synergistically effective in promoting ethylene synthesis in defense responses	Wang *et al.* 2006
Oryza sativa	Salt and heat stress	Induced activities of ROS-scavenging enzymes and also generated higher quantum yield for PSII	Uchida *et al.* 2002
Lycopersicon esculentum	Cold stress	Root application of H_2O_2 decreased cold induced damage and improved cold response of tomato	Iseri *et al.* 2013
Tobacco	Oxidative stress	Leaves sprayed with H_2O_2 provided protection against oxidative stress by inducing CAT, APX, and guaiacol peroxidases	Gechev *et al.* 2002
Agrostis stolonifera	Heat stress	Foliar application of H_2O_2 induced tolerance to heat stress by reducing oxidative damage	Larkindale and Huang 2004
Zoysia tenuifolia and *Zoysia matrella*	Chilling stress	Improved the tolerance to chilling stress	Wang *et al.* 2010
Zea mays	Salt stress	Reduced the deleterious effects of salinity on seedling growth	Gondim *et al.* 2012
Vigna radiata	Chilling stress	Enhanced tolerance to chilling stress and also increased the glutathione content	Yu *et al.* 2003
Vigna radiata	Cold	Induced chilling tolerance comparable to cold acclimation	Hung *et al.* 2007
Festuca arundinacea and *Lolium perenne*	Heat	Increased the activities of POX, CAT, APX, GR, GPX, and glutathione pool	Wang *et al.* 2014
Cucumis sativus	Heat	Affected the heat-induced alteration of DNA methylation	Cao *et al.* 2013
Lycopersicon esculentum	Low temperature	Increased the growth characteristics, SPAD chlorophyll, activities of POX, PPO and fruits yield	Orabi *et al.* 2015
Zea Mays	Osmotic stress	Improved tolerance to osmotic stress by increasing some metabolites	Terzi *et al.* 2014
Vigna radiata	Chilling	Increased the glutathione content	Yu *et al.* 2003
Triticum aestivum	Aluminium	Aluminium-induced oxidative stress mitigation in wheat seedlings	Xu *et al.* 2011
Triticum aestivum	Salt	Decreased the deleterious effect of salt stress on growth of wheat	Li *et al.* 2011
Phaseolus vulgaris	Drought	Enhanced the root growth and fresh mass	Abass and Mohamed 2011
Triticum aestivum	Drought	Improved the photosynthetic rate and antioxidant system	He *et al.* 2009
Glycine max	Drought	Increased in the mRNA levels of d-myo-inositol 3-phosphate synthase 2 (GmMIPS2) and galactinol synthase (GolS)	Ishibashi *et al.* 2011

Calcium ions and hydrogen peroxide crosstalk

Ca^{2+} has been implicated as a secondary messenger and it is one of the major components in the cellular signalling (Sanders *et al.* 1999). The influx of Ca^{2+} through cation channels occurs in the tonoplast, endoplasmic reticulum, and plasma membrane and generates cytosolic Ca^{2+} $[Ca^{2+}]_{cyt}$ concentration that initiates cellular responses to a diverse range of developmental cues and environmental challenges (White 2000, Sanders *et al.* 2002). Various studies have revealed that transient variation in $[Ca^{2+}]_{cyt}$ plays an important role in signalling induced by various stresses (Monroy and Dhindsa 1995, Sanders *et al.* 1999). Cold shock induces transient increases in $[Ca^{2+}]_{cyt}$ content in tobacco and *Arabidopsis* (Knight *et al.* 1991, Knight *et al.* 1996, Polisensky and Braam 1996, Lewis *et al.* 1997). In the light of above mentioned studies, it could be believed that intracellular concentration of calcium was maintained through its influx which plays a key role in the cold shock response. Further, Pei *et al.* (2000) suggested that both Ca^{2+} and H_2O_2 are involved in a signalling cascade that leads to closure of stomata in *Arabidopsis*. H_2O_2-activated Ca^{2+} channels, mediate the influx of Ca^{2+} in the protoplasts along with the simultaneous increase in $[Ca^{2+}]_{cyt}$ in intact guard cells. However, this could be autocatalytic, because H_2O_2 production in the oxidative burst requires a constant Ca^{2+} influx, which activates the plasma membrane-localized NADPH oxidase (Lamb and Dixon 1997, Xing *et al.* 1997, Grant *et al.* 2000, Yang and Poovaiah 2002). Moreover, the $[Ca^{2+}]_{cyt}$ stimulates the calmodulin (a calcium sensor) and consequently passes the signal to a downstream target, *i.e.* CAT which finally downregulates H_2O_2 contents by catalysing its breakdown. The combination of H_2O_2 and Ca^{2+} may play essential roles in plants under both stress and stress-free conditions. Various plants, even different parts of the same plant, may have diverse modulation mechanisms. Thus, interaction between H_2O_2 and Ca^{2+} signalling in plants is very complex. The detailed mechanism of interaction between H_2O_2 and Ca^{2+} needs to be unraveled in detail.

Hydrogen peroxide activation of MAPK cascade and regulation of gene expression

H_2O_2 has been considered as a secondary messenger for gene activation in mammalian cells as well as in plants. However, in plants an increased content of H_2O_2 encourages the expression of defence as well as resistance genes (Mittler *et al.* 2004). H_2O_2 is also involved in modulation of many activities of signalling components, such as protein phosphatases, protein kinases (González *et al.* 2012), and transcription factors (TFs) (Cheng and Song 2006). H_2O_2 also communicates with other signal molecules and pathway forming part of the signalling network that controls responses downstream of H_2O_2 (Neill *et al.* 2002). Several studies have revealed that H_2O_2 participates in the downstream genes regulation. For example, mitogen-activated protein kinase (MAPK) cascades appear to be functional downstream of H_2O_2. MAPK in plants form a large system implicated in a number of functions, such as relay of H_2O_2 signals (Zhang *et al.* 2006, Xing *et al.* 2008). They activate *Nicotiana* protein kinase 1 (NPK1) in a MAPK cascade that transduces extracellular stimuli to gene expression for defence (Grant *et al.* 2000, Kovtun *et al.* 2000, Desikan *et al.* 2001). H_2O_2 rapidly activates MAPKs in shoots, even when applied to the roots (Capone *et al.* 2004). It has been reported that H_2O_2 controls seed dormancy and germination by triggering the induction of ABA catabolism genes (Liu *et al.* 2010). Zinc-finger transcription factor is generally involved in the regulation of ROS-related defence genes. It was revealed that the ZAT7 and ZAT12 zinc-finger proteins of *Arabidopsis* are strongly upregulated by oxidative stress in *apx* knockout mutants in response to H_2O_2 and methyl viologen (MV) treatment (Rizhsky 2004). ZAT10 plays a dual role both as repressor and inducer of ROS-responsive genes under salt, drought, and osmotic stresses (Sakamoto *et al.* 2004, Mittler 2006). ZAT6 positively regulates tolerance to chilling, drought, and salt stress, as well as resistance to bacterial infection, by modifying ROS contents and SA-related gene expression (Shi *et al.* 2014).

Based on above discussion, a suggested model of H_2O_2 signalling pathway has been outlined (Fig. 1). An H_2O_2 signal may be perceived by a cell surface receptor resulting in elevated $[Ca^{2+}]_{cyt}$. The increased content of $[Ca^{2+}]_{cyt}$ may trigger a signalling protein, such as protein kinase or phosphatase, to activate a cascade thus mediating phosphorylation or dephosphorylation of a transcription factor. In addition to this, H_2O_2 may activate transcription by directly oxidising H_2O_2-responsive transcription factors *via* oxidation of thiols of cysteine residues in protein. The modified (activated) transcription factor moves into the nucleus, interacts with its corresponding *cis*-acting element on the target promoter to regulate gene expression related to cold.

Hydrogen peroxide toxicity in plants

Despite the reported signalling role of H_2O_2, its excessive concentrations in the plants may be harmful. Chen *et al.* (2009) confirmed that the higher concentrations of H_2O_2 caused oxidative stress; on the other hand, at low concentration it acts as a signalling molecule regulating cell growth and development, cell proliferation, cell stress response, and signal transduction (Fukao and Bailey-Serres 2004, Mittler *et al.* 2004). High concentrations of H_2O_2 can directly or indirectly oxidize ascorbic acid and glutathione pool and alter the overall redox state of the cells. Such high concentrations of H_2O_2 can also damage a number of biomolecules, such as lipids, proteins, and nucleic acids that are essential for the activity and integrity of the cells (Mittler 2002).

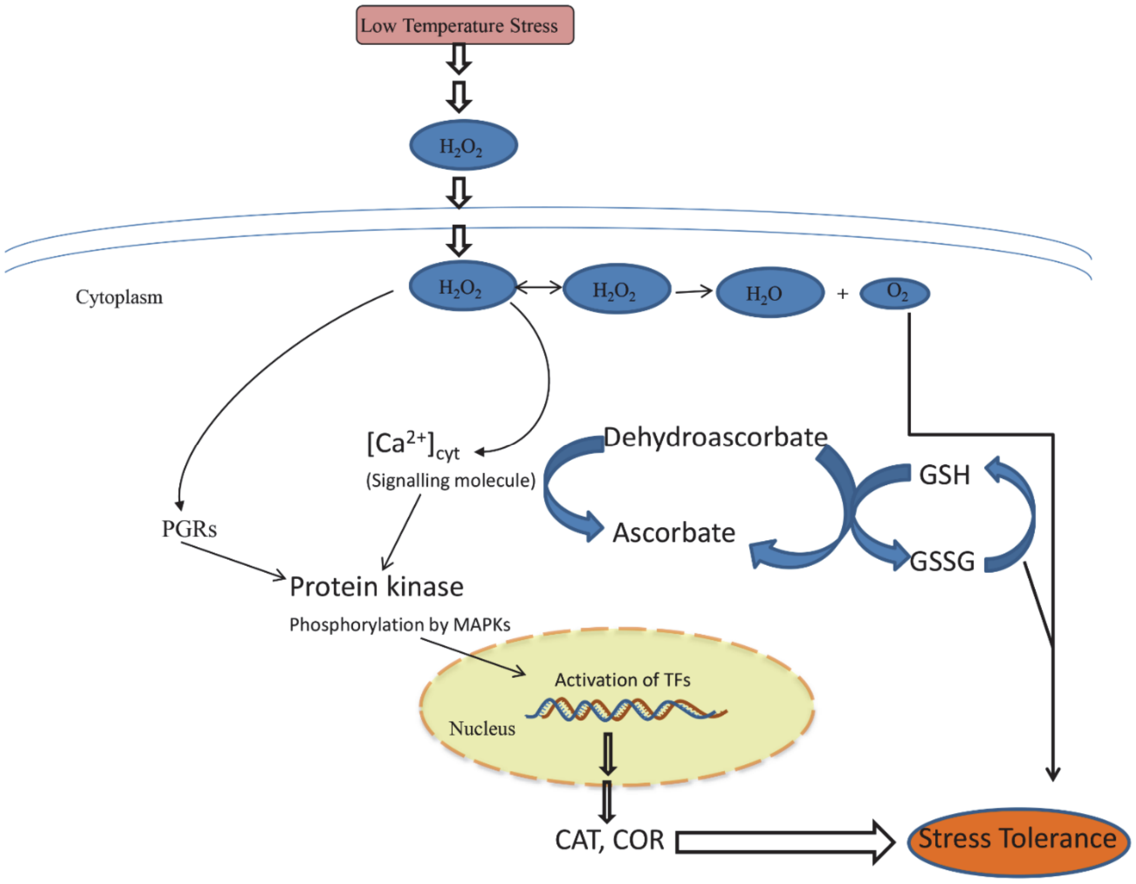

Fig. 1. A model of H_2O_2 signalling cascade for low temperature stress. H_2O_2 – hydrogen peroxide; PGRs – plant growth regulators; CAT – catalase; COR – cold regulated gene; GSH – glutathione; GSSG – glutathione disulphide; MAPKs – mitogen-activated protein kinases; TFs – transcription factors.

Conclusions: It has been established that H_2O_2 functions as the signalling molecule in plants depending on its concentration and crop species. It is imperative that a homeostasis should be maintained between generation and utilization of H_2O_2 inside the cells. Cells have evolved strategies to use ROS as biological signals that activate and control various stress responses at the level of gene. Therefore, it is established that H_2O_2 acts as a signalling molecules with tremendous impact on plant growth and development. Recent studies have shown that optimal H_2O_2 concentrations are important for proper plant growth, photosynthetic performance, and antioxidant activity and also for acclimation to various environmental stresses. Therefore, many of the signalling pathways mediated by H_2O_2 during various abiotic stresses have extensively been studied and still there is ample scope of additional work that could unravel the pathway mediated by H_2O_2 to confer tolerance against the various stresses. Although a significant progress has been made in the last few years, which contributed to overall understanding related to H_2O_2 mediated physiology, but many components in its signalling network are yet to be unveiled. These findings are of not only fundamental, but also of practical importance.

References

Abass S.M., Mohamed H.I.: Alleviation of adverse effects of drought stress on common bean (*Phaseolus vulgaris* L.) by exogenous application of hydrogen peroxide. – Bangladesh J. Bot. **41**: 75-83, 2011.

Ahmad P., Umar S., Sharma S.: Mechanism of free radical scavenging and role of phytohormones in plants under abiotic stresses. – In: Ashraf M., Ozturk M., Ahmad M.S.A. (ed.): Plant Adaptation and Phytoremediation. Pp. 99-118. Springer, Dordrecht – Heidelberg – London – New York, Springer 2010.

Ahmad P.: Oxidative Damage to Plants – Antioxidant Networks and Signaling. Pp. 65-88. Academic Press, Elsevier Inc., New York 2014.

Anjum N.A., Sofo A., Scopa A. *et al.*: Lipids and proteins – major targets of oxidative modifications in abiotic stressed plants. – Environ. Sci. Pollut. R. **22**: 4099-4121, 2015.

Alscher R.G., Erturk N., Heath L.S.: Role of superoxide dismutases (SODs) in controlling oxidative stress in plants. – J. Exp. Bot. **53**: 1331-1341, 2002.

Apel K., Hirt H.: Reactive oxygen species: metabolism, oxidative stress, and signal transduction. – Annu. Rev. Plant Biol. **55**: 373-399, 2004.

Apostol I., Heinstein P.F., Low P.S.: Rapid stimulation of an oxidative burst during elicitation of cultured plant cells: role in defense and signal transduction. – Plant Physiol. **90**: 109-116, 1989.

Ashfaque F., Khan M.I.R., Khan N.A.: Exogenously applied H_2O_2 promotes proline accumulation, water relations, photosynthetic efficiency and growth of wheat (*Triticum aestivum* L.) under salt stress. – Ann. Res. Rev. Biol. **4**: 105-120, 2014.

Ashraf M., Foolad M.R.: Roles of glycine betaine and proline in improving plant abiotic stress resistance. – Environ. Exp. Bot. **59**: 206-216, 2007.

Ashraf M.A., Rasheed R., Hussain I. *et al.*: Hydrogen peroxide modulates antioxidant system and nutrient relation in maize (*Zea mays* L.) under water-deficit conditions. – Arch. Agron. Soil Sci. **61**: 207-523, 2015.

Azevedo-Neto A.D., Prisco J.T., Enéas-Filho J. *et al.*: Hydrogen peroxide pre-treatment induces salt stress acclimation in maize plants. – J. Plant Physiol. **162**: 1114-1122, 2005.

Baier M., Noctor G., Foyer C.H. *et al.*: Antisense suppression of 2-cys peroxiredoxin in *Arabidopsis thaliana* specifically enhances the activites and expression of enzymes associated with ascorbate metabolism, but not glutathione metabolism. – Plant Physiol. **124**: 823-832, 2000.

Banu N.A., Hoque A., Watanabe-Sugimoto M. *et al.*: Proline and glycinebetaine induce antioxidant defense gene expression and suppress cell death in cultured tobacco cells under salt stress. – J. Plant Physiol. **166**: 146-156, 2009.

Barba-Espin G., Diaz-Vivancos P., Clemente-Moreno M.J. *et al.*: Interaction between hydrogen peroxide and plant hormones during germination and the early growth of pea seedlings. – Plant Cell Environ. **33**: 981-994, 2010.

Becana M., Moran J., Iturbe-Ormaetxe I.: Iron-dependent oxygen free radical generation in plants subjected to environmental stress: toxicity and antioxidant protection. – Plant Soil **201**: 137-147, 1998.

Bhattacharjee S.: An inductive pulse of hydrogen peroxide pretreatment restores redox homeostasis and mitigates oxidative membrane damage under extremes of temperature in two rice cultivars (*Oryza sativa* L., cultivars Ratna and SR 26B). – Plant Growth Regul. **68**: 395-410, 2012.

Bhattacharyya S., Das B., Ghose T.K. *et al.*: Investigation on seed germination of *Nyctanthes arbour-tristis* (Oleraceae) in relation to the phenol content. – Seed Sci. Tech. **27**: 321-327, 1999.

Burdon R.H., Alliangana D., Gill V.: Hydrogen peroxide and the proliferation of BHK-21 cell. – Free Radic. Res. **23**: 471-486, 1995.

Cao Y.Y., Gao Y., Sun W.J. *et al.*: Role of hydrogen peroxide pretreatment in heat-induced alteration of DNA methylation in cucumber leaves. – Sci. Hortic.-Amsterdam **151**: 173-183, 2013.

Capone R., Tiwari B.S., Levine A.: Rapid transmission of oxidative and nitrosative stress signals from roots to shoots in *Arabidopsis*. – Plant Physiol. Bioch. **42**: 425-428, 2004.

Carol R.J., Dolan L.: The role of reactive oxygen species in cell growth: lessons from root hairs. – J. Exp. Bot. **57**: 1829-1834, 2006.

Çavusoglu K., Kabar K.: Effects of hydrogen peroxide on the germination and early seedling growth of barley under NaCl and high temperature stresses. – EurAsian J. Biol. Sci. **4**: 70-79, 2010.

Chien C.T., Lin T.P.: Mechanism of hydrogen peroxide in improving the germination of *Cinnamonum camphora* seed. - Seed Sci. Tech. **22**: 231-236, 1994.

Chen X.Y., Ding X., Xu S. *et al.*: Endogenous hydrogen peroxide plays a positive role in the upregulation of heme oxygenase and acclimation to oxidative stress in wheat seedling leaves. – J. Integr. Plant Biol. **51**: 951-960, 2009.

Cheng Y., Song C.: Hydrogen peroxide homeostasis and signaling in plant cells. – Sci. China C Life Sci. **49**: 1-11, 2006.

Cheng X.X., Yu M., Zhang N. *et al.*: Reactive oxygen species regulate programmed cell death progress of endosperm in winter wheat (*Triticum aestivum* L.) under waterlogging. – Protoplasma **253**: 311-327, 2015.

Das K., Roychoudhury A.: Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. – Front. Environ. Sci. **2**: 53, 2014.

Deng X.P., Cheng Y.J., Wu X.B. *et al.*: Exogenous hydrogen peroxide positively influences root growth and exogenous hydrogen peroxide positively influences root growth and metabolism in leaves of sweet potato seedlings. – Aust. J Crop. Sci. **6**: 1572-1578, 2012.

Desikan R., Hancock J.T., Neill S.J.: Oxidative stress signalling. – In: Hirt H., Shinozaki K. (ed.): Plant Responses to Abiotic Stress. Topics in Current Genetics. Pp. 121-149, Springer, Berlin, Heidelberg, 2003.

Desikan R.S., Mackerness A.H., Hancock J.T. *et al.*: Regulation of the *Arabidopsis* transcriptome by oxidative stress. – Plant Physiol. **127**: 159-172, 2001.

Dietz K.J., Mittler R., Noctor G.: Recent progress in understanding the role of reactive oxygen species in plant cell signaling. – Plant Physiol. **171**: 1535-1539, 2016.

Dunand C., Crevecoeur M., Penel C.: Distribution of superoxide and hydrogen peroxide in *Arabidopsis* root and their influence on root development: possible interaction with peroxidases. – New Phytol. **174**: 332-341, 2007.

Fan Y., Huang Y.: The effective peroxidase-like activity of chitosan- functionalized $CoFe_2O_4$ nanoparticles for chmiluminescence sensing of hydrogen peroxide and glucose. – Analyst **137**: 1225-1231, 2012.

Fariduddin Q., Khan T.A., Yusuf M.: Hydrogen peroxide mediated tolerance to copper stress in the presence of 28-homobrassinolide in *Vigna radiata*. – Acta Physiol. Plant. **36**: 2767-2778, 2014.

Fontaine O., Huault C., Pavis N. *et al.*: Dormancy breakage of *Hordeum vulgare* seeds: Effect of hydrogen peroxide and stratification on glutathione level and glutathione reductase activity. – Plant Physiol. Bioch. **32**: 677- 683, 1994.

Foyer C.H., Noctor G.: Redox sensing and signalling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. – Physiol. Plantarum **119**: 355-364, 2003

Foyer C.H., Noctor G.: Oxidant and antioxidant signalling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. – Plant Cell Environ. **28**: 1056-1071, 2005.

Foyer C.H., Souriau N., Perret S. *et al.*: Over-expression of glutathione reductase but not glutathione synthetase leads to increases in antioxidant capacity and improved photosynthesis in poplar (*Populus tremula*× *P. alba*) trees. – Plant Physiol. **109**: 1047-1057, 1995.

Fukao T., Bailey-Serres J.: Plant responses to hypoxia-is survival a balancing act. – Trends Plant Sci. **9**: 449-456, 2004.

Gao Y., Guo Y.K., Lin S.H. *et al.*: Hydrogen peroxide pretreatment alters the activity of antioxidant enzymes and protects chloroplast ultrastructure in heat stressed cucumber leaves. – Sci. Hortic.-Amsterdam **126**: 20-26, 2010.

Ge X.M., Cai H.L., Lei X. *et al.*: Heterotrimeric G protein mediates ethylene-induced stomatal closure via hydrogen peroxide synthesis in *Arabidopsis*. – Plant J. **82**: 138-150, 2015.

Gechev T., Gadjev I., van Breusegem F. *et al.*: Hydrogen peroxide protects tobacco from oxidative stress by inducing a set of antioxidant enzymes. – Cell Mol. Life Sci. **59**: 708-714, 2002.

Gechev T.S., Hille J.: Hydrogen peroxide as a signal controlling plant programmed cell death. – J. Cell Biol. **8**: 17-20, 2005.

Gill S.S., Tuteja N.: Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. – Plant Physiol. Bioch. **48**: 909-930, 2010.

Gondim F.A., Gomes-Filho E., Costa J.H. *et al.*: Catalase plays a key role in salt stress acclimation induced by hydrogen peroxide pretreatment in maize. – Plant Physiol. Bioch. **56**: 62-71, 2012.

Gondim F.A., Miranda R.S., Gomes-Filho E. *et al.*: Enhanced salt tolerance in maize plants induced by H_2O_2 leaf spraying is associated with improved gas exchange rather than with non-enzymatic antioxidant system. – Theor. Exp. Plant Physiol. **25**: 251-260, 2013.

Gong M., Chen B., Li Z.G. *et al.*: Heat-shock-induced cross adaptation to heat, chilling, drought and salt stress in maize seedlings and involvement of H_2O_2. – J. Plant Physiol. **158**: 1125-1130, 2001.

González A., de los Ángeles Cabrera M., Henríquez M.J. *et al.*: Cross talk among calcium, hydrogen peroxide, and nitric oxide and activation of gene expression involving calmodulins and calcium-dependent protein kinases in *Ulva compressa* exposed to copper excess. – Plant Physiol. **158**: 1451-1462, 2012.

Grant J.J., Yun B.W., Loake G.J.: Oxidative burst and cognate redox signaling reported by luciferase imaging: identification of a signal network that functions independently of ethylene, SA and Me-JA but is dependent on MAPKK activity. – Plant J. **24**: 569-582, 2000.

Guzel S., Terzi R.: Exogenous hydrogen peroxide increases dry matter production, mineral content and level of osmotic solutes in young maize leaves and alleviates deleterious effects of copper stress. – Bot. Stud. **54**: 26, 2013.

Hasan S.A., Irfan M., Masrahi Y.S. *et al.*: Growth, photosynthesis, and antioxidant response of *Vigna unguiculata* L. treated with hydrogen peroxide. – Cogent Food Agri. **2**: 1155331, 2016.

He L., Gao Z., Li R.: Pretreatment of seed with H_2O_2 enhances drought tolerance of wheat (*Triticum aestivum* L.) seedlings. – Afr. J. Biotech. **8**: 6151-6157, 2009.

Hernández J.A., Ferrer M.A., Jiménez A. *et al.*: Antioxidant systems and O_2^-/ H_2O_2 production in the apoplast of pea leaves. Its relation with salt-induced necrotic lesions in minor veins. – Plant Physiol. **127**: 817-831, 2001.

Hernández-Barrera A., Velarde-Buendía A., Zepeda I. *et al.*: Hyper, a hydrogen peroxide sensor, indicates the sensitivity of the *Arabidopsis* root elongation zone to aluminum treatment. – Sensors **15**: 855-867, 2015.

Hippeli S., Elstner E.F.: Mechanisms of oxygen activation during plant stress: biochemical effects of air pollutants. – J. Plant Physiol. **148**: 249-257, 1996.

Holländer-Czytko J., Grabowski I., Sandorf K. *et al.*: Tocopherol content and activities of tyrosine aminotransferase and cystine lyase in *Arabidopsis* under stress conditions. – J. Plant Physiol. **162**: 767-770, 2005.

Holmberg N., Bülow L.: Improving stress tolerance in plants by gene transfer. – Trends Plant Sci. **3**: 61-66, 1998.

Horling F., Lamkemeyer P., König J. *et al.*: Divergent light-, ascorbate- and oxidative stress-dependent regulation of expression of the peroxiredoxin gene family in *Arabidopsis*. – Plant Physiol. **131**: 317-325, 2003.

Hossain M.A., Fujita M.: Hydrogen peroxide priming stimulates drought tolerance in mustard (*Brassica juncea* L.) seedlings. – Plant Gene Trait. **4**: 109-123, 2013.

Hossain M.A., Bhattacharjee S., Armin S.M. *et al.*: Hydrogen peroxide priming modulates abiotic oxidative stress tolerance: insights from ROS detoxification and scavenging. – Front. Plant Sci. **6**: 420, 2015.

Hu Y., Ge Y., Zhang C. *et al.*: Cadmium toxicity and translocation in rice seedlings are reduced by hydrogen peroxide pretreatment. – Plant Growth Regul. **59**: 51-61, 2009.

Hung S.H., Wang C.C., Ivanov S.V. *et al.*: Repetition of hydrogen peroxide treatment induces a chilling tolerance comparable to cold acclimation in mung bean. – J. Am. Soc. Hortic. Sci. **132**: 770-776, 2007.

Hung S.H., Yu C.W., Lin C.H.: Hydrogen peroxide functions as a stress signal in plants. – Bot. Bull. Acad. Sci. **46**: 1-10, 2005.

Işeri O.D., Körpe D.A., Sahin F.I. *et al.*: Hydrogen peroxide pretreatment of roots enhanced oxidative stress response of tomato under cold stress. – Acta Physiol. Plant. **35**: 1905-1913, 2013.

Ishibashi Y., Yamaguchi H., Yuasa T. *et al.*: Hydrogen peroxide spraying alleviates drought stress in soybean plants. – J. Plant Physiol. **168**: 1562-1567, 2011.

Jahan A.A., Anis M.: Changes in antioxidative enzymatic responses during acclimatization of *in vitro* raised plantlets of *Cardiospermum halicacabum* L. against oxidative stress. – J. Plant Physiol. Pathol. **4**: 2, 2014.

Jiang Y., Cheng F., Zhou Y. *et al.*: Hydrogen peroxide functions as a secondary messenger for brassinosteroids-induced CO_2 assimilation and carbohydrate metabolism in *Cucumis sativus*. – J. Zhejiang Univ.-Sci. B **13**: 811-823, 2012.

Kamal-Eldin L.A., Appelqvist.: The chemistry and antioxidant properties of tocopherols and tocotrienols. – Lipids **31**: 671-701, 1996.

Kapoor D., Sharma R., Handa N. *et al.*: Redox homeostasis in plants under abiotic stress: role of electron carriers, energy metabolism mediators and proteinaceous thiols. – Front. Environ. Sci. **3**: 13, 2015.

Karpinski S., Reynolds H., Karpinska B. *et al.*: Systemic signaling in response to excess excitation energy in *Arabidopsis*. – Science **284**: 654-657, 1999.

Karuppanapandian T., Moon J.C., Kim C. *et al.*: Reactive oxygen species in plants: their generation signal transduction, and scavenging mechanisms. – Aust. J. Crop Sci. **5**: 709, 2011.

Katzman, L.S., Taylor A.G., Langhans R.W.: Seed enhancements to improve spinach germination. – HortScience **36**: 979-981, 2001.

Khan T.A., Yusuf M., Fariduddin Q.: Seed treatment with H_2O_2 modifies net photosynthetic rate and antioxidant system in mung bean (*Vigna radiata* L. Wilczek) plants. – Israel J. Plant Sci. **62**: 167-175, 2015.

Khan M.I.R., Khan N.A., Masood A. *et al.*: Hydrogen peroxide alleviates nickel-inhibited photosynthetic responses through increase in use-efficiency of nitrogen and sulfur, and glutathione production in mustard. – Front. Plant Sci. **7**: 44, 2016.

Khandaker M.M., Boyce A.N., Osman N.: The influence of hydrogen peroxide on the growth, development and quality of wax apple (*Syzygium samarangense*, [Blume] Merrill & L.M. Perry var. jambu madu) fruits. – Plant Physiol. Bioch. **53**: 101-110, 2012.

Knight H., Trewavas A.J., Knight M.R.: Cold calcium signalling in *Arabidopsis* involves two cellular pools and a change in calcium signature after acclimation. – Plant Cell **8**: 489-503, 1996.

Knight M.R., Campbell A.K., Smith S.M. *et al.*: Transgenic plant aequorin reports the effects of touch and cold-shock and elicitors on cytoplasmic calcium. – Nature **352**: 524-526, 1991.

Kovtun Y., Chiu W.L., Tena G. *et al.*: Functional analysis of oxidative stress-activated mitogen-activated protein kinase cascade in plants. – P. Natl. Acad. Sci. USA **97**: 2940-2945, 2000.

Krifka S., Hiller K.A., Spagnuolo G. *et al.*: The influence of glutathione on redox regulation by antioxidant proteins and apoptosis in macrophages exposed to 2-hydroxyethyl methacrylate (HEMA). – Biomaterials **33**: 5177-5186, 2012.

Kubiś J., Floryszak-Wieczorek J., Arasimowicz-Jelonek M.: Polyamines induce adaptive responses in water deficit stressed cucumber roots. – J. Plant Res. **127**: 151-158, 2014.

Lamb C., Dixon R.A.: The oxidative burst in plant disease resistance. – Annu. Rev. Plant Phys. **48**: 251-275, 1997.

Larkindale J., Huang B.: Thermo tolerance and antioxidant systems in *Agrostis stolonifera*: involvement of salicylic acid, abscisic acid, calcium, hydrogen peroxide, and ethylene. – J. Plant Physiol. **161**: 405-413, 2004.

Leshem Y., Wills R.B.H., Ku V.: Evidence for the function of the free radical gas-nitric oxide (NO) as an endogenous maturation and senescence regulating factor in higher plants. – Plant Physiol. Bioch. **36**: 825-833, 1998.

Lewis B.D., Karlin-Neumann G., Davis R.W. *et al.*: Ca_2^+-activated anion channels and membrane depolarizations induced by blue light and cold in *Arabidopsis* seedlings. – Plant Physiol. **114**: 1327-1334, 1997.

Li J.T., Qiu Z.B., Zhang X.W. *et al.*: Exogenous hydrogen peroxide can enhance tolerance of wheat seedlings to salt stress. – Acta Physiol. Plant. **33**: 835-842, 2011.

Liao W.B., Huang G.B., Yu J.H. *et al.*: Nitric oxide and hydrogen peroxide alleviate drought stress in marigold explants and promote its adventitious root development. – Plant Physiol. Bioch. **58**: 6-15, 2012.

Lin Q., Chen Y., Wang Z. *et al.*: Study on the possibility of hydrogen peroxide pretreatment and plant system to remediate soil pollution. – Chemosphere **57**: 1439-1447, 2004.

Liu X., Xing D., Li L. *et al.*: Rapid determination of seed vigor based on the level of superoxide generation during early imbibitions. – Photoch. Photobio. Sci. **6**: 767-774, 2007.

Liu X.M., Kim K.E., Kim K.C. *et al.*: Cadmium activates *Arabidopsis* MPK3 and MPK6 via accumulation of reactive oxygen species. – Phytochemistry **71**: 614-618, 2010.

Lum H.K., Butt Y.K.C., Lo S.C.L.: Hydrogen peroxide induces a rapid production of nitric oxide in mung bean (*Phaseolus aureus*). – Nitric Oxide **6**: 205-213, 2002.

Ma F., Wang L.J., Li J.L. *et al.*: Interaction between HY1 and H_2O_2 in auxin-induced lateral root formation in *Arabidopsis*. – Plant Mol. Biol. **85**: 49-61. 2014.

May M.J., Vernoux T., Leaver C. *et al.*: Glutathione homeostasis in plants: implications for environmental sensing and plant development. – J. Exp. Bot. **49**: 649-667, 1998.

Mittler R., Vanderauwera S., Gollery M. *et al.*: Reactive oxygen gene network of plants. – Trends Plant Sci. **9**: 490-498, 2004.

Mittler R.: Oxidative stress, antioxidants and stress tolerance. – Trends Plant Sci. **7**: 405-410, 2002.

Mittler R., Vanderauwera S., Suzuki N. *et al.*: ROS signaling: the new wave? – Trends Plant Sci. **16**: 300-309, 2011.

Mittler R.: Abiotic stress, the field environment and stress combination. – Trends Plant Sci. **11**: 15-19, 2006.

Monroy A.F., Dhindsa R.S.: Low temperature signal transduction: induction of cold acclimation-specific genes of alfalfa by calcium at 25ºC. – Plant Cell **7**: 321-331, 1995.

Morita S., Kaminaka H., Masumura T. *et al.*: Induction of rice cytosolic ascorbate peroxidase mRNA by oxidative stress: the involvement of hydrogen peroxide in oxidative stress signalling. – Plant Cell Physiol. **40**: 417-422, 1999.

Mostofa M.G., Seraj Z.I., Fujita M.: Exogenous sodium nitroprusside and glutathione alleviate copper toxicity by reducing copper uptake and oxidative damage in rice (*Oryza sativa* L.) seedlings. – Protoplasma **251**: 1373-1386, 2014.

Müller K., Linkies A., Vreeburg R.A.M. *et al.*: *In vivo* cell wall loosening by hydroxyl radicals during cross seed germination and elongation growth. – Plant Physiol. **150**: 1855-1865, 2009.

Nahar K., Hasanuzzaman M., Alam M.M. *et al.*: Exogenous glutathione confers high temperature stress tolerance in mung bean (*Vigna radiata* L.) by modulating antioxidant defense and methylglyoxal detoxification system. – Environ. Exp. Bot. **112**: 44-54, 2015.

Neill S.J., Desikan R., Clarke A. *et al.*: Hydrogen peroxide and nitric oxide as signalling molecules in plants. – J. Exp. Bot. **53**: 1237-1247, 2002.

Neill S.J., Desikan R., Hancock J.: Hydrogen peroxide signaling. – Curr. Opin. Plant Biol. **5**: 388-395, 2002.

Noctor G., Foyer C.: Ascorbate and GSH: keeping active oxygen under control. – Annu. Rev. Plant Phys. **49**: 249-279, 1998.

Noctor G., Mhamdi A., Foyer C.H.: The roles of reactive oxygen metabolism in drought: not so cut and dried. – Plant Physiol. **164**: 1636-1648, 2014.

Nogues S., Baker N.R.: Effects of drought on photosynthesis in Mediterranean plants grown under enhanced UV-B radiation. – J. Exp. Bot. **51**: 1309-1317, 2000.

Ogawa K., Iwabuchi M.: A mechanism for promoting the germination of *Zinnia elegans* seeds by hydrogen peroxide. – Plant Cell Physiol. **42**: 286-291, 2001.

Okuda T., Matsuda Y., Yamanaka A. *et al.*: Abrupt increase in the level of hydrogen peroxide in leaves of winter wheat is caused by cold treatment. – Plant Physiol. **97**: 1265-1267, 1991.

Orabi S.A., Dawood M.G., Salman S.R.: Comparative study between the physiological role of hydrogen peroxide and salicylic acid in alleviating the harmful effect of low temperature on tomato plants grown under sand-ponic culture. – Sci. Agri. **9**: 49-59, 2015.

Oracz K., El-Maarouf-Bouteau H., Kranner I. *et al.*: The mechanisms involved in seed dormancy alleviation by hydrogen cyanide unravel the role of reactive oxygen species as key factors of cellular signalling during germination. – Plant Physiol. **150**: 494-505, 2009.

Pastori G.M., Foyer C.: Common components, networks and pathways of cross-tolerance to stress. The central role of 'redox' and abscisic acid-mediated controls. – Plant Physiol. **129**: 460-468, 2002.

Payton P., Webb R., Kornyeyev D. *et al.*: Protecting cotton photosynthesis during moderate chilling at high light intensity by increasing chloroplastic antioxidant enzyme activity. – J.

Exp. Bot. **52**: 2345-2354, 2001.

Pei Z.M., Murata Y., Benning G. *et al.*: Calcium channels activated by hydrogen peroxide mediate abscisic acid signalling in guard cells. – Nature **406**: 731-734, 2000.

Peng L.T., Jiang Y.M., Yang S.Z. *et al.*: Accelerated senescence of fresh-cut Chinese water chestnut tissues in relation to hydrogen peroxide accumulation. – J. Plant Phys. Mol. Biol. **31**: 527-532, 2005.

Pinhero R., Rao M., Paliyath G. *et al.*: Changes in activities of antioxidant enzymes and their relationship to genetic and paclobutrazol-induced chilling tolerance of maize seedlings. – Plant Physiol. **114**: 695-704, 1997.

Polisensky D.H., Braam J.: Cold-shock regulation of the *Arabidopsis* TCH genes and the effects of modulating intracellular calcium levels. – Plant Physiol. **111**: 1271-1279, 1996.

Prasad T., Anderson M., Martin B. *et al.*: Evidence for chilling-induced oxidative stress in maize seedlings and a regulatory role for hydrogen peroxide. – Plant Cell **6**: 65-74, 1994a.

Prasad T., Anderson M., Stewart C.: Acclimation, hydrogen peroxide, and abscisic acid protect mitochondria against irreversible chilling injury in maize seedlings. – Plant Physiol. **105**: 619-627, 1994b.

Ranganayakulu G.S., Veeranagamallaiah G., Sudhakar C.: Effect of salt stress on osmolyte accumulation in two groundnut cultivars (*Arachis hypogaea* L.) with contrasting salt tolerance. – Afr. J. Plant Sci. **12**: 586-592, 2013.

Ren C.G., Li X., Liu X.L. *et al.*: Hydrogen peroxide regulated photosynthesis in C4-pepc transgenic rice. – Plant Physiol. Bioch. – **74**: 218-229, 2014.

Rizhsky L., Davletova S., Liang H., Mittler R.: The zinc finger protein Zat12 is required for cytosolic ascorbate peroxidase 1 expression during oxidative stress in *Arabidopsis*. – J. Biol. Chem. **279**: 11736-11743, 2004.

Roxas V.P., Smith R.K., Allen E.R. *et al.*: Overexpression of glutathione S-transferase/glutathione peroxidase enhances the growth of transgenic tobacco seedlings during stress. – Nat. Biotechnol. **15**: 988-991, 1997.

Roxas V.P., Lodhi S.A., Garrett D.K. *et al.*: Stress tolerance in transgenic tobacco seedlings that overexpress glutathione *S*-transferase/glutathione peroxidase. – Plant Cell Physiol. **41**: 1229-1234, 2000.

Sakamoto H., Maruyama K., Sakuma Y. *et al.*: *Arabidopsis* Cys2/His2-type zinc-finger proteins function as transcription repressors under drought, cold, and high-salinity stress conditions. – Plant Physiol. **136**: 2734-2746, 2004.

Sanders D., Brownlee C., Harper J.F.: Communicating with calcium. – Plant Cell **11**: 691-706, 1999.

Sanders D., Pelloux J., Brownlee C. *et al.*: Calcium at the crossroads of signalling. – Plant Cell **14**: S401-S417, 2002.

Sarath G., Hou G., Hou L.M. *et al.*: Reactive oxygen species, ABA and nitric oxide interactions on the germination of warm-season C4-grasses. – Planta **226**: 697-708, 2007.

Sharma P., Jha A.B., Dubey R.S. *et al.*: Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. – J. Bot. **2012**: 217037, 2012.

Shi H., Wang X., Ye T. *et al.*: The Cysteine2/Histidine2-type transcription factor ZINC FINGER OF *Arabidopsis thaliana* 6 modulates biotic and abiotic stress responses by activating salicylic acid-related genes and C-REPEAT-BINDING FACTOR genes in *Arabidopsis*. – Plant Physiol. **165**: 1367-1379, 2014.

Sofo A., Scopa A., Nuzzaci M. *et al.*: Ascorbate peroxidase and catalase activities and their genetic regulation in plants subjected to drought and salinity stresses. – Int. J. Mol. Sci. **16**: 13561-13578, 2015.

Tanou G., Job C., Rajjou L. *et al.*: Proteomics reveals the overlapping roles of hydrogen peroxide and nitric oxide in the acclimation of citrus plants to salinity. – Plant J. **60**: 795-804, 2009.

Tao K.L.J., Buta J.G.: Differential effects of camptothecin and interaction with plant hormones on seed germination and seedling growth. – Plant Growth Regul. **4**: 219-226, 1986.

Terzi R., Kadioglu A., Kalaycioglu E. *et al.*: Hydrogen peroxide pretreatment induces osmotic stress tolerance by influencing osmolyte and abscisic acid levels in maize leaves. – J. Plant Interact. **9**: 559-565, 2014.

Türkan I., Demiral T.: Recent developments in understanding salinity tolerance. – Environ. Exp. Bot. **67**: 2-9, 2009.

Uchida A., Jagendorf A.T., Hibino T. *et al.*: Effects of hydrogen peroxide and nitric oxide on both salt and heat stress tolerance in rice. – Plant Sci. **163**: 515-523, 2002.

van Breusegem F., Dat J.F.: Reactive oxygen species in plant cell death. – Plant Physiol. **141**: 384-390, 2006.

van Camp W.: Yield enhancement genes: seeds for growth. – Curr. Opin. Biotechnol. **16**: 147-153, 2005.

Vavilala S.L., Gawde K.K., Sinha M. *et al.*: Programmed cell death is induced by hydrogen peroxide but not by excessive ionic stress of sodium chloride in the unicellular green alga *Chlamydomonas reinhardtii*. – Eur. J. Phycol. **50**: 422-438, 2015.

Verma K., Mehta S.K., Shekhawat G.S.: Nitric oxide (NO) counteracts cadmium induced cytotoxic processes mediated by reactive oxygen species (ROS) in *Brassica juncea*: cross-talk between ROS, NO and antioxidant responses. – Biometals **26**: 255-269, 2013.

Wahid A., Perveen M., Gelani S. *et al.*: Pretreatment of seed with H_2O_2 improves salt tolerance of wheat seedlings by alleviation of oxidative damage and expression of stress proteins. – J. Plant Physiol. **164**: 283-294, 2007.

Wahid A., Noreen A., Basra S.M.A. *et al.*: Priming-induced metabolic changes in sunflower (*Helianthus annuus*) achenes improve germination and seedling growth. – Bot. Stud. **49**: 343-350, 2008.

Wang C., Croft K.P.C., Järlfors U. *et al.*: Subcellular localization studies indicate that lipoxygenases 1 to 6 are not involved in lipid mobilization during soybean germination. – Plant Physiol. **120**: 227-236, 1999.

Wang Y., Feng H., Qu Y. *et al.*: The relationship between reactive oxygen species and nitric oxide in ultraviolet- B-induced ethylene production in leaves of maize seedlings. – Environ. Exp. Bot. **57**: 51-61, 2006.

Wang Y., Li J., Wang J. *et al.*: Exogenous H_2O_2 improves the chilling tolerance of manila grass and mascarene grass by activating the antioxidative system. – Plant Growth Regul. **61**: 195-204, 2010.

Wang Y., Zhang J., Li J. *et al.*: Exogenous hydrogen peroxide enhanced the thermotolerance of *Festuca arundinacea* and *Lolium perenne* by increasing the antioxidative capacity. – Acta Physiol. Plant. **36**: 2915-2924, 2014.

White P.J.: Calcium channels in higher plants. – BBA-Biomembranes **1465**: 171-189, 2000.

Wingate V.P.M., Lawton M.A., Lamb C.J.: Glutathione causes a massive and selective induction of plant defense genes. – Plant Physiol. **87**: 206-210, 1998.

Wojtyla Ł., Lechowska K., Kubala S. *et al.*: Different modes of hydrogen peroxide action during seed germination. – Front. Plant Sci. **7**: 66, 2016.

Xia X.J., Wang Y.J., Zhou Y.H. *et al.*: Reactive oxygen species are involved in brassinosteroid-induced stress tolerance in cucumber. – Plant Physiol. **150**: 801-814, 2009.

Xing T., Higgins V.J., Blumwald E.: Race-specific elicitors of *Cladosporium fulvum* promote translocation of cytosolic components of NADPH oxidase to the plasma membrane of tomato cells. – Plant Cell **9**: 249-259, 1997.

Xing Y., Jia W., Zhang J.: AtMKK1 mediates ABA-induced *CAT1* expression and H_2O_2 production via AtMPK6-coupled signalling in *Arabidopsis*. – Plant J. **54**: 440-451, 2008.

Xu F.J., Jin C.W., Liu W.J. *et al.*: Pretreatment with H_2O_2 alleviates aluminum-induced oxidative stress in wheat seedlings. – J. Integr. Plant Biol. **53**: 44-53, 2011.

Yang T., Poovaiah B.W.: Hydrogen peroxide homeostasis: activation of plant catalase by calcium/calmodulin. – P. Natl. Acad. Sci. USA **99**: 4097-4102, 2002.

Yu C.W., Murphy T.M., Lin C.H.: Hydrogen peroxide-induced chilling tolerance in mung beans mediated through ABA-independent glutathione accumulation. – Funct. Plant Biol. **30**: 955-963, 2003.

Zeinalabedini M., Majourhat K., Hernández J.A. *et al.*: Breaking seed dormancy in long-term stored seeds from Iranian wild almond species. – Seed Sci. Tech. **37**: 267-275, 2009.

Zhang A., Jiang M., Zhang J. *et al.*: Mitogen-activated protein kinase is involved in abscisic acid-induced antioxidant defense and acts downstream of reactive oxygen species production in leaves of maize plants. – Plant Physiol. **141**: 475-487, 2006.

Zhang J., Cui S., Li J. *et al.*: Protoplasmic factors, antioxidant responses, and chilling resistance in maize. – Plant Physiol. Bioch. **33**: 567-575, 1995.

Zhou J., Wang J., Shi K. *et al.*: Hydrogen peroxide is involved in the cold acclimation-induced chilling tolerance of tomato plants. – Plant Physiol. Bioch. **60**: 141-149, 2012.