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EFFECT OF WATER DEFICIT STRESS AND FOLIAR APPLICATION OF SALICYLIC ACID ON ANTIOXIDANTS ENZYMES ACTIVITY IN LEAVES OF *THYMUS DAENENSIS* SUBSP. *LANCIFOLIUS*

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ABSTRACT. In order to study the effects of water deficit stress and foliar application of salicylic acid (SA) on the activity of five antioxidant enzymes (catalase - CAT; EC 1.11.1.6, ascorbate peroxidase - APX; EC 1.11.1.11, glutathione reductase - GR; EC 1.6.4.2, peroxidase - POD; EC 1.11.1.7 and polyphenol oxidase - PPO; 1.14.18.1) of *Thymus daenensis* (subsp. *lancifolius*), an experiment was conducted in factorial based on completely randomized design with three replicates, during 2013. Drought treated seedlings showed elevated levels of reactive oxygen species (ROSs), with a concomitant increase in the activities of the enzymes CAT, APX, GR, POD and PPO, compared to controls. Under medium water deficit, APX and PPO activities significantly increased by higher SA concentration (2 mM), but under control and sever water deficit conditions, there was no significant difference between 1 mM and 2 mM concentrations regarding APX and PPO activity. Under all levels of available water, increase in SA concentration from 0.1 mM to1 mM induced significant increase in GR activity. The maximum amount of GR (under medium water deficit condition) achieved from 1mM of SA. While the maximum amounts of APX, PPO (under medium water deficit condition), CAT and POD (under sever water deficit condition) achieved from 2 mM of SA. In total, our results suggest that application of SA (as a trigger of signal cascade) could be advantageous against water deficit stress, and could protect thyme plants in mentioned conditions.

Key words: Antioxidant enzymes; Thyme; Reactive oxygen species; Water deficit stress.

INTRODUCTION

Lamiaceae (syn. *Labiatae*) herb family consists of more than 252 genus and 7000 species (Hedge,

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1992). The genus *Thymus* L. (*Labiatae*) consists of about 215 species of herbaceous perennials and subshrubs. This genus is represented in Iranian flora by 14 species, four of which (*Thymus carmanicus, Thymus daenensis* subsp. *daenensis* and *T. daenensis* subsp. *lancifolius, Thymus persicus* and *Thymus trautvetteri)* are endemic (Rechinger, 1982). Thyme species are considered as medicinal plants, due to their pharmacological and biological properties. *Thymus daenensis* is an endemic species of Iran. The aerial parts and volatile constituents of thyme, a perennial dwarf shrub, are used as a medicinal herb. Infusion and decoction of aerial parts of thyme species are used to produce a tonic, carminative, digestive, antispasmodic, anti-inflammatory, antitussive, and expectorant and for the treatment of colds in Iranian traditional medicine (Zargari, 1990; Nickavar *et al*. 2005).

Water deficit (commonly known as drought) can be defined as the absence of adequate moisture necessary for a plant to grow normally and complete its life cycle (Zhu, 2002). Drought stress is serious obstacle for medical plants and field crops in further areas of the world, especially in arid and semiarid regions. Drought stress leads to suppression of plant growth and development at all growth stages, however, depending upon plant species, certain stages such as germination, seedling or flowering stage could be the most critical stages for drought stress. The yield and the quality of the essential oil are considerably affected by drought stress. Physiological and environmental factors (such as drought stress) as well as processing conditions may play an important role while defining the chemistry and chemical composition of essential oils (Masotti *et al*., 2003; Angioni *et al*., 2006).

In addition to this, an important consequence of drought stress in plants is the excessive generation of reactive oxygen species (ROS), particularly in chloroplast and mitochondria (Mittler, 2002).

ROSs are molecules like hydrogen peroxide (H_2O_2), ions like the hypochlorite ion, radicals like the hydroxyl radical (OH°) and the superoxide anion (O_2^-). ROSs are a group of very reactive, short-lived chemicals produced during normal metabolism or after an oxidative reaction (Sun, 1990). ROSs are known to damage cellular membranes by inducing lipid peroxidation (Ramadevi and Prasad, 1998). They also can damage DNA, proteins, lipids and chlorophylls (Mittova *et al*., 2000).

Plants have developed an array of defense strategies (antioxidant system) to cope up with oxidative stress. The antioxidative system includes both enzymatic and non-enzymatic systems. The non enzymatic system includes ascorbic acid (vitamin C); α-tocopherol, cartenes etc., and enzymic system include superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX), glutathione reductase (GR) and polyphenol oxidase (PPO) etc. The

function of this antioxidant system is to scavenge the toxic radicals produced during oxidative stress and thus help the plants to survive through such conditions. (Noctor and Foyer, 1998). For instance, SOD catalyses the dismutation of superoxide to hydrogen peroxide and oxygen. However, hydrogen peroxide is also toxic to cells and has to be further detoxified by CAT and/or peroxidases to water and oxygen.

In plants, salicylic acid (SA) plays an important role in signaling both local and systemic defense responses. SA has been recognized as a regulatory signal mediating plant response to abiotic stresses such as drought (Munné-Bosch and Peñuelas, 2003) and osmotic stress (Borsani *et al*., 2001).

SA action is tightly related to the generation of various ROS (Kawano and Muto, 2000). ROS acts as signaling molecules that triggers the cascade of protective reactions in plants (Tarchevskii, 2002), including activation of antioxidant enzymes. Treatment of wheat seedlings with SA caused a transitory enhancement of O_2^- and H_2O_2 production by plants and simultaneous increase in the activity of SOD. Consequently, enhancement of the generation of H_2O_2 in SA treated seedlings is accompanied by the activation of peroxidase (Alscher *et al*., 2002). Which acts as a hardening process, increasing the surviving capacity of the plants.

We need the information for understanding the mechanisms of the antistress effects of SA in medicinal plants, which is a prerequisite to justify the use of this natural growth regulator for increasing *T. daenensis* resistance to drought. Therefore, the purposes of the present research were to assess the effect of different irrigation regimes and foliar application of salicylic acid (SA) on antioxidants enzymes activity in leaves of *Thymus daenensis* subsp. *lancifolius*.

MATERIALS AND METHODS

This study was carried out at climatic greenhouse in order to investigate the effect of salicylic acid (SA) and different irrigation regimes on the antioxidants enzymes activity in leaves of thyme. Three levels of irrigation, including control (FC), medium water deficit (70% FC) and sever water deficit (30% FC) and four concentrations of SA (0, 0.1, 1 and 2 mM) were considered as treatments. The experimental design was a factorial experiment, completely randomized in three replicates.

Enzyme extractions

A quantity of 0.1g of fresh foliar tissue from fresh seedlings (uppermost leaves) were harvested, weighed, washed with distilled water and then homogenized with a mortar and pestle with 5 ml chilled sodium phosphate buffer (50 mM, pH 7.8). The homogenates were centrifuged at 15,000 g for 15 min at 4°C. Three replicates per treatment were used. The supernatant was stored at 4°C and used for CAT, APX, GR, POD and PPO assays.

Protein determination

Protein concentration of the various extracts and solutions was determined by the dye binding method of Bradford (1976), using bovine serum albumin as standard.

Enzyme assays

GR activity was determined by following the rate of GSSG-dependent oxidation of NADPH, through the decrease in the absorbance at 340 nm (Di Baccio *et al.,* 2004). The assay mixture (1 ml final volume) was composed of 0.4 mM potassium phosphate buffer (pH 7.5), 0.4 mM Na_2EDTA, 5.0 mM GSSG and 100 µl of crude extract. The reaction was initiated by the addition of 2.0 mM NADPH. Corrections were made for the background absorbance at 340 nm, without NADPH. Activity was expressed as units (µmol of NADPH oxidized per minute) per mg of protein.

POD activity was determined spectrophotometrically, by measuring the oxidation of o-dianisidine (3,3'-dimethoxybenzidine) at 460 nm (Ranieri *et al.,* 2000). The reaction mixture contained 20 mM phosphate buffer (pH 5.0), 1 mM dianisidine, 3 mM H_2O_2 and 50 µl of extract. POD specific activity was expressed as units (µmol of dianisidine oxidized per minute) per mg of protein.

APX activity was measured by the methods of Nakano and Asada (1981). The reaction mixture contained 500 ml of 100 mM K-P buffer (pH 7.0), 100 ml of 5 mM ascorbate, 250 ml of distilled water and 50 ml of enzyme extract. APX activity was measured by ascorbate oxidation at 290 nm in the presence of 100 ml of 1 mM H_2O_2. The final reaction volume was adjusted to 1 ml. The unit for APX activity was micromoles of ascorbate oxidized per minute per milligram of protein.

CAT activity was measured by the method of Blume and McClure (1980). The reaction mixture contained 500 ml of 100 mM K-P buffer (pH 7.8), 200 ml of distilled water, and 200 ml of enzyme extract. The reaction was started by adding 100 ml of 50 mM H_2O_2 in a final volume of 1 ml and absorbance was measured at 240 nm. The unit for CAT activity was micromoles of hydrogen peroxide oxidized per minute per milligram of protein.

Polyphenol oxidase: the assay mixture (3 ml) of contained 10 mM pirogalol, 25 mM phosphate buffer (pH 6.8) and 200 µl enzyme extract. Enzyme activity determined in 420 nm, its molar extension coefficient is 2.47 l $mM^{-1}cm^{-1}$.

Statistical analysis

The experimental design was a factorial experiment, completely randomized in three replicates. Graphs were drawn using Microsoft Office Excel 2013 software.

RESULTS AND DISCUSSION

As shown in *Fig. 1*, generally, in compared with control condition, lower available water levels led to increase in CAT activity. There were no significant difference between low levels of SA (0 and 0.1 mM) in the all irrigation treatments. Increase in SA concentration from 0.1 mM to 2 mM induced greater CAT activity. Under sever condition (30% FC), higher level of SA induced greater CAT activity while there was no significant difference between SA levels (1 and 2 mM) under sever (30 % FC) water deficit condition.

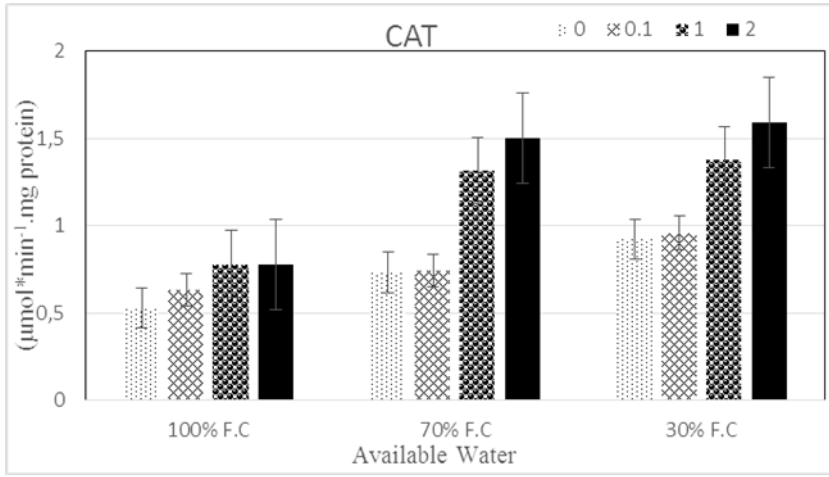

Figure 1 - Effect of different concentrations of SA on CAT activity in thyme plants under control (FC), medium water deficit (70% FC) and sever water deficit (30% FC) conditions. Values are the means ± SE of three replicates. Means with different letters are significantly different (p<0.05).

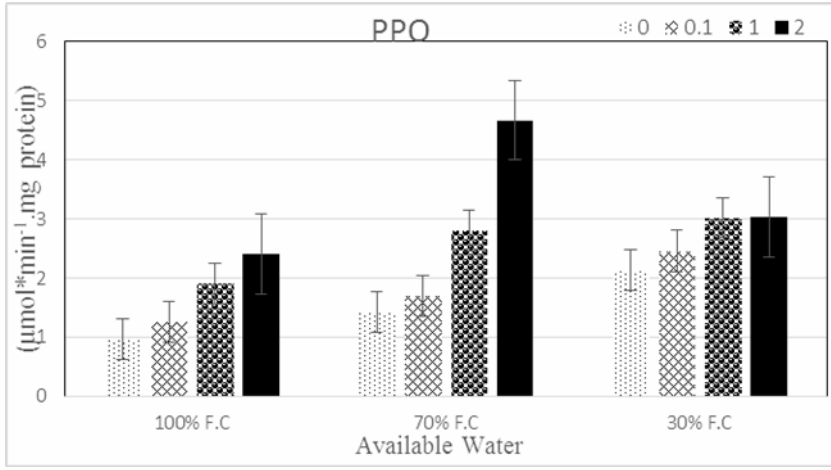

Figure 2 - Effect of different concentrations of SA on PPO activity in thyme plants under control (FC), medium water deficit (70% FC) and sever water deficit (30% FC) conditions. Values are the means ± SE of three replicates. Means with different letters are significantly different (p<0.05).

The response of PPO activity to SA concentration was different under different levels of available water. As presented in *Fig. 2*, while under medium water deficit, PPO activity significantly increased by higher SA concentration, under control and sever water deficit conditions, there was no

significant difference between 1 mM and 2 mM concentrations regarding PPO activity.

Increasing water deficit was associated with increase in POD activity (*Fig. 3*). At all levels of SA, the lowest POD activity was observed under control condition (*Fig. 3*). As shown in *Fig. 3*, higher levels of SA induced greater POD activity under sever condition yet under sever water deficit, there was no significant difference between 1 mM and 2 mM concentrations of SA about POD activity.

Under all levels of available water, increase in SA concentration from 0.1 mM to 2 mM induced significant increase in APX activity. Higher concentrations of SA had the maximum effect on APX activity in the medium water deficit condition. But in the sever water deficit (30% FC) conditions there was no significant difference between 1 and 2 mM concentrations (*Fig. 4*).

In compared with other antioxidant enzymes, GR activity exhibited lower response to SA concentration and water available (*Fig. 5*). Whereas 1mM concentration of SA induced significant increase in GR activity, increase in SA concentration to two caused no significant change in GR activity, when compared with 1 mM concentration at all levels of available water. Plants treated with 0.1 mM and 2 mM of SA, exhibited no significant change in GR activity by reduction in available water but treated plants with 1 mMSA, exhibited intensified GR activity by reduced available water to 70% FC (*Fig. 5*).

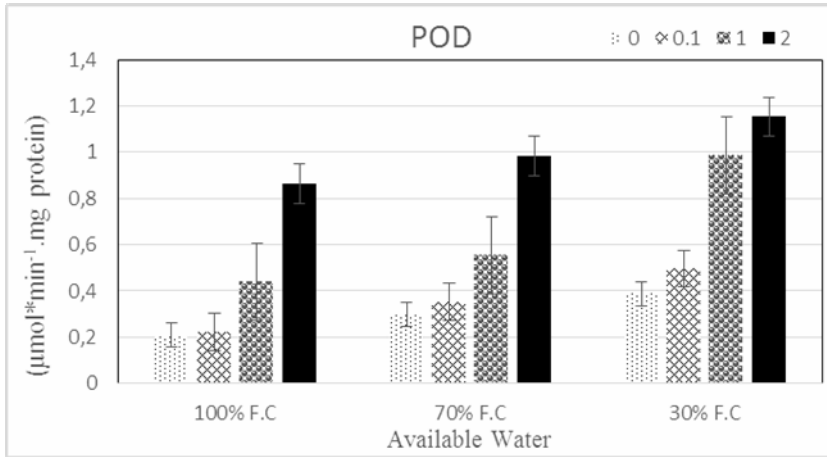

Figure 3 - Effect of different concentrations of SA on POD activity in thyme plants under control (FC), medium water deficit (70% FC) and sever water deficit (30% FC) conditions. Values are the means ± SE of three replicates. Means with different letters are significantly different (p<0.05).

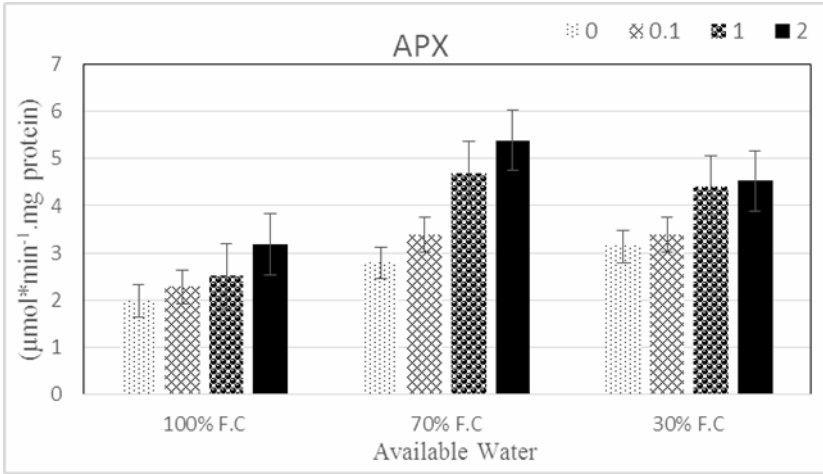

Figure 4 - Effect of different concentrations of SA on APX activity in thyme plants under control (FC), medium water deficit (70% FC) and sever water deficit (30% FC) conditions. Values are the means ± SE of three replicates. Means with different letters are significantly different (p<0.05).

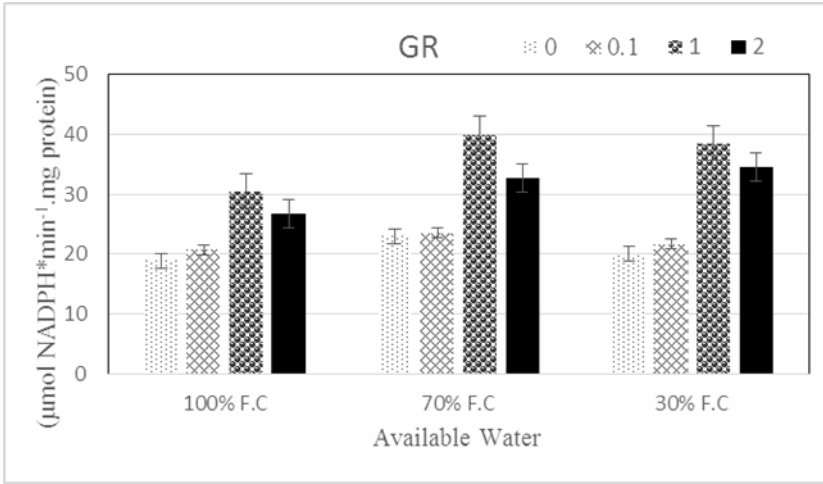

Figure 5 - Effect of different concentrations of SA on GR activity in *Thymus daenensis* plants under control (FC), medium water deficit (70% FC) and sever water deficit (30% FC) conditions. Values are the means ± SE of three replicates. Means with different letters are significantly different (p<0.05).

A secondary effect of osmotic stress is the increase of reactive oxygen species (ROS) (Smirnoff, 1998; Bartels, 2001; Apel and Hirt, 2004). The alleviation of oxidative damage and increased resistance to environmental stresses is often correlated with an efficient

antioxidative system (Shalata *et al*., 2001; Kranner *et al*., 2002). Overproduction of antioxidant enzymes have been shown to improve oxidative stress tolerance in transgenic plants (Roxas *et al*., 1997). To scavenge ROSs, plants either synthesize different antioxidant compounds or activate antioxidant enzymes. Salicylic acid (SA) plays an important role in abiotic stress tolerance, and considerable interests have focused on SA due to its ability to induce a protective effect on plants under stress (Sakhabutdinova *et al*., 2003; Shakirova *et al*., 2003). In current study, generally, SA induced greater antioxidant enzymes activity under water deficit condition. The role of SA as a defense signal has been well established in plants (Ganesan and Thomas, 2001). SA has qualified as a plant hormone due to its physiological and biological roles in plants (Raskin, 1992). SA has been suggested as signal transducer or messenger under stress conditions (Klessig and Malamy, 1994).

CAT is tetrameric heme containing enzyme that is abundant in the glyoxysomes of lipid storing tissues (Fornazier *et al*., 2004). The combined action of SOD and CAT converts the toxic O_2 and H_2O_2 to water and molecular oxygen, averting the cellular damage under unfavorable conditions such as drought stress (Reddy *et al*., 2000; Chaitanya *et al*., 2002). POD plays a key role in decreasing H_2O_2 content accumulation, eliminating MDA resulting cell peroxidation of membrane lipids and maintaining cell membrane integrity (Jaleel *et al*., 2008b). Increased POD activity was reported in drought stressed soybean (Zhang *et al*., 2006) and chives plants (Egert and Tevini, 2002). APX is thought to play the most essential role in scavenging ROS and protecting cells in higher plants, algae, euglena and other organisms. APX is involved in scavenging of H_2O_2 in water-water and ASH-GSH cycles and utilizes ASH as the electron donor (Gill and Tuteja, 2010). GR is a flavoprotein oxidoreductase, found in both prokaryotes and eukaryotes (Romero-Puertas *et al.,* 2006). It is a potential enzyme of the ASH-GSH cycle and plays an essential role in defense system against ROS by sustaining the reduced status of GSH. In coordination with obtained data from this study, already convincing data have been obtained about the role of SA in the resistance of wheat seedlings to salinity (Shakirova and Bezrukova, 1997), and water deficit (Bezrukova *et al.,* 2001), of maize to low temperature (Janda *et al*., 1999), of tomato and bean plants to low and high temperature (Senaratna *et al.,* 2000).

CONCLUSIONS

Drought stress caused dramatic increase in antioxidant activities in *Thymus daenensis* (subsp. *lancifolius*). Deleterious effects of drought stress was more severe in untreated plants than in treated plants. Treatments with SA enhanced

seedling total antioxidant capacity. The enhancement of antioxidant capacity in thyme plants could have contributed to the drought tolerance. Therefore, it is safe to suggest that treatment with SA could confer plant tolerance to drought stress by acting as direct ROS scavengers or binding to antioxidant enzyme molecules to scavenge free radicals.

REFERENCES

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

Angioni A., Barra A., Coroneo V., Dessi S., Cabras P., 2006 - Chemical composition, seasonal variability, and antifungal activity of *Lavandula stoechas* L. ssp. *stoechas* essential oils from stem/leaves and flowers. J. Agr. Food Chem., 54: 4364-4370.

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

Bartels D., 2001 - Targeting detoxification pathways: an efficient approach to obtain plants with multiple stress tolerance. Trends Plant Sci., 6:284-286.

Bezrukova M.V., Sakhabutdinova A.R., Fatkhutdinova R.A., Kyldiarova I.A., Shakirova F.M., 2001 - The role of hormonal changes in protective action of salicylic acid on growth of wheat seedlings under water deficit, Agrochemya (Russ.), 2: 51-54.

Blume D.E., McClure J., 1980 - Developmental effects of Sandoz 6706 on activities of enzymes of phenolic and general metabolism in barely shoots grown in the dark or under low of high intensity light. Plant Physiol., 65:234-238.

Borsani O., Valpuesta V., Botella M.A., 2001 - Evidence for a role of salicylic acid in the oxidative damage generated by NaCl and osmotic stress in Arabidopsis seedlings. Plant Physiol., 126: 1024-1030.

Bradford M.M., 1976 - A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein-dye binding. Anal. Biochem., 72: 248-254.

Chaitanya K.V., Sundar D., Masilamani S., Ramachandra Reddy A., 2002 - Variation in heat stress-induced antioxidant enzyme activities among three mulberry cultivars. Plant. Growth Regul., 36: 175-180.

Di Baccio D., Navari-Izzo F., Izzo R., 2004 - Seawater irrigation: antioxidant defense responses in leaves and roots of a sunflower (*Helianthus annuus* L.) ecotype. J. Plant Physiol., 161: 1359-1366.

Ganesan V., Thomas G., 2001 - Salicylic acid response in rice: influence of salicylic acid on H_2O_2 accumulation and oxidative stress. Plant. Sci.,160: 1095-106.

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

Egert M., Tevini M., 2002 - Influence of drought on some physiological parameters symptomatic for oxidative stress in leaves of chives (*Allium schoenoprasum*). Environ. Exp. Bot., 48: 43-49.

Fornazier R.F., Ferreira R.R., Pereira G.J.G., Molina S.M.G., Smith R.J., Lea P.J., Azevedo R.A., 2004 - Cadmium stress in sugarcane in callus cultures: effects on antioxidant enzymes. Plant Cell Tiss Org., 71: 125-131.

Hedge C., 1992 - A global survey of the biogeography of the *Labiatae*. *In* Harley R.M. and Reynolds T. (Eds) Advances in Labiatae Science. Royal Botanic Gardens, Kew, 7-17.

Jaleel C.A., Gopi R., Manivannan P., Gomathinayagam M., Sridharan R., Panneerselvam R., 2008 - Antioxidant potential and indole alkaloid profile variations with water deficits along different parts of two varieties of *Catharanthus roseus.* Colloid Surface B, 62: 312-318.

Janda T., Szalai G., Tari I., Páldi E., 1999 - Hydroponic treatment with salicylic acid decreases the effects of chilling injury in maize (*Zea mays* L.) plants. Planta, 208: 175-180.

Kawano T., Muto S., 2000 - Mechanism of peroxidase actions for salicylic acid-induced generation of active oxygen species and an increase in cytosolic calcium in tobacco cell suspension culture. J. Exp. Bot., 51: 685-693.

Klessig D.F., Malamy J., 1994 - The salicylic acid signal in plants. Plant Mol. Biol., 26: 1439-58.

Kranner I., Beckett R.P., Wornik S., Zorn M., Pfeifhofer H.W., 2002 - Revival of resurrection plant correlates with its antioxidant status. Plant J, 31:13-24.

Masotti V., Juteau F., Bessiere J.M., Viano J., 2003 - Seasonal and phonological variations of the essential oil from the narrow endemic species *Artemisia molinieri* and its biological activities. J Agr Food Chem, 51: 7115-7121.

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

Mittova V ., Volokita M., Guy M., Tal M., 2000 - Activities of SOD and the ascorbate- lutathione cycle enzymes in subcellular compartments in leaves and roots of the cultivated tomato and its wild salt-tolerant relative *Lycopersicon pennellii*. Physiol. Plant, 110(1): 42-51.

Munné-Bosch S., Peñuelas J., 2003 - Photo- and antioxidative protection, and a role for salicylic acid during drought and recovery in field grown *Phillyrea angustifolia* plants. Planta, 217: 758-766.

Nakano Y., Asada K., 1981 - Hydrogen peroxide is scavenged by ascorbate specific peroxidase in spinach chloroplast. Plant Cell Physiol, 22:867-880.

Nickavar B., Mojab F., Dolat-Abadi R., 2005 - Analysis of the essential oils of two Thymus species from Iran. Food Chem, 90: 609-611.

Noctor G., Foyer C.H., 1998 - Ascorbate and glutathione: keeping active oxygen under control. Annu Rev Plant Physiol Plant Mol Biol, 49: 249-279.

Ramadevi S., Prasad M.N.V., 1998 - Copper toxicity in *Ceratophyllum demersum* L. (Coontail), a free floating macrophyte: response of antioxidant enzymes and antioxidants. Plant Sci, 138-157.

Ranieri A., Petacco F., Castagna A., Soldatini G.F., 2000 - Redox state and peroxidase system in sunflower plants exposed to ozone. Plant Sci, 159: 159-168.

Raskin I., 1992 - Role of salicylic acid in plants. Annu Rev Plant Physiol Mol Biol, 43: 439-463.

Rechinger K.H., 1982 - Flora Iranica (Vol. 152). Graz: Akademische Druck und Verlagsanstalt.

Reddy A.R., Chaitanya K.V., Sundar D., 2000 - Water stress-mediated changes in antioxidant enzymes activity of mulberry (*Morus alba* L.). J Seri Sci Jpn, 69: 169-175.

Romero-Puertas M.C., Corpas F.J., Sandalio L.M., Leterrier M., Rodriguez-Serrano M., del Rio L.A., Palma J.M., 2006 - Glutathione reductase from pea leaves: response to abiotic stress and characterization of the peroxisomal isozyme, New Phytol, 170: 43-52.

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

Sakhabutdinova A.R., Fatkhutdinova D.R., Bezrukova M.V., Shakirova F.M., 2003 - Salicylic acid prevents damaging action of stress factors on wheat plants. Bulg J Plant Physiol., 214-219.

Senaratna T., Touchell D., Bunn E., Dixon K., 2000 - Acetyl salicylic acid (aspirin) and salicylic acid induce multiple stress tolerance in bean and tomato plant. Plant Growth Reg, 30: 157-161.

Shakirova F.M., Bezrukova M.V., 1997 - Induction of wheat resistance against environmental salinization by salicylic acid, Biol Bull (Izv. Russ. Acad. Sci.), 24: 109-112.

Shakirova F.M., Sakhabutdinova A.R., Bezrukova M.V., Fatkhutdinova R.A., Fatkhutdinova D.R., 2003 - Changes in hormonal status of wheat seedlings induced by salicylic acid and salinity. Plant Sci., 164: 317-322.

Shalata A., Mittova V., Volokita M., Guy M., Tal M., 2001 - Response of the cultivated tomato and its wild salt-tolerant relative *Lycopersicon pennellii* to salt-dependent oxidative stress: the root antioxidative system. Physiol Plant, 112:487-494.

Smirnoff N., 1998 - Plant resistance to environmental stress. Curr Opin Plant Biol, 9:214-219.

Sun Y., 1990 - Free radicals, antioxidant enzymes, and carcinogenesis. Free Radic Biol Med, 8(6): 583-599.

Tarchevskii L.A., 2002 - Signal'nye sistemy kletok rastenii (Signal Systems of Plant Cells). Nauka, Moscow, 294 p.

Zargari A., 1990 - Medicinal plants. Tehran University Press, Tehran, pp. 28-42.

Zhang J., Jia W., Yang J., Ismail A.M., 2006 - Role of ABA in integrating plant responses to drought and salt stresses. Field Crops Res, 97: 111-119.

Zhu J.K., 2002 - Salt and drought stress signal transduction in plants, Annu Rev Plant Biol, 53: 247-273.